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AN INTEGRATED STUDY ON LATE CISURALIAN (EARLY PERMIAN) PALAEOENVIRONMENTS AND PALAEOCLIMATE OF SOUTHERN ALPS

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CHAPTER 4 – The Tregiovo conifers – a morphological and geochemical study

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ABSTRACT

The transition from ice-house to green-house conditions that characterized the Permian (289–252 million years ago) climate passed through several glacial and interglacial phases and an increase of aridity, which affected the palaeoequatorial regions. The causes behind this increase, which led to several important changes within the terrestrial ecosystems, are still poorly understood. During the Permian, extrabasinal floras, mainly composed of drought-tolerant plants such as conifers and other gymnosperms, started to spread and move into the lowlands, progressively replacing the hygrophytic lowland floras that characterized the Carboniferous peat-forming forests. These climate changes and terrestrial biotic turnover left an important imprint in the carbon stable isotopic composition of the atmospheric CO_2, and consequently, of the terrestrial organic matter. However, the step-wise nature of the Permian palaeofloristic transition and the low-resolution of $\delta^{13}C$ data on the terrestrial organic matter make it difficult to clearly reconstruct what happened to the Permian palaeoequatorial ecosystems. A palaeoenvironmental and palaeoclimate reconstruction of the Kungurian (Cisuralian, early Permian) Tregiovo Basin (NE-Italy) is here provided. A multidisciplinary study has been carried out, through which two sections of the Tregiovo Formation, respectively "Le Fraine" and Tregiovo village sections, have been investigated for sedimentology, geochemistry, palaeobotany and palynology. The taxonomical study on the two rich palaeobotanical assemblages of the "Le Fraine" section revealed a very diverse and abundant flora, composed of sphenophytes (*Annularia*), ginkgophytes (?*Sphenobaiera*), pteridosperms (*Peltaspermum*), conifers (e.g., *Hermitia*, *Feysia, Quadrocladus, Dolomitia*) and taxa with uncertain botanical affinity like taeniopterids (*Taeniopteris*), sphenopterids (*Sphenopteris*) and two *incertae sedis* "morphotypes". The palaeobotanical and palynological study indicates a xerophytic character for the Tregiovo flora, mainly dominated by conifers and sphenopterids. A thorough taxonomical study on these two plant groups showed a remarkable diversity, which allowed to pre-date the first appearance of genus *Dolomitia* to be moved back to the Kungurian, and to identify a new sphenopterid species, *Sphenopteris valentinii*. Sedimentological studies from the two sections indicate a playa-lake environment alternating with stable lacustrine conditions. Lake phases are indicated by common microbial carbonates, whereas playa-lake phases are indicated by the occurrence of mud-cracks and tetrapod footprints. Stable isotopic analyses on bulk organic carbon and conifer coalified tissues from the two Tregiovo sections highlighted a distinct negative shift of the $\delta^{13}C$ curve on the terrestrial organic carbon within the Tregiovo Formation, well-constrained to the middle Kungurian by radiometric data, that correlates very well with the negative shift recorded by other authors for the Kungurian. This work represents a contribution to the comprehension of the complex picture of Permian palaeoenvironments and palaeoclimate, filling a gap on the knowledge about the early Permian eastern palaeoequatorial ecosystems.

RIASSUNTO

Il Permiano (289–252 milioni di anni) rappresenta un periodo di transizione da condizioni di ice-house a condizioni di green-house, avvenuto attraverso diverse fasi glaciali e interglaciali. Questo cambiamento è stato caratterizzato da un incremento di aridità che interessò le regioni paleoequatoriali della Pangea. Le cause principali di questo incremento e di altri importanti cambiamenti che hanno interessato gli ecosistemi terrestri sono ancora poco chiare. Nel Permiano, le flore che occupavano le aree al di fuori dei bacini, costituite soprattutto da conifere ed altre gimnosperme che meglio tollerano periodi di aridità, cominciarono a migrare all'interno dei bacini, rimpiazzando progressivamente le flore più igrofitiche che avevano caratterizzato le foreste pluviali Carbonifere. Tali cambiamenti, sia climatici che relativi al biota terrestre, lasciarono un'impronta considerevole sulla composizione isotopica della CO_2 atmosferica, e di conseguenza, della materia organica terrestre. La natura discontinua della transizione paleofloristica Permiana e la scarsa risoluzione dei dati riguardanti il $\delta^{13}C$ della materia organica terrestre, rendono difficile una chiara visione di quello che accadde agli ecosistemi Permiani paleoequatoriali. In questa ricerca, viene proposta una ricostruzione paleoclimatica e paleoambientale del bacino Kunguriano (Cisuraliano, Permiano inferiore) di Tregiovo (NE-Italia). Attraverso uno studio multidisciplinare, le due sezioni di "Le Fraine" e del villaggio, appartenenti alla Formazione Tregiovo, sono state investigate dal punto di vista sedimentologico, geochimico, paleobotanico e palinologico. Lo studio tassonomico sui due depositi a piante di "Le Fraine" ha rivelato una flora molto ricca e diversificata, composta da sfenofite (*Annularia*), ginkgofite (?*Sphenobaiera*), pteridosperme (*Peltaspermum*), conifere (e.g., *Hermitia*, *Feysia, Quadrocladus, Dolomitia*) e taxa con affinità incerta come taeniopteridi (*Taeniopteris*), sfenopteridi (*Sphenopteris*) e due morfotipi *incertae sedis*. Gli studi paleobotanico e palinologico indicano un carattere xerofitico per la flora di Tregiovo, dominata da conifere e sfenopteridi. L'approfondito studio tassonomico di questi due gruppi ha svelato una notevole diversità, ha permesso di retrodatare al Kunguriano la prima comparsa del genere *Dolomitia*, e ha consentito di identificare una nuova specie di sfenopteride, *Sphenopteris valentinii*. Gli studi sedimentologici su entrambe le sezioni hanno indicato un'alternanza tra condizioni di playa-lake e lacustri stabili. Le fasi di playa-lake sono indicate dalla presenza di mud-cracks ed impronte di tetrapodi, mentre quelle lacustri stabili sono indicate dalla presenza abbastanza comune di carbonati microbiali. Le analisi isotopiche sul carbonio stabile contenuto nel bulk e nei tessuti carbonificati provenienti dalle due sezioni, hanno evidenziato uno shift negativo della curva del $\delta^{13}C$ della Formazione di Tregiovo. Quest'ultima, radiometricamente datata Kunguriano medio, è molto ben correlabile con lo shift negativo registrato da altri autori per il Kunguriano. Il presente lavoro rappresenta un notevole contributo alla comprensione del complesso, e tuttora incompleto, quadro degli ecosistemi e del clima Permiani, che va a colmare una lacuna nelle conoscenze riguardante gli ecosistemi paleoequatoriali Permiani della Pangea orientale.

INTRODUCTION

The Carboniferous–Permian was a time characterized by many important climate and palaeoenvironmental changes. During the Carboniferous, the most important ice-age of the Phanerozoic took place, which lead to the formation of several ice centers that, during its maximum expansion, covered the greater part of the southern hemisphere (e.g., Frakes et al., 1992; Isbell et al., 2003). The last phases of consolidation of Pangaea formed the Central Pangean Mountains, which caused the fragmentation of the humid palaeoequatorial belt that characterized the Carboniferous with its coal-forming forests (e.g., DiMichele et al., 2001; 2008). The Permian in turn was characterized by the transition from ice-house to green-house conditions, passing through several glacial and interglacial phases and an increase of aridity, which was reflected in the palaeoequatorial regions (e.g., Montañez et al., 2007; DiMichele et al., 2008; 2009; Tabor and Montañez, 2004; Montañez and Poulsen, 2013; Michel et al., 2015). The causes that may have triggered the increase of aridity in the palaeoequatorial areas are several, among which, as suggested by some authors, the high levels of CO_2 in the atmosphere (Montañez et al., 2007; 2016).

These important changes heavily influenced the Permian palaeoequatorial ecosystems, and led to the stepwise replacement of spore-producing plants by more drought-tolerant seed plants, in which the conifers were a dominant element (e.g., DiMichele et al., 2006; 2008; Looy and Stevenson, 2014). This replacement proceeded from western to eastern Pangea during most of the Permian. The first evidences of conifers date back to the Middle Pennsylvanian, with the earliest occurrence in the Euramerican flora. The early conifers were small shrubs belonging to the walchian conifers (Mapes, 1987), which occupied well-drained extrabasinal areas (e.g., Rothwell et al., 1997). With the strong climatec oscillation (Rosenau et al., 2013a, 2013b) and the trend of increase of aridity which characterized the Permian palaeoequatorial regions, drought-tolerant taxa started to spread and move into the lowlands, occupying also basinal habitats, where the potential of preservation is higher (the so-called "window of preservation" of Looy et al., 2014). This step is crucial for those taxa that become more common in the fossil record, revealing important information about the formerly extrabasinal communities, where most likely, in the more challenging extrabasinal environments, the major body-plan innovation originated. We here endorse the view that early conifers are "Methuselah taxa", i.e., derived forms that unexpectedly occur early in the evolution of a taxonomical group and become widespread only much later (Looy et al., 2014). For this reason, early conifers are extremely important to reconstruct the evolution of this plant lineage.

The object of this PhD research project is the small Kungurian sedimentary basin of Tregiovo in northern Italy (Trento province, Trentino-Alto Adige region), which yielded an extraordinarily rich and diverse lower flora dominated by conifers. The aim of the research was to provide a palaeoenvironmental and palaeoclimatic reconstruction or the Cisuralian of the Southern Alps, and to add a mosaic tile to the complex and incomplete early Permian picture. To this end, a multidisciplinary approach has been applied on the study of the Tregiovo Basin. Here, two new sections, respectively "Le Fraine" section and Tregiovo village section, which belong to the Tregiovo Formation, have been investigated for palaeobotany, palynology, sedimentology and geochemistry. The Tregiovo flora comes from two distinct horizons of "Le Fraine" section, separated by ca. 60 meters. The taxonomical study of the Tregiovo flora represented a fundamental starting point of the research. The composition of the flora gave important information about the palaeoenvironmental and the palaeoclimate conditions of Tregiovo, and showed a change in the flora composition between the two assemblages of the "Le Fraine" section. Along with the study of the macroflora, a palynological study was carried out for three main reasons: 1) to obtain important information about the floral composition at a wider (regional) scale; 2) to obtain further palaeoenvironmental/palaeoclimate information to be compared to that obtained from the macroflora; 3) to check if any taphonomical and/or collecting biases affected the macroflora collection.

For the sedimentological part of the work, the studies of the Tregiovo village section and a new interpretation of the "Le Fraine" section were carried out. The sedimentological results from the study of the two sections allowed us to support the information about the palaeoenvironmental conditions and their variations through time. Moreover, it permitted to the correlation of the two Tregiovo sections, a correlation that is supported by the geochemical study as well.

The last part of this work regards a study of the carbon stable isotopic composition at Tregiovo, here carried out for the first time. The study focused on the organic carbon, and was done on both sections. Initially, the isotopic study was focused on the geochemical study of the organic carbon contained in the bulk rock. The aim was to obtain a well time constrained, high resolution Kungurian $\delta^{13}C_{org}$ curve, comparable with other $\delta^{13}C_{org}$ records of the continental Permian (e.g., Faure et al., 1995; Zhang et al., 1999; Peters-Kottig et al., 2006). It is known that the $\delta^{13}C$ of terrestrial organic matter ranges between – 22.9‰ and – 25.5‰ for the Permian. In particular, for the Cisuralian, the average value of terrestrial organic $\delta^{13}C$ is –22.9‰ VPDB (Strauss and Peter-Kottig, 2003), which is comparable to that of modern C3 plants (from – 34‰ to – 20‰; O'Leary, 1988). This is in line with the notion that during the Paleozoic C4 and CAM photosynthetic plants had not yet evolved (Bocherens et al., 1993). This is also the case of Tregiovo, in which the $\delta^{13}C_{org}$ values from bulk are in the range of C3 plants. Nonetheless the Tregiovo $\delta^{13}C_{org}$ curve shows also a negative shift that seems to have been recorded by other authors for the Kungurian (e.g., Faure et ap., 1995; Zhang et al., 1999; Peters-Kottig et al., 2006). The second part of the isotopic study was focused on the coalified tissues of plant remains. In fact, one of the first hypotheses to explain the negative shift recorded by bulk rock was that, being terrestrial plants are the most important component of the bulk organic carbon, the change in the flora composition between the two plant assemblages of the "Le Fraine" section could have affected the carbon isotopic composition of the bulk. For these reasons, the coalified tissues of plant remains have been analyzed on a variety of taxa from the two assemblages.

The data and results obtained within this research project have been interpreted and structured in four different papers, one already published, one under revision, one submitted and one still at the stage of manuscript draft. Each of these papers represents on chapter of this thesis, and are briefly introduced below.

The first chapter represents a paper submitted at the end of the second year of PhD to the journal "Review of Palaeobotany and Palynology", and published in 2017. It is a study on the dominant group of plants of Tregiovo, the conifers, in which we show the diversity of this group of plants, based on the study of their dwarf shoots. Through the description of the morphology and the comparison with other Permian taxa, we provided descriptions of three new morphotypes (A, B and C) and extended back to the middle Kungurian the appearance of the genus *Dolomitia* Clement-Westerhof 1987, previously only known from the Lopingian (upper Permian) of the Southern Alps.

The second chapter consists of a paper submitted during the end of the third year to the journal "Review of Palaeobotany and Palynology", for which a request of minor revisions has been received. These revisions are incorporatedin this thesis and are at present under consideration at the journal. The sphenopterids, an eterogeneous group that includes ferns and possibly seed plants, represent a very important group of plants in the Tregiovo flora, in which they show a remarkable diversity and an increase of abundance, parallel to the decrease of conifers, in the younger plant assemblage of "Le Fraine". In this paper, we discussed the diversity and the distribution of the genus *Sphenopteris* during the Permian, and the variability of the genus *Sphenopteris* in the Tregiovo flora, also describing a new species, *Sphenopteris valentinii* nov. sp. Forte et Kerp, from the "Le Fraine" section of Tregiovo.

The third chapter is a paper in press, which was submitted at the end of the third year to the journal “Palaeogeography, Palaeoclimatology, Palaeoecology”. It consists of a palaeoenvironmental and palaeoclimate reconstruction of the Tregiovo Basin based on a multidisciplinary palaeobotanical, palynological sedimentological and geochemical study of the two Tregiovo sections.

Finally, the fourth chapter is a manuscript draft, which represents a further taxonomical and morphological and geochemical study on the Tregiovo conifers, on the basis of their vegetative shoots. In this work, we performed a morphological comparison between the Tregiovo taxa and other Permian conifers, and taxon-specific isotopic analysis on the coalified tissues of the Tregiovo conifers. These latest geochemical results have been discussed and compared with the isotopic results obtained from the two Tregiovo sections, presented in the third chapter.

References

Bocherens, H., Friis, E.M., Mariotti, A., Pedersen, K.R., 1993. Carbon isotopic abundances in Mesozoic and Cenozoic fossil plants: palaeoecological implications. Lethaia 26, 347–358.

Clement-Westerhof, J.A., 1987. Aspects of Permian palaeobotany and palynology, VII. The Majonicaceae, a new family of Late Permian conifers. Rev. Palaeobot. Palynol. 52, 375–402.

DiMichele, W.A., Pfefferkorn, H.W., Gastaldo, R.A., 2001. Response of Late Carboniferous and Early Permian plant communities to climate change. Annu. Rev. Earth Planet. Sci. 29,461–487.

DiMichele, W.A., Kerp, H., Tabor, N.J., Looy, C.V., 2008. The so-called "Paleophytic-Mesophytic" transition in equatorial Pangea – Multiple biomes and vegetational tracking of climate change through geological time. Paleogeography, Palaeoclimatology, Palaeoecology 268, 152–163.

DiMichele, W.A., Tabor, N.J., Chaney, D.S., Nelson, W.J., 2006. From wetlands to wet spots: environmental tracking and fate of Carboniferous elements in Early Permian tropical floras. In: Grab, S.F., DiMichele, W.A., (Eds.), Wetlands Through Time. Geological Society of America Special Paper 399, pp. 223–248.

DiMichele, W.A., Montañez, I.P., Poulsen, C.J., Tabor, N.J., 2009. Climate and vegetational regime shifts in the late Paleozoic ice age earth. Geobiology 7(2), 200–226.

Faure, K., Wit, W.J., Willis, J.P., 1995. Late Permian cola hiatus linked to 13C-depleted CO2 flux into the atmosphere during the final consolidation of Pangea. Geology 23(6), 507–510.

Frakes, L.A., Francis, J.E., Syktus, J.I., 1992. Climate modes of the Phanerozoic. New York: Cambridge University Press, 274 pp.

Isbell, J.L., Miller, M.F., Wolfe, K.L., Lenaker, P.A., 2003. Timing of the late Palaeozoic glaciation in Gondwana: was glaciation responsible of the development of northern hemisphere cyclothems? In: Chan, M.A., Archer, A.W. (Eds.), Extreme Depositional Environments: Mega End Members in Geologic Time. Geol. Soc. Of Am. Spec. Pap., vol. 370, pp. 5–24.

Looy, C.V., Stevenson, R.A., 2014. Earliest occurrence of autorotating seeds in conifers: the Permian (Kungurian–Roadian) Manifera talaris gen. et sp. nov. International Journal of Plant Sciences 175(7), 841–854.

Looy, C.V., Kerp, H., Duijnstee, I.A.P., DiMichele, W.A., 2014. The late Paleozoic ecological-evolutionary laboratory, a land-plant fossil record perspective. The Sedimentary Record 12(4), 4–10.

Mapes, G. 1987. Ovule inversion in the earliest conifers. American Journal of Botany 74, 1205–1210.

Michel, L.A., Tabor, N.J., Montañez, I.P., Schmitz, M.D., Davydov, V.I., 2015. Chronostratigraphy and paleoclimatology of the Lodève Basin, France: evidence for a pan-tropical aridification event across the Carboniferous–Permian boundary. Palaeogeography, Palaeoclimatology, Palaeoecology 430, 118–131.

Montañez, I.P., Poulsen, C.J., 2013. The Late Paleozoic ice age: an evolving paradigm. Annu. Rev. Earth Planet. Sci. 41, 629–656.

Montañez, I.P., Tabor, N.J., Niemeier, D., DiMichele, W.A., Frank, T.D., Fielding, C.R., Isbell, J.L., Birgenheier, L.T., Rygel, M., 2007. CO2-forced climate and vegetation instability during Late Paleozoic glaciation. Science 315, 87–91.

Montañez, I.P., McElwain, J.C., Poulsen, C., White, J.D., DiMichele, W.A., Wilson, J.P., Griggs, G., Hren, M.T., 2016. Cimate, pCO2 and terrestrial carbon cycle linkages during late Palaeozoic glacial-interglacial cycles- Nature Geoscience 9, 824–828.

Peters–Kottig, W., Strauss, H., Kerp, H., 2006. The land plant δ13C record and plant evolution in the Late Palaeozoic. Palaeogeography, Palaeoclimatology, Palaeoecology 240, 237–252.

Rosenau, N.A., Tabor, N.J., Elrick, S.D., Nelson, W.J., 2013a. Polygenetic history of paleosols in middle–upper Pennsylvanian cyclothems of the Illinois Basin, U.S.A.: Part I. Characterization of paleosol types and interpretation of pedogenetic processes. J. Sediment. Res. 83, 606–636.

Rosenau, N.A., Tabor, N.J., Elrick, S.D., Nelson, W.J., 2013b. Polygenetic history of paleosols in middle–upper Pennsylvanian cyclothems of the Illinois Basin, U.S.A.: Part II. Integrating geomorphology, climate and glacioestasy. J. Sediment. Res. 83, 637–668.

Rothwell, G.W., Mapes, G., Mapes, R.H., 1997. Late Paleozoic conifers of North America: structure, diversity and occurrences. Review of Palaeobotany and Palynology 95, 95–113.

Strauss, H., Peter-Kottig, W., 2003. The Paleozoic to Mesozoic carbon cycle revisited: The carbon isotopic composition of terrestrial organic matter. Geochemistry, Geophysics, Geosystems 10, 1525–2027.

Tabor, N.J., Montañez, I.P., 2004. Morphology and distribution of fossil soils in the Permo–Pennsylvanian Wichita and Bowie Group, north-central Texas, USA: implications for western equatorial Pangean palaeoclimate during icehouse-greenhouse transition. Sedimentology 51, 851–884.

Zhang, H., Shen, G., He, Z., 1999. A carbon Isotopic Stratigraphic Pattern of the Late Palaeozoic Coals in the North China Platform and Its Palaeoclimatic Implications. Acta Geologica Sinica, 72(1), 111–119.

CHAPTER 1

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, sphenopterids, and sphenopsids. 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, which typically resemble late Pennsylvanian and early Permian walchian 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 walchian- 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.

Keywords: Permian, Kungurian, Fossil conifers, *Dolomitia*, Dwarf-shoots, *Pseudovoltzia*

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 walchian conifers (walchian Voltziales), a paraphyletic group of trees with plagiotropic branching patterns. The walchian conifers originated during the middle 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 walchian 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 ginkgo. In eastern Euramerica, late Cisuralian and Guadalupian sequences are rare and in- complete, and generally do not contain plant remains. Until now, evidence for the timing of the transition from walchian- 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 walchian 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.

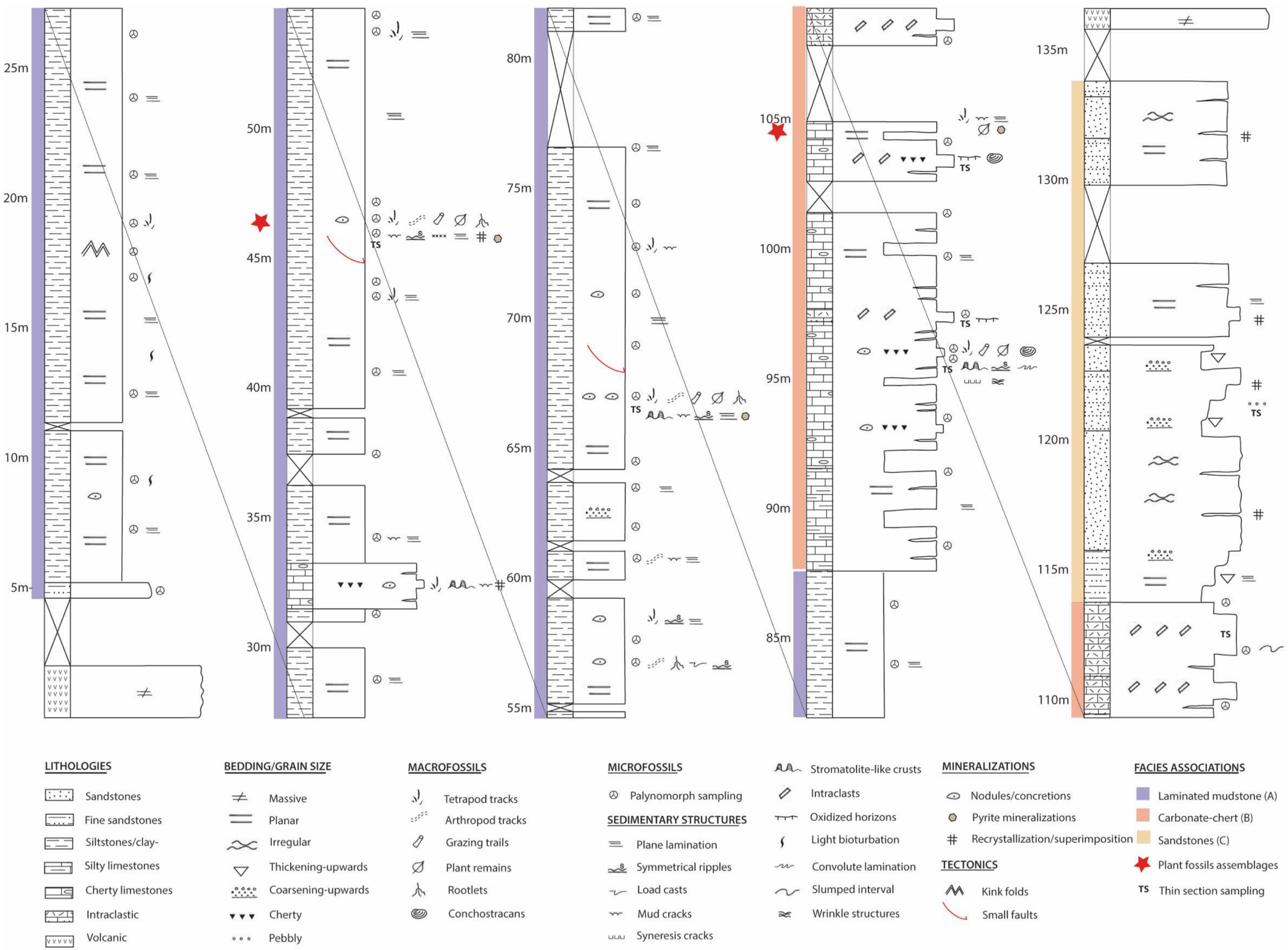

Fig. 1. Stratigraphic section of "Le Fraine", from Marchetti et al. (2015) (modified).

2. Materials 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 limestones 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., submitted).

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 of 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 I, 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 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.

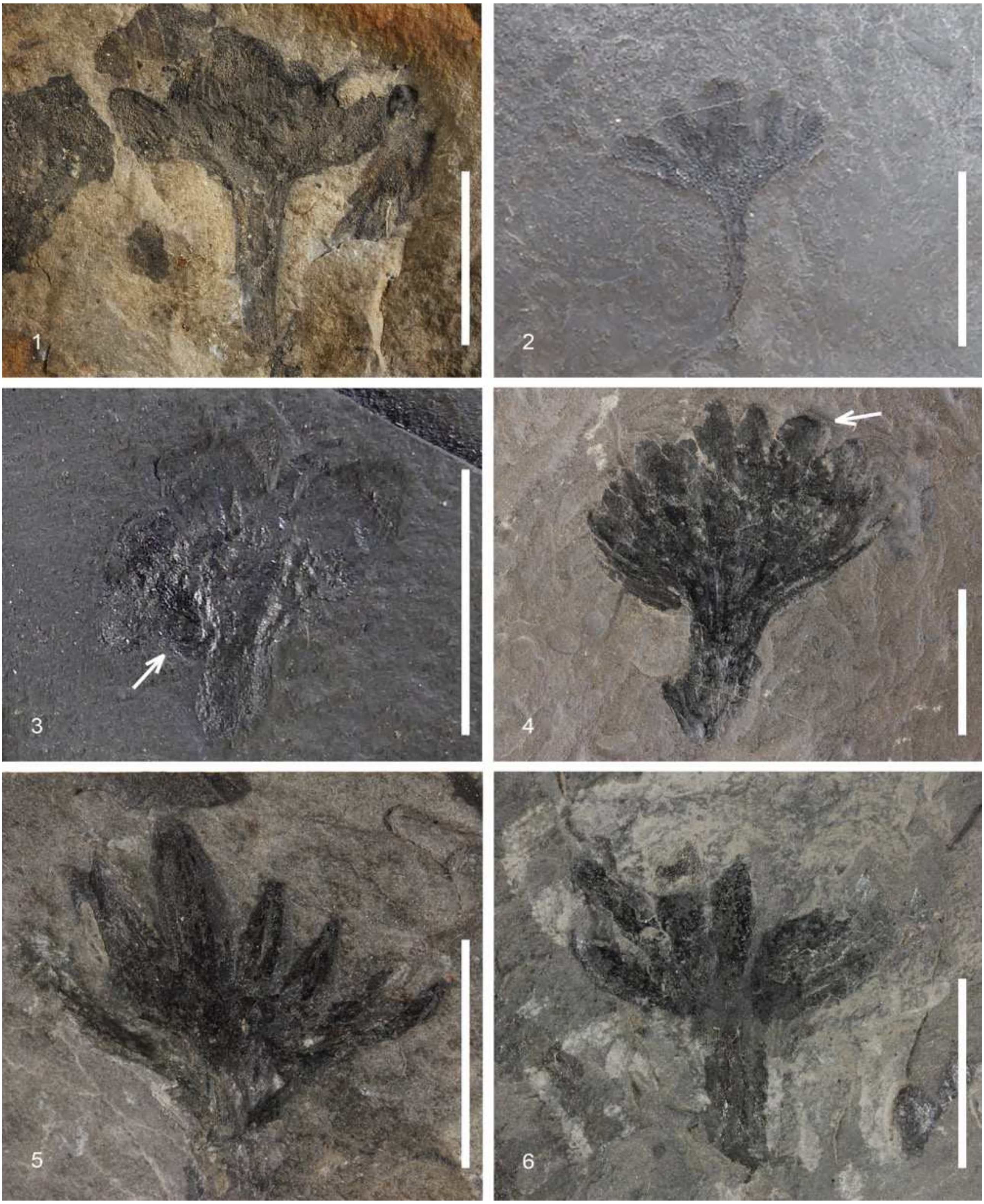

Plate I. 1. Dwarf shoot of *Dolomitia* sp. (MUSE PAG 7315); 2. *Pseudovoltzia*-like dwarf shoot (TREG P1600859), from the upper flora; 3. *Pseudovoltzia*-like dwarf shoot laterally folded (MUSE PAG 7389), from the lower flora; the arrow indicates ovoid coaly structure that may be attribute to an ovule 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; 5. Type C dwarf shoot (TREG 0038) with a well-defined stalk-like base, lanceolate scales free down to their base; scale bar 1 cm.

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 cittertiae* 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. cittertiae* 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. cittertiae*, 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.

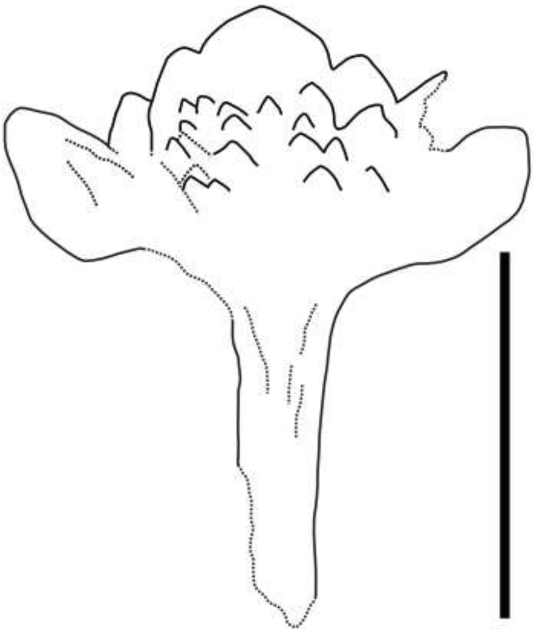

Fig. 2. Reconstruction of dwarf shoot of *Dolomitia* sp. (MUSE PAG 7315), showing several acute sterile scales (17–19) and three main rounded fertile scales; scale bar 1 cm.

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 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.

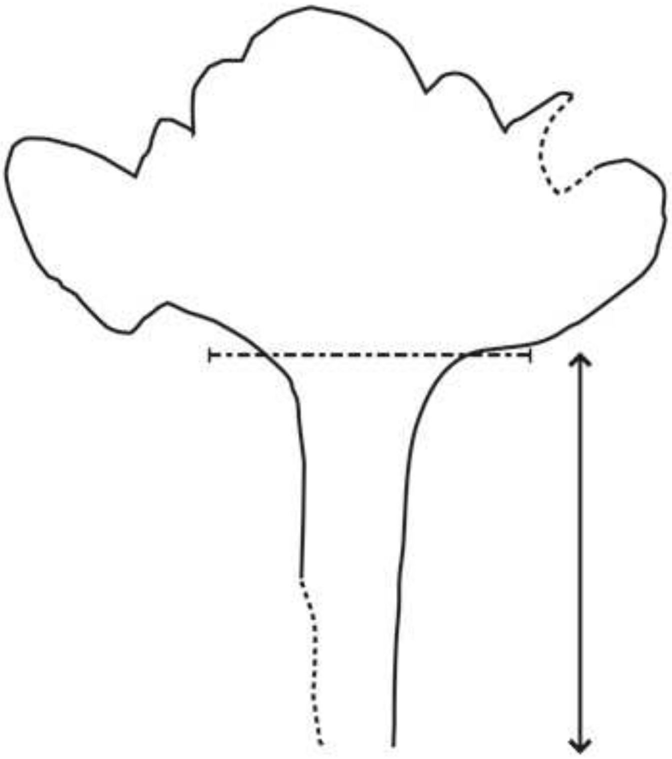

Fig. 3. Indication of the length of *Dolomitia* sp. stalk-like base; the dotted line links the two maximum curvature point of the upper portion down.

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 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).

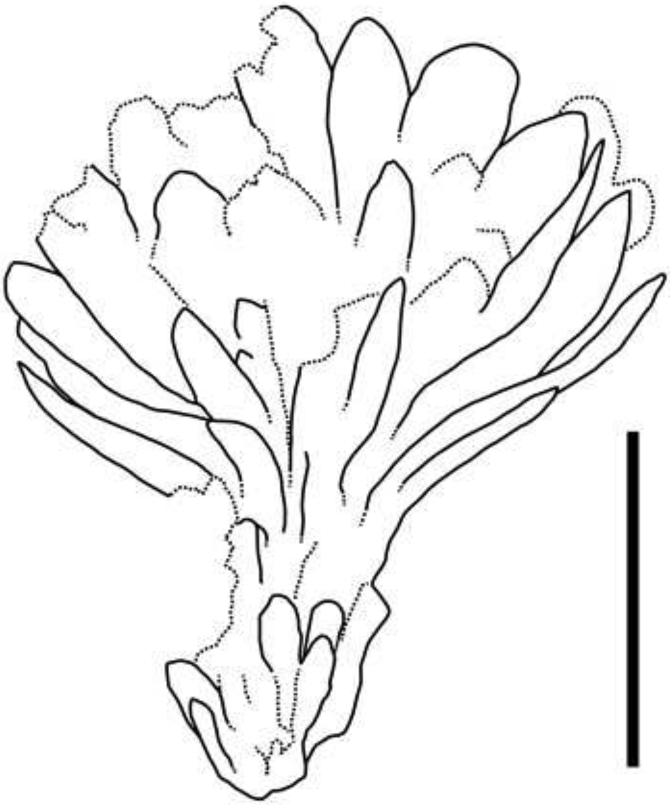

Fig. 4. Reconstruction of Type A dwarf shoot (TRE 526), showing several rows of scales that also cover the stalk-like base; scale bar 1 cm.

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, bi- laterally 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* Mädler, 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 (Mädler, 1957), but it was also reported from a mixed "Rotliegend-Zechstein" assemblage from northern Germany (Mädler, 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 Majonicaceae. 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 Majonicaceae 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 Majonicaceae, was so far only known from the late Permian of the Southern Alps. *Dolomitia cittertiae* 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

Majonicaceae by having a relatively high number of small sterile scales positioned on the ab- axial 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 be- tween the walchian conifers and the Majonicaceae (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 walchian conifers like *Emporia*, *Otovicia* and *Ortiseia* too. This may suggest a close walchian 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* (Majonicaceae, 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 walchian and voltzian taxa. Originally established for the late Permian taxa in Europe, the Majonicaceae 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 Majonicaceae 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 walchian 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 extrabasinal 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.

Acknowledgements

We want to thank Mr. Ferruccio Valentini (Tuenno) for meticulously collecting material over the years and making his collection available. Without him and his deep love for nature that he never fails to transmit, this paper would not have been possible. We thank also dr. Massimo Bernardi (MUSE, Trento) and Dr. Lorenzo Marchetti (Urweltmuseum GEOSKOP) for their support, and the MUSE Museo delle Scienze of Trento for the access to the collection. The paper was improved by the thoughtful comments of Bill DiMichele and one anonymous reviewer.

References

Avanzini, M., Bargossi, G., Borsato, A., Castiglioni, G.B., Cucato, M., Morelli, C., Prosser, G., Sapelza, A., 2007. Note illustrative della Carta Geologica d'Italia alla scala 1:50.000, Foglio 026 Appiano. Servizio Geologico d'Italia APAT, Dipartimento Difesa del Suolo, Roma (184 pp.).

Broutin, J., Kerp, H., 1994. Aspects of Permian palaeobotany and palynology. XIV. A new form-genus of broad-leaved Late Carboniferous and Early Permian Northern Hemisphere conifers. Rev. Palaeobot. Palynol. 83, 241–251.

Cassinis, G., Doubinger, J., 1991. On the geological time of the typical Collio and Tregiovo continental beds in the Southalpine Permian (Italy), and some additional observations. Atti Ticinesi di Scienze della Terra 34, 1–20.

Cassinis, G., Doubinger, J., 1992. Artinskian to Ufimian palynomorphs assemblages from the Central Southern Alps, Italy and their regional stratigraphic implications. In: Nairn, A.E.M., Koroteev, V. (Eds.), Contributions to Eurasian Geology, Papers Presented at the International Congress Permian System of the World, Part I. University of South Carolina, Columbia, pp. 9–18.

Cecil, C.B., Dulong, F.T., 2003. Precipitation models for sediment supply in warm climates. SEPM Spec. Publ. 77, 21–27.

Clement-Westerhof, J.A., 1984. Aspects of Permian palaeobotany and palynology. IV. The conifer Ortiseia Florin from the Val Gardena Formation of the Dolomites and the Vicentinian Alps (Italy) with special reference to a revised concept of the Walchiaceae (Göppert) Schimper. Rev. Palaeobot. Palynol. 41, 51–166.

Clement-Westerhof, J.A., 1987. Aspects of Permian palaeobotany and palynology, VII. The Majonicaceae, a new family of Late Permian conifers. Rev. Palaeobot. Palynol. 52, 375–402.

Clement-Westerhof, J.A., 1988. Morphology and phylogeny of Palaeozoic conifers. In: Beck, C. (Ed.), Origin and Evolution of Gymnosperms. Columbia University Press, New York, pp. 298–337.

DiMichele, W.A., Mamay, S.H., Chaney, D.S., Hook, R.W., Nelson, W.J., 2001. An early Permian flora with late Permian and Mesozoic affinities from North-Central Texas. J. Paleontol. 75 (2), 449–460.

DiMichele, W.A., Hook, R.W., Nelson, W.J., Chaney, D.S., 2004. An unusual Middle Permian flora from the Blaine Formation (Pease River group, Leonardian-Guadalupian series) of King County, west Texas. J. Paleontol. 78, 765–782.

DiMichele, W.A., Tabor, N.J., Chaney, D.S., Nelson, W.J., 2006. From wetlands to wet spots: environmental tracking and the fate of Carboniferous elements in Early Permian tropical floras. In: Greb, S.F., DiMichele, W.A. (Eds.), Wetlands Through Time. Geological Society of America Special Paper 399, pp. 223–248.

DiMichele, W.A., Kerp, H., Tabor, T.J., Looy, C.V., 2008. The so-called “Paleophytic-Mesophytic” transition in equatorial Pangea: multiple biomes and vegetational tracking of climate change through geological time. Palaeogeogr. Palaeoclimatol. Palaeoecol. 286, 152–163.

DiMichele, W.A., Montañez, I.P., Poulsen, C.J., Tabor, N.J., 2009. Climate and vegetational regime shifts in the late Paleozoic ice age earth. Geobiology 7 (2), 200–226.

Falcon-Lang, H.J., Lucas, S.G., Kerp, H., Krainer, K., Montañez, I.P., Vachard, D.V., Chaney, D.S., Elrick, S.D., Contreras, D.L., Kurzawe, F., DiMichele, W.A., Looy, C.V., 2015. Early Permian (Asselian) vegetation from a seasonally dry coast in western equatorial Pangea: paleoecology and evolutionary significance. Palaeogeogr. Palaeoclimatol. Palaeoecol. 433, 158–173.

Florin, R., 1927. Preliminary descriptions of some Palaeozoic genera of Coniferae. Arkiv för Botanik 21 (A), 1–7.

Florin, R., 1964. Über *Ortiseia leonardii* n. gen. et sp. eine Konifere aus den Grödener Schichten in Alto Adige (Südtirol). Memorie Geopaleontologiche dell'Università di Ferrara 1 (1), 3–11.

Forte, G., Kustatscher, E., Van Konijnenburg-van Cittert, J.H.A., Kerp, H., submitted. Sphenopterid Diversity in the Kungurian of Tregiovo.

Hernandez-Castillo, G.R., Rothwell, G.W., Mapes, G., 2001. Thucydiaceae fam. nov., with a review and reevaluation of Paleozoic walchian conifers. Int. J. Plant Sci. 162, 1155–1185.

Hernandez-Castillo, G.R., Rothwell, G.W., Stockey, R.A., Mapes, G., 2003. Growth architecture in *Thucydia mahoningensis*, a model for primitive walchian conifer plants. Int. J. Plant Sci. 164, 443–452.

Horton, D.E., Poulsen, C.J., Montañez, I.P., DiMichele, W.A., 2012. Eccentricity-paced late Paleozoic climate change. Palaeogeogr. Palaeoclimatol. Palaeoecol. 331–332, 150–161.

Kerp, H., Clement-Westerhof, J.A., 1991. Aspect of Permian palaeobotany and palynology XII. The form-genus *Walchiostrobus* Florin reconsidered. Neues Jahrb. Geol. Palaontol. Abh. 183 (1–3), 257–268.

Kerp, J.H.F., Poort, R.J., Swinkels, H.A.J.M., Verwer, R., 1990. Aspect of Permian palaeobotany and palynology. IX. Conifer-dominated Rotliegend floras from the Saar-Nahe Basin (Late Carboniferous-Early Permian; SW-Germany) with special reference to the reproductive biology of early conifers. Rev. Palaeobot. Palynol. 62, 205–248.

Kozur, H., 1980. Beiträge zur Stratigraphie des Perms. Teil III (2): Zur Korrelation der überwiegend kontinentalen Ablagerungen des obersten Karbons und Perms von Mittel- und Westeuropa. Freib. Forsch. C348, 69–172.

Looy, C.V., 2007. Extending range of derived Late Paleozoic conifers: *Lebowskia* gen. nov. (Majonicaceae). Int. J. Plant Sci. 168, 957–972.

Looy, C.V., Stevenson, R.A., 2014. Earliest occurrence of autorotating seeds in conifers: the Permian (Kungurian–Roadian) *Manifera talaris* gen. et sp. nov. Int. J. Plant Sci. 175, 841–854.

Looy, C.V., Kerp, H., Duijnstee, I.A.P., DiMichele, W.A., 2014. The late Paleozoic ecological-evolutionary laboratory, a land-plant fossil record perspective. Sediment. Rec. 12 (4), 4–9.

Mädler, K., 1957. *Ullmannia*-Blätter und andere Koniferenrete aus dem Zechstein der Bohrung Friederich Heinrich 57. Geol. Jahrb. 73, 75–90.

Mädler, K.A., 1992. Die Rotliegend-Zechsteinflora von Lieth bei Elmshorn, Schleswig- Holstein. Geologisches Jahrbuch, A 133, 3–31.

Mapes, G., Rothwell, G.W., 2003. Validation of the names Emporiaceae, *Emporia*, and *Emporia lockardii*. Taxon 52, 327–328.

Marchetti, L., Forte, G., Bernardi, M., Wappler, T., Hartkopf-Fröder, C., Krainer, K., Kustatscher, E., 2015. Reconstruction of a Late Cisuralian (Early Permian) floodplain lake environment: palaeontology and sedimentology of the Tregiovo Basin (Trentino-Alto Adige, Northern Italy). Palaeogeogr. Palaeoclimatol. Palaeoecol. 440, 180–200.

Marocchi, M., Morelli, C., Mair, V., Klotzli, U., Bargossi, G.M., 2008. Evolution of large silicic magma systems: remarks new U-Pb zircon data on the NW Permian Athesian Volcanic Group (Southern Alps, Italy). J. Geol. 116, 480–498.

Michel, L.A., Tabor, N.J., Montañez, I.P., Schmitz, M.D., Davydov, V.I., 2015. Chronostratigraphy and paleoclimatology of the Lodève Basin, France: evidence for a pan-tropical aridification event across the Carboniferous–Permian boundary. Palaeogeogr. Palaeoclimatol. Palaeoecol. 430, 118–131.

Montañez, I.P., Poulsen, C.J., 2013. The Late Paleozoic ice age: an evolving paradigm. Annu. Rev. Earth Planet. Sci. 41, 629–656.

Montañez, I.P., Tabor, N.J., Niemeier, D., DiMichele, W.A., Frank, T.D., Fielding, C.R., Isbell, J.L., Birgenheier, Rygel, M.C., 2007. CO2-forced climate and vegetation instability during Late Paleozoic deglaciation. Science 315, 87–91.

Neri, C., Avanzini, M., Bampi, T., Bargossi, G.M., Mair, V., Morelli, C., Pittau, P., Ronchi, A., Sapelza, A., 1999. The Tregiovo area and related volcanics in the Tregiovo section. 1.2. The Tregiovo section. The Continental Permian, International Congress, 15–25 Sept., 1999, Brescia, Italy—Stratigraphy and Facies of the Permian Deposits Between Eastern Lombardy and the Western Dolomites, Field Trip Guidebook, 23–25 Sept. 1999. Earth Science Department, Pavia University, Pavia, pp. 81–82.

Peyser, C.E., Poulsen, C.J., 2008. Controls on Permo–Carboniferous precipitation over tropical Pangea: a GCM sensitivity study. Palaeogeogr. Palaeoclimatol. Palaeoecol. 268, 181–192.

Remy, W., Remy, R., 1978. Die Flora des Perms im Trompia-Tal und die Grenze Saxon/ Thuring in den Alpen. Argumenta Palaeobotanica 5, 57–90.

Rothwell, G.W., Mapes, G., Hernandez-Castillo, G.R., 2005. *Hanskerpia* gen. nov. and phylogenetic relationships among the most ancient conifers (Voltziales). Taxon 54, 733–750.

Schweitzer, H.J., 1963. Der weibliche Zapfen von *Pseudovoltzia liebeana* und seine Bedeutung für die Phylogenie der Koniferen. Palaeontographica B 113, 1–29.

Schweitzer, H.J., 1996. *Voltzia hexagona* (Bisschof) Geinitz aus dem mittleren Perm Westdeutschlands. Palaeontographica 239 (1–3), 1–22.

Tabor, N.J., Montañez, I.P., 2004. Morphology and distribution of fossil soil in the Permo–Pennsylvanian Wichita and Bowie Group, north-central Texas, USA: implications for western equatorial Pangea palaeoclimate during icehouse-greenhouse transition. Sedimentology 51, 851–884.

Tabor, N.J., Poulsen, C.J., 2008. Palaeoclimate across the Late Pennsylvanian-Early Permian tropical palaeolatitudes: a review of climate indicators, their distribution, and relation to palaeophysiographic climate factors. Palaeogeogr. Palaeoclimatol. Palaeoecol. 268, 293–310.

Vacek, M., 1882. Vorlage der geologischen Karte des Nonsberges. Verhandl. k.-k. geol. Reichsanst. 3, 42–47.

Vacek, M., 1894. Ueber die geologischen Verhältnisse des Nonsberges. Verhandl. k.-k. geol. Reichsanst. 16, 431–446.

Vacek, M., Hammer, W., 1911. Erläuterungen zur Geologischen Karte, der im Reichsrate vertretenen Königreiche und Länder der Österr.-ungar. Monarchie. SW-Gruppe Nr. 79 Cles. Verhandl. k.-k. geol. Reichsanst., Wien.

Visscher, H., Kerp, J.H.F., Clement-Westerhof, J.A., 1986. Aspects of Permian palaeobotany and palynology. VI. Towards a flexible system of naming Palaeozoic conifers. Acta Bot. Neerlandica 35 (2), 87–99.

Visscher, H., Kerp, J.H.F., Clement-Westerhof, J.A., Looy, C.V., 2001. Permian floras of the Southern Alps. Natura Bresciana 25, 117–123.

Wang, Z.Q., Wang, L.X., 1986. Late Permian fossil plants from the lower part of the Shiqianfeng (Shihchienfeng) Group in North China. Bull. Tianjin Inst. Geol. Miner. Res. 15, 1–120 (in Chinese with extended English Abstract).

Wardlaw, B.R., 2005. Age assignment of Pennsylvanian–Early Permian succession of North Central Texas. Permophiles 44, 25–28.

CHAPTER 2

Sphenopterid diversity in the Kungurian of Tregiovo (Trento, NE-Italy)

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Abstract

The lower Permian fossiliferous deposit of Tregiovo, in the upper Val di Non (Trento Province, N-Italy), is known from the beginning of last century, since it has yielded invertebrate and vertebrate footprints, palynomorphs, conchostracans, and especially plant remains. In recent years, a new section in the Tregiovo Formation, called "Le Fraine", located along the Lauregno provincial road, has been discovered. Two fossiliferous layers in this new section, one in the lower and one in the upper part of the section, yielded different plant assemblages. The radiometric dating of the volcanic formations under- and overlying the Tregiovo Formation, indicates a middle Kungurian age for the fossil-bearing sequence. More than 1000 specimens, impressions and compressions but without cuticles, have been found. The two plant assemblages are rich and diverse, and both are dominated by conifers (e.g., *Feysia*, *Hermitia*, *Dolomitia*) that range from 60 to 80% of the total assemblage, but also sphenophytes (*Annularia*), taeniopterids (*Taeniopteris*) and ginkgophytes (*Sphenobaiera*) occur. Most remarkable of these two assemblages is the high diversity of sphenopterids that are sometimes preserved as complete fronds. At least five different species can be attributed to the genus *Sphenopteris*, i.e. *S. kukukiana*, *S. suessii, S.* sp. cf. *S. geinitzii, Sphenopteris* sp. and a morphotype that represents a new species, *S. valentinii*. Most species look pretty stiff and have strongly dissected pinnules with very narrow, linear rigid segments, apparently being an adaptation to arid conditions. The Tregiovo flora is of great importance, not only because of its richness and diversity, especially with regard to sphenopterids, but also because it is one of the very few well-dated Kungurian floras from Euramerica.

Keywords: Cisuralian, lower Permian, southern Alps, *Sphenopteris*, lake deposits

1. Introduction

During the late Carboniferous sphenopterids were common and diverse (e.g., Brousmiche, 1983), but they became much rarer in the Permian with a limited number of species. No less than 13 species of *Sphenopteris* (Brongniart) Sternberg, 1825 were reported from the Stephanian of Central France (Blanzy: Langiaux, 1982; Saint-Étienne Basin: Doubinger et al., 1995). In contrast, the number of species reported from the classical Rotliegend and Autunian sequences of Europe (Asselian–Sakmarian) is surprisingly low (e.g., Barthel, 2006, 2016; Šimůnek and Martínek, 2009; Fig. 1). They comprise two species that were first described from the Stephanian (*Sphenopteris mathetii* Zeiller, 1888 and *S. picandetii* Zeiller, 1888), and one species (*S. germanica* Weiss, 1869; Fig. 1), originally described from lower Permian strata of Radogosz, Silesia, Poland (Weiss, 1879). The latter species is very rare and in many European Rotliegend basins even absent. However, it has recently been recognized in the south-western United States, where it can be locally abundant in the upper Pennsylvanian and may occur as low as the middle Pennsylvanian (Lucas et al., 2013; DiMichele et al., 2013, 2017). In addition, two species were recorded from the Collio Formation (Artinskian) in Val Trompia, northern Italy, i.e. *S. suessii* Geinitz, 1965 and *S. kukukiana* Gothan et Nagalhard, 1921

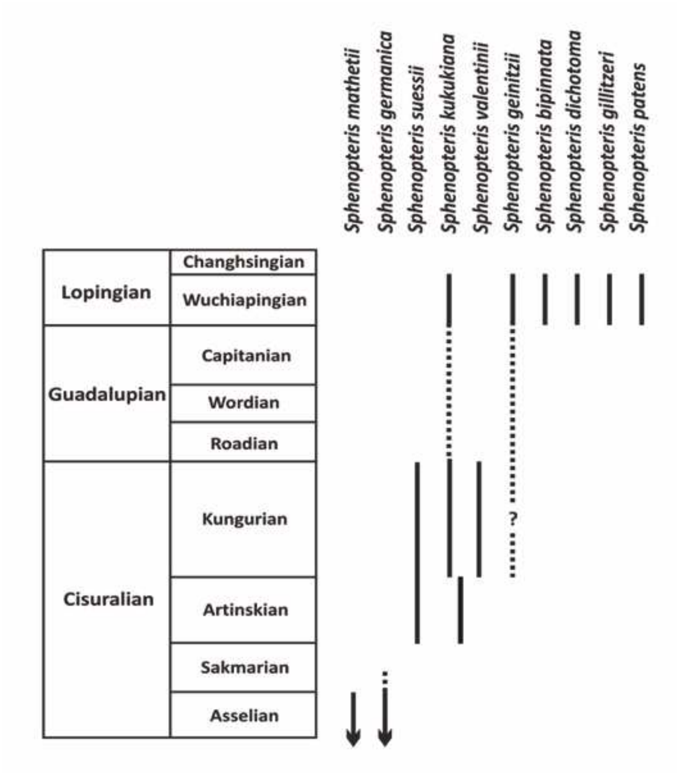


Fig. 1. Distribution of the genus *Sphenopteris* in the European area during the Permian.

(Geinitz, 1869; Remy and Remy, 1978; Visscher et al., 2001). The first species was established on fossils from Val Trompia, whereas the latter was originally described from the Zechstein of the Niederrhein, Germany (Fig. 1). None of these species is really common, some are even known from a few localities only. Other species from the lower Permian originally assigned to *Sphenopteris* were later transferred to other genera, i.e. *Ovopteris dechenii* (Weiss) Potonié, 1893 and *O. lebachensis* (Weiss) Archangeli, 1895. Sphenopterids were quite diverse in the upper Permian, and Schweitzer (1960) listed seven *Sphenopteris* species from the German Zechstein although some are known from small fragments only. The preservation is generally poor to very poor and all species are from the Kupferschiefer. However, the number of species per locality is limited; from some localities only a single species is known. The discovery of a middle Kungurian flora in Tregiovo, Val di Non, northern Italy, with five species of *Sphenopteris*, including one new species, *Sphenopteris valentinii* sp. nov., is therefore of great interest. The Tregiovo Formation is one of the few fossil-bearing localities in Kungurian strata in Euramerica (see also Forte et al., 2017).

2. Geographical and geological setting

The Tregiovo Basin is a small sedimentary basin within the Athesian Volcanic Complex. The Tregiovo Formation is intercalated between two volcanic formations, i.e. the Auer/Ora Formation and the Gargazzon/Gargazzone Formation. Plant fossils from the Tregiovo Formation were described by Remy and Remy (1978), Visscher et al. (2001), and Marchetti et al. (2015). In addition, palynomorphs, conchostracans and vertebrate footprints were reported. Various ages were suggested based on palynomorphs, i.e. Artinskian–Kungurian (Mostler, 1966), Kungurian–Capitanian (Cassinis and Doubinger, 1991, 1992), and Kungurian–Ufimian (Barth and Mohr, 1994; Neri et al., 1999). Tetrapod footprints would support an Artinskian–Kungurian age (Conti et al., 1997, 1999), general palaeontological data suggest a middle Kungurian–early Roadian age (Cassinis et al., 2002). Recent radiometrical dating of the overlying Auer/Ora Formation and the underlying Gargazon/Gargazzone Formation attribute respectively 274.1 ± 1.6 Ma and 276.5 ± 1.1 Ma to the two formations (Avanzini et al., 2007; Marocchi et al., 2008), which confines the age of the Tregiovo Formation to the middle Kungurian.

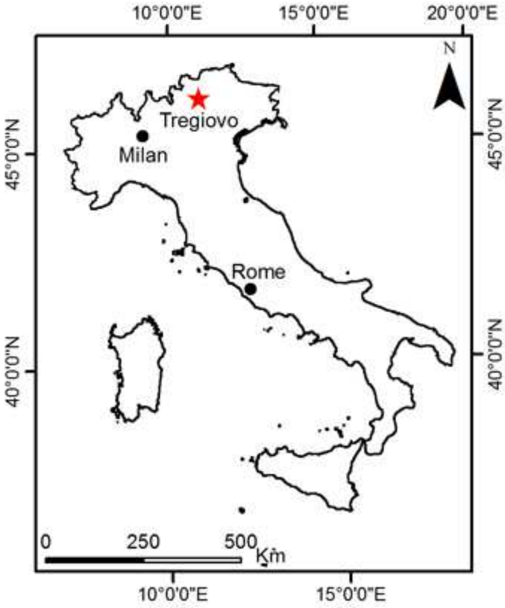


Fig. 2. Location of the Tregiovo village.

The “Le Fraine” section is located in the upper Val di Non, near the village of Tregiovo (Trento Province, NE-Italy; Fig. 2). The section extends from the Pescara creek to the village with a total thickness of about 130 m (Fig. 3). At its base, the section consists of very finely laminated dark siltstones and claystones, and in the upper part of marly limestones and sandstones (Marchetti et al., 2015). The finely laminated plant-bearing sediments are interpreted as lacustrine deposits, and show a cyclical variation of the lake level. Moreover, they are very rich in organic matter and sometimes traces of pyritization occur, which indicate sub- to anoxic conditions at the bottom of the lake (Marchetti et al., 2015).

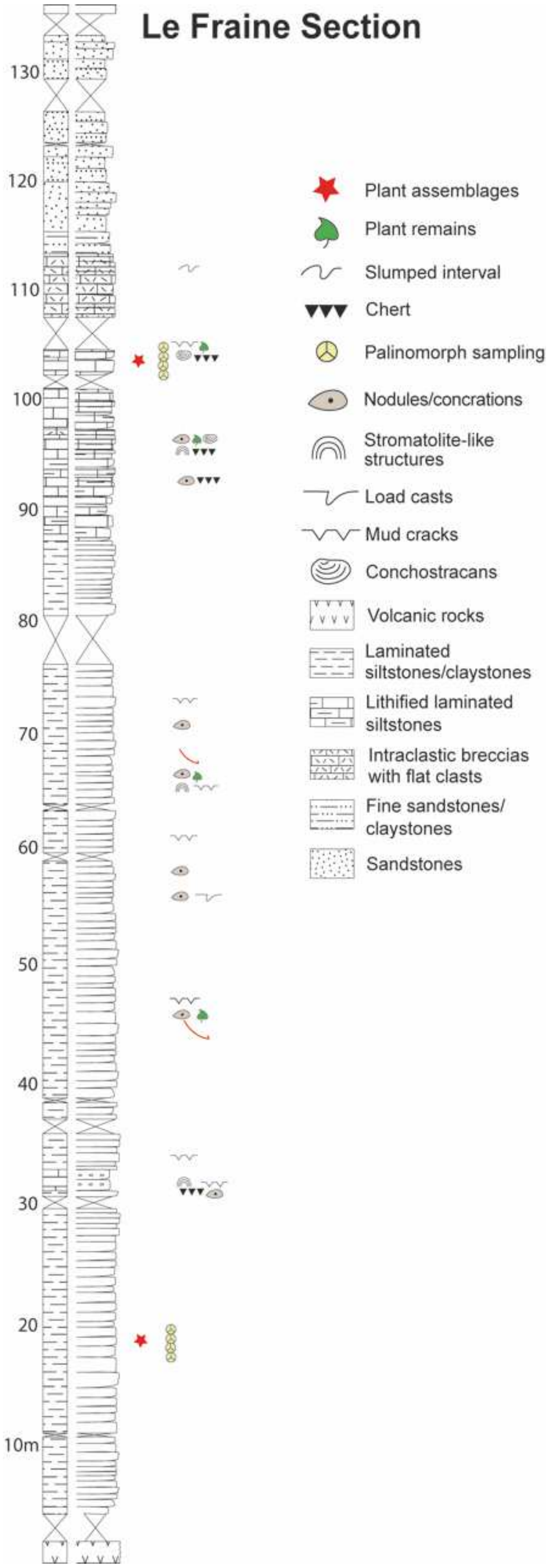


Fig. 3. Simplified scheme of the “Le Fraine” section (modified from Marchetti et al., 2015).

3. Material and methods

The material from the "Le Fraine" section is temporary stored in the MUSE, Museo delle Scienze of Trento (Italy), labelled with the prefix "MUSE PAG", followed by a progressive number. The recently collected material (collection Valentini) has a provisional prefix (e.g., TREG, followed by a progressive number); the holotype of *Sphenopteris valentinii* sp. nov. Forte et Kerp is stored at the Museum of Geology and Palaeontology of the University of Padova, labelled with the number MGP-PD 31970.

The specimens come from two different plant assemblages, respectively at ca. 45 m and 105 m from the base of the section (Fig. 3), and are part of a collection that consists of more than 1000 specimens. The lowermost plant assemblage is characterized by the dominance of foliated conifer shoots (*Hermitia* Kerp et Clement-Westerhof, 1986, *Feysia* Broutin et Kerp 1994, *Quadrocladus* Mädler, 1957). Furthermore, several conifer dwarf-shoots (e.g., *Dolomitia* Clement-Westerhof 1987, *Pseudovoltzia*-like, Type A–C; Forte et al., 2017), sphenophytes (*Annularia* Sternberg, 1821), ginkgophytes (*Sphenobaiera* Florin, 1936), pteridosperms (*Peltaspermum* Harris 1937 and *Lodevia*-like foliage), taeniopterids (*Taeniopteris* Brongniart, 1828) and twelve frond fragments of *Sphenopteris* (Marchetti et al., 2015) are known. The upper assemblage is dominated by the same conifer genera as the lower assemblage, and further contains pteridosperms (*Peltaspermum*), and taeniopterids, and a higher abundance and greater variety of sphenopterids. The material consists of adpressions without cuticle due to high coalification and the specimens are often pyritized. The ones from the upper assemblage are better preserved and more complete than those from the lower assemblage. Some fronds are remarkably complete including the base of the frond. All specimens were photographed with a Canon EOS 550D and were studied under a dissecting stereomicroscope (SZ-ST Olympus), measured with a calliper and also digitally with the free software ImageJ64®.

4. Systematic palaeontology

4.1. Genus *Sphenopteris* (Brongniart 1822) Sternberg 1825

Sphenopteris (Brongniart, 1822) Sternberg, 1825 is a genus for fossil wide diversity of fern-like foliage with usually small, deeply lobed, dissected or segmented pinnules having linear, rounded, oval, obovate, or sometimes wedge-shaped pinnule segments. This fossil genus is based on morphological criteria only and includes morphologically similar but not necessarily related species. A fairly large number species originally assigned *Sphenopteris* have been reclassified and assigned to other genera on the basis of morphological criteria and/or their natural affinity. Several species originally assigned to *Sphenopteris* have been recognized as pteridosperms (see e.g., Van Amerom, 1975), whereas others can be assigned to different fern genera (see e.g., Brousmiche, 1983). However, there is still a fairly large, morphologically very diverse group of species that cannot be classified in any of the segregate genera of *Sphenopteris* and of which the natural affinity cannot proven; the generic name *Sphenopteris* is retained for this group of species. The forked fronds seen in two of the *Sphenopteris* species here described from Tregiovo strongly suggests that at least these forms were pteridosperms.

No less than five different morphotypes of sphenopterids have been recovered from the Le Fraine section near Tregiovo. Three of them can be attributed to known species, whereas one appears to be new. A fifth type cannot be assigned to any known species, but the generic assignment is clear. These forms are described and discussed below. The main features are summarized in Table 1a, 1b together with other Lopingian species for comparison.

4.1.1. Sphenopteris kukukiana Gothan et Nagalhard 1922

Plate I, 3, Pl. II

Description: Frond bifurcate, bipinnate, more or less triangular in outline (e.g., Plate I, 3, Plate II). Specimens are 58–112 mm long and 51–66 mm wide, with up to at least 10 pinna pairs attached at and above the bifurcation; lower part of the rachis (below the bifurcation) naked (TREG 649), widening towards the base. The frond rachis is 5.1 mm wide at the base, 2.8 mm at the bifurcation; the rachides of the frond segments above the bifurcation are 1.5–2 mm wide; the angle of bifurcation is c. 40–50°. Pinnae are alternate to subopposite, widely spaced in the lower part of the frond segments and more densely positioned in the upper half, where they are partly overlapping. In the interior part of the frond, pinnae are smaller than in the external part, especially immediately above the bifurcation. Pinnae become smaller towards the frond apex; apex of the frond segments is acute in outline. Pinnae are up to 370 mm long and 170 mm wide, more or less straight in outline with rounded apices. Pinna rachides are remarkably stiff, straight to very slightly bent upward, attached an angle of 40–100°. Pinnules vary from simple (Plate I, 3, TREG 126), bilobed to pinnately lobed with narrow, very stiff segments with rounded, sometimes slightly widened apices. They vary from 2–10 mm in length and from 0.8–5.5 mm in width; venation unclear. Pinnae are usually terminating in two simple lobes (Plate II, TREG 649).

Discussion: Sphenopteris kukukiana is the most common sphenopterid in the Tregiovo flora. The species is easily recognizable by its very regularly arranged pinnae and pinnules, both having a very stiff appearance. The lack of intercalary pinnules distinguishes *S. kukukiana* from callipterids with superficially similar pinnules, such as *Gracilopteris bergeronii* (Zeiller) Kerp, Naugolnykh et Haubold, 1991 and *Arnhardtia scheibei* (Gothan) Haubold et Kerp, 1988. Its forked rachis suggests an affinity with the seedferns.

Plate I. 1. Almost complete frond of *Sphenopteris suessii* Geinitz 1869 from the upper plant assemblage, TREG 565; 2. frond fragment of *Sphenopteris* sp. cf. *Sphenopteris geinitzii* (Geinitz 1848) Göppert 1864 from the lower plant assemblage, MUSE PAG 7309; 3. frond fragment of *Sphenopteris kukukiana* Gothan et Nagalhard 1921 from the upper plant assemblage, TREG 126.

The species was first described by Gothan and Nagalhard (1922) from the Zechstein (Wuchiapingian) of the Niederrhein (Lower Rhine) in Germany, where some 30 specimens were collected. Three of the specimens from Germany show the basal dichotomy (Gothan and Nagalhard, 1922; Schweitzer, 1960, 1962, 1986). In the most complete specimen (Schweitzer, 1962, pl. 2, 1) the frond rachis is little thinner and pinnae are less well preserved. Nevertheless, the similarities with the material from Tregiovo are very clear.

Several larger specimens are known from Tregiovo, including three nearly or largely complete fronds clearly showing the frond architecture (see e.g., Plate II). In addition, a large number of small pinna fragments have been recovered, especially in the upper flora (Plate I, 3). The Tregiovo material nicely illustrates the considerable variability in pinnule morphology within this species. The largest frond bears simple pinnules as well as pinnately compound pinnules (Table 1a). Incomplete, smaller frond portions only bear smaller pinnules. The size and the complexity of pinnule morphology is apparently related to the position of the pinnules in the frond and the size of the frond. Small fronds and fronds of young plants only had simple and/or once bifurcated pinnules. With increasing frond size, the pinnules become pinnately lobed; the most strongly lobed ones occur in the central portion of the frond. This feature, heteroblastic development, is known from many other species e.g., *Rhachiphyllum schenkii* (Heyer 1886) Kerp, 1988.

Sphenopteris kukukiana has also been reported from the Collio Formation (Artinskian) from Monte Colombine, Val Trompia, northern Italy (Remy and Remy, 1978; Visscher et al., 2001). Remy and Remy (1978) illustrated a rather small specimen with a slightly bent rachis with very stiff pinnae; the pinnules are mostly simple and some show two lobes. Although the pinnules do not reach the degree of complexity as in the specimen on our Plate II, it fits very well within *S. kukukiana*. Some specimens from the upper part of the Meisenheim Formation, M8 near Oberhausen/Appel, Saar-Nahe Basin (Germany), identified as *Sphenocallipteris* sp. cf. *S. bergeronii* (Zeiller) Haubold et Kerp, 1988 (Kerp, 1990, pl. 2, 8–11) and from the same formation M5 near Alsenz /Appel, Saar-Nahe Basin listed as *Gracilopteris bergeronii* (Lausberg and Kerp, 2000), look remarkably similar to *Sphenopteris kukukiana*. However, identifications were based on very incomplete specimens not showing the bipinnate nature of the foliage. The type of *Gracilopteris bergeronii* (al. *Callipteris bergeronii* Zeiller, 1898) is a callipterid frond with well-developed intercalary pinnules (Zeiller, 1898). The material from Oberhausen/Appel and Alsenz/Appel comes from lacustrine deposits dominated by conifers. Larger specimens of *G. bergeronii* are extremely rare but isolated pinnules are very common. If these specimens from the Asselian–Sakmarian of the Saar-Nahe Basin would indeed belong to *S. kukukiana*, the record would even be extended further down.

Plate II. Complete frond of *Sphenopteris kukukiana* Gothan et Nagalhard 1921 from the upper plant assemblage, TREG 649.

4.1.2. Sphenopteris valentinii Forte et Kerp sp. nov.

Plates III, IV

Holotype: MGP-PD 31970 bifurcated frond fragment (Plate V), here designated.

Repository: Museum of Geology and Palaeontology of the University of Padova, palaeobotanical collection number MGP-PD 31970.

Type locality: Le Fraine Section, Tregiovo, upper flora, at 105 m above the base of the section Tregiovo, Val di Non, Trento Province, northern Italy.

Stratigraphic Type Horizon and age: Tregiovo Formation (middle Kungurian, Cisuralian, Permian).

Etymology: the epithet refers to Mr. Ferruccio Valentini who discovered the new fossil site near Tregiovo and collected the here described material.

Diagnosis: Frond bifurcated, bipinnate, triangular in outline. Pinnae long, triangular in outline, densely spaced, partly overlapping, inserted above the bifurcation at acute angles. Pinnules pinnately arranged, quite narrow, inserted at acute angles, stiff, simple to once bifurcated near the pinnule base. First pinna and pinnule arising on the basiscopic (catadromic) side.

Description: The available material consists of one complete frond (Plate III), several larger frond portions (Plate IV) and a number of smaller pinnae fragments. The frond fragment MGP-PD 31970 (Plate III) is more or less triangular in outline, 110 mm long and 75 mm wide at the tip. Pinnae are catadromically inserted at angles of 55° basally to 20° apically; pinnae are 14–81 mm long and 6–32 mm wide. The lowermost ones are small but they rapidly increase in length and the longest ones are found about halfway to the apex, then the pinnae become progressively shorter, giving the frond apex a blunt appearance. Pinnules are also arising catadromically and are densely spaced, simple or once bifurcated near their base and with rounded apices. Pinnules, respectively pinnule segments are long, narrow and remarkably stiff, free down to their base but often overlying each other (Plate III, IV); they are 0.4–38 mm long and 1–1.5 mm wide. The longest pinnules are found in the middle of the pinnae, and then they decrease in length resulting in a blunt pinna apex.

Comparisons: *Sphenopteris valentinii* is easily recognizable by its blunt-ending pinnae and pinnules that are less regularly arranged and much longer than other species. In *S. kukukiana* pinnae are ending acutely, and pinnae are more regularly arranged and evenly spaced, and pinnules and pinnule segments are often slightly club-shaped and all more or less of the same size. *Sphenopteris*

Plate III. Holotype of *Sphenopteris valentinii* Forte et Kerp sp. nov. from the upper plant assemblage, MGP-PD 31970.

valentinii resembles *S. suessii* but can be distinguished by the shape of the pinnae, and the apices, which are blunt in *S. valentinii*, whereas they are acute in *S. suessii*. Moreover, *S. valentinii* fronds appear to be more compact with more densely positioned pinnae and pinnules, which may overlap. However, it should be noted that small, fragmentary specimens may be difficult to distinguish.

Discussion: *Sphenopteris valentinii* is only known from the upper plant assemblage. Although at first sight quite similar to *S. suessii*, we think that the suite of characters that distinguishes this form justifies the erection of a new species (see also Table 1a).

Its forked rachis suggests that it belonged to the seedferns, just as *Sphenopteris kukukiana.*

Remarks: The counterpart of the holotype of *Sphenopteris valentinii* (Plate IV, TREG 232) consists of the complete frond, which also includes the lower part with the rachis and the bifurcation, some pinnules from the apical part of the frond. The frond, 180 mm long and 95 mm wide, bifurcates at about one third of its length, the angle of the bifurcation is c. 35°; the lowermost pinnules are inserted slightly below the middle of the frond. The frond rachis is up to 4.4 mm wide below the bifurcation and the rachides of the frond segments above the bifurcation are up to 2.8 mm wide.

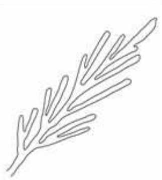
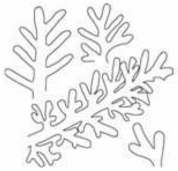
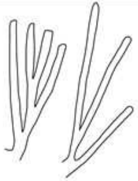
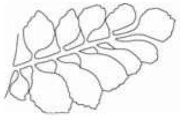
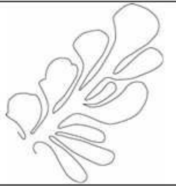
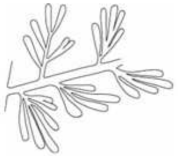
Since the complete frond is part of a private collection (Collezione Valentini), and the specimen MGP-PD 31970 shows the suite of distinctive characters of the new species, we designate the latter as the holotype.

4.1.3. Sphenopteris suessii Geinitz 1869

Plate I, 1

Description: One large bipinnate rhomboid frond portion and several isolated pinnae have been found (Plate I, 1, TREG 565). The largest specimen is a 150 mm long and 80 mm wide frond portion with pinnae in alternating position; however, several of the pinnae are incomplete or missing. The frond rachis is straight, up to 2 mm thick but shows a slight overtopping below the apex. The frond segment ends in a pseudodichotomy. The pinnae are very loosely spaced, arising at an angle of 40–56°; pinnae are up to 52 mm long and 20 mm wide. Pinna axes are straight in the lower half but the upper part may be curved. Pinnules alternate and vary from simple to twice bifurcated; usually one of the segments bifurcates again, the other not, giving the pinnules an asymmetrical appearance (Plate I, 1; Table 1a). Pinnules are 4.5–12 mm long and 0.5–1 mm wide; the basal ones are short, they reach their maximum length in or just above the middle of the pinna and then become shorter towards the pinna apex. Pinnule segments are narrow, linear, and sometimes bi- or trifurcated.

Plate IV. Complete frond of *Sphenopteris valentinii* Forte et Kerp sp. nov. from the upper plant assemblage (TREG 232, counterpart of the holotype).

		S. suessii	*S. kukukiana*	*S. valentinii*	*S. geinitzii*	*Sphenopteris* sp.	*S. bipinnata*	*S. dichotoma*	*S. gillitzeri*	*S. patens*
										
Frond architecture		pseudodichotomous, pinnate-bipinnate	bifurcate, triangular in outline	bifurcate, triangular in outline	bifurcate, pinnate-pinnatifid	bifurcate, pinnate	bifurcate, bipinnate	bifurcate, pinnate	bifurcate, pinnate	bifurcate, pinnate
Pinnules	**shape**	narrow, linear and sometimes bi- or three-furcate	varying from simple, bilobed, pinnately lobed, narrow stiff, segments with rounded apices	pinnules long, narrow, simple or bifurcated near their base, rounded apices, remarkably stiff, free for all their length	elongate, more or less tongue-shaped in outline with many lobes, only few lobes free until the base	laminar appearance, simple rounded/obovate shape or pinnately arranged lobes.	pinnules spatulate, entire-margined, some with small lobes in the apical part	pinnules with alternating ob-ovate segments; segments usually entire-margined, sometimes lobed	pinnules long, narrow, simple or bifurcated near their base	flabellate, with deep, slightly club-shaped lobes, ±emerging from a single point
	spacing	rather loose	rather loose	dense, often overlapping	rather dense	rather dense	dense, partly overlapping (?or partly fused)	dense, partly overlapping	rather loose	loose to rather dense
	venation	unclear	unclear	unclear	with a clear midvein	some pinnules show 2–3 ridges arising from the central part of the pinnule	unclear	pinnules with a clear, ±flexuous midvein/axis; venation of individual lobes palmate	unclear	unclear
	length	4.5–12 mm	2–10 mm	0.5–38 mm	7–40 mm	1.5 mm	3–14 mm	20–45 mm	3–(?)15 mm	4–15 mm
	width	0.5–1 mm	0.8–5.5 mm	1–1.5 mm	4–16 mm	0.5–1.5 mm	1.5–4 mm	12–20 mm	up to 1 mm, usually less	1–4 mm
Occurrence		Mt. Collio, Val Trompia, I; Tregiovo, Val di Non, I	Niederrhein, D; Val di Non, Val Trompia, I	Tregiovo, Val di Non, I	Tregiovo, Val di Non, I (?); Gera, Ilmenau, D	Tregiovo, Val di Non, I	Richelsdorf, D; Hilton, Eden Valley, Westmoreland, UK	Gera, Mansfeld, Richelsdorf, D	Mansfeld, D	Gera, Richelsdorf, D
Stratigraphy		Collio Fm., Artinskian; Tregiovo Fm., Kungurian	Tregiovo Fm., Kungurian, Collio Fm., Artinskian; Zechstein, Wuchiapingian	Tregiovo Fm., Kungurian	Tregiovo Fm., Kungurian?, Zechstein, Wuchiapingian	Tregiovo Fm., Kungurian	Zechstein, Wuchiapingian	Zechstein, Wuchiapingian	Zechstein, Wuchiapingian	Collio Fm., Artinskian, Zechstein, Wuchiapingian
Remarks			Thus far, this species was only known from the Niederrhein				Only two poorly preserved specimens have ever been figured; in our opinion, it is questionable whether both specimens belong to the same species		Very similar to *S. patens*, but smaller and pinnules are more densely spaced. Some superficial similarity to *S. valentinii* but much smaller.	

Tab. 1. Summary table that includes morphological characters, stratigraphy and occurrences of the *Sphenopteris* from the Tregiovo section of “Le Fraine” and other Lopingian species.

Discussion: The material from Tregiovo includes the best-preserved specimens of *Sphenopteris suessii* known to date (e.g., Plate I, 1, TREG 565). The species occurs in the upper assemblage only. Isolated pinnae are quite frequent. The species was originally described from the Collio Formation, Monte Colombine in Val Trompia, northern Italy (Geinitz, 1869; Remy and Remy, 1978). The very loose but regular with narrow segments that are partly twice bifurcated (Table 1a).

4.1.4. Sphenopteris sp. cf. *Sphenopteris geinitzii* (Geinitz 1848) Göppert 1864

Plate I, 2

Description: There is a single 42 mm long and 22 mm wide pinna fragment with alternating pinnules (Pl. I, 2). Pinna rachis is 2.2 mm wide, tapering towards the pinna apex; the rachis looks like it is overtopping slightly. Pinnules, arising at an angle of 45–60° from the pinna rachis, are 6.6–14 mm long and 3.8–5.2 mm wide, pinnately lobed with largely free segments in the basal part and partially fused or overlapping segments at the pinnule apices. Segments are 2–7 mm long and 4–10 mm wide, arise at an angle of 40–60°, and are narrowing near their base and ending more or less club-shaped (Table 1a).

Discussion: Only a single small fragment (MUSE PAG 7309, 7304, respectively part and counterpart) is known from the lower assemblage in Tregiovo. We provisionally identified this specimen as *Sphenopteris* sp. cf. *S. geinitzii*, because it shows the strongly segmented pinnules with slightly club-shaped, densely spaced, partly overlapping segments. The holotype from the Zechstein (Wuchiapingian) of Ilmenau, Thuringia, Germany, illustrated by Geinitz (1848) has been refigured repeatedly but never as a photograph. According to Schweitzer (1960) only two other specimens from Gera have been assigned to this species; we are not aware of any more recently published records.

4.1.5. Sphenopteris sp.

Plate V

Description: A single, largely complete but only partially well-preserved specimen was collected from the lower plant-bearing level (Plate V, TREG 328). It is a bifurcated, bipinnate frond, 85 mm long and 57 mm wide. The angle of bifurcation is c. 40°. The frond rachis varies in width from 3.3 to 4.4 mm. The first small pinnules are attached just below the bifurcation. Above the bifurcation

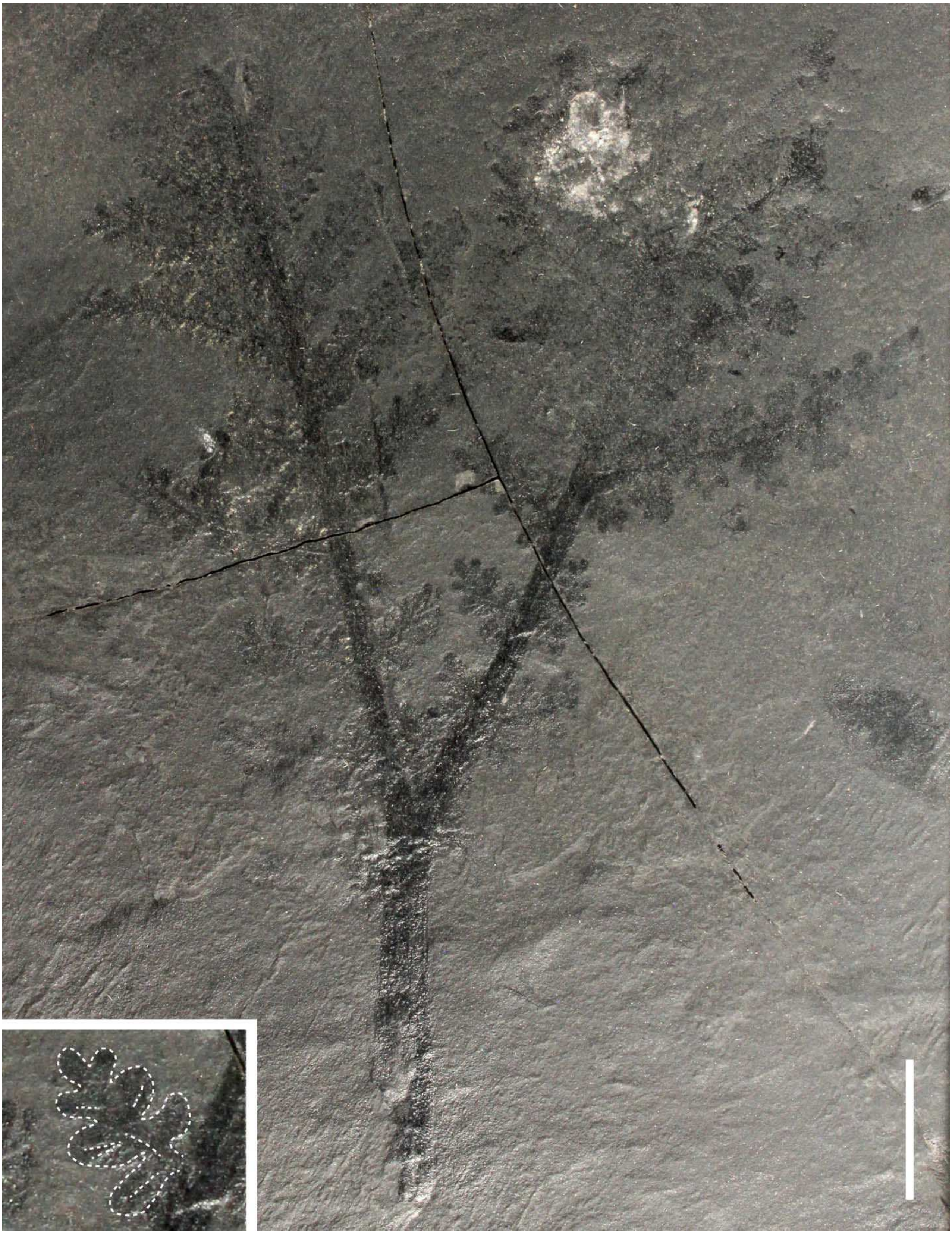


Plate V. Complete bifurcate frond of *Sphenopteris* sp. from the lower plant assemblage (TREG 232).

pinnules rapidly increase in size and are then replaced by pinnae. Pinnae are widely spaced, alternating, 6–25 mm long and 3.8–6.7 mm wide, and arise at an angle of 40–60°; those in the interior portion of the frond being shorter than the exterior ones. Pinnules have a laminar appearance with small rounded to slightly obovate, pinnately arranged lobes. In some pinnules each lobe shows two or three conspicuous ridges arising from the central part of the pinnules (e.g., see enlarged pinnule in Plate V, TREG 328). The pinnules are up to 1.5 mm long and 1.5 mm wide. Unfortunately, the upper part of the frond is not well enough preserved to show details of the pinnule morphology. In addition, one specimen (part and counterpart) with two fragments of bifurcated fronds was recovered from the upper plant-bearing level. Also several smaller pinnae portions were found.

Discussion: This is the only species, together with *Sphenopteris* sp. cf. *S. geinitzii*, that has laminar pinnules, which easily distinguishes it from the other species. It differs from *S. geinitzii* in having loosely arranged lobes that are largely free; *S. geinitzii* has longer, narrow, closely spaced lobes that partly overlap each other. The venation of this form is unclear. Some pinnule lobes show conspicuous ridges that are reminiscent of veins. However, because they are only observed in a few pinnules and not seem to be a consistent feature, they may have another nature. They also could correspond to folds in the lamina. Such folds are likely to be found in forms with thick fleshy pinnules.

This form shows some vague similarities to some callipterids, notably *Rhachiphyllum diabolica* (Zeiller 1892) Kerp, 1988, a species originally described from the lower Permian of the Brive Basin, France and also reported from Lodève (Zeiller 1892, 1898). This latter species has a very robust frond axis with closely spaced pinnae. Our material from Tregiovo does not show the presence of intercalary pinnules. Because the material is rather poorly preserved and some essential details are not clear, we refrain from establishing a new species, even though it does not resemble any other species of *Sphenopteris.*

5. General discussion

Because nothing is known about the natural affinity of the here described forms, and because there are no other, more narrow-defined fossil-genera to include the here described species, we prefer to classify them in the fossil-genus *Sphenopteris*.

The diversity of the Tregiovo flora is not very high, although it should be noted that the preservation of the material often hampers a precise identification. Many of the plant fossils are very small, and, due to the high degree of thermal alteration, the material lacks cuticles, which are often crucial for precise identifications, especially in conifers. The Tregiovo flora is dominated by conifers, but it is difficult to determine the exact number of species without having cuticles; at least four different types of dwarf shoots have been recognized (Forte et al., 2017). The presence of five species of *Sphenopteris* in the Tregiovo floras, particularly those with remarkably complete fronds in the upper assemblage, is very noteworthy. Although the preservation of the Tregiovo material is not ideal, it is better than the previously described specimens; a new species, *Sphenopteris valentinii*, a nearly complete frond is also known.

All species from Tregiovo have strongly dissected pinnules, mostly with narrow linear segments. In this respect, they differ from the sphenopterids from the classical Rotliegend/Autunian sequences of Germany, Poland and the Czech Republic (Asselian–Sakmarian), which all have broader, more "laminar" pinnules/lobes. These latter species are already known from the Stephanian or strongly reminiscent of forms known from the Stephanian. The only two species known from the Collio Formation (Artinskian) in northern Italy, *Sphenopteris suessii* and *S. kukukiana*, occur in Tregiovo (middle Kungurian) together with three other species. The species known from the Collio Formation and most species from the classical Zechstein (Wuchiapingian) have strongly dissected pinnules with very narrow segments. As far as more or less complete fronds are known, all the species from Tregiovo and from the classical Zechstein have very small fronds, rarely exceeding 20 cm in length. The stiffness of the pinnules and pinnule segments of *S. suessii*, *S. kukukiana* and *S. valentinii* suggests that they were more or less elliptical or circular in cross section, giving them a succulent appearance. The reduced frond size and the stiffness of the pinnules are here interpreted as adaptations to drier conditions. This is also suggested by the conifer foliage from the Tregiovo flora, which are all rather broad- and thick-leaved forms, different from the strongly decurrent, needle-like leaves of most Stephanian and Rotliegend conifers. Altogether, the physiognomy of the Tregiovo plants reflects a trend of increasing aridity that is known for the Permian (e.g., Tabor and Montañez, 2002, 2004, Roscher and Schneider, 2006; DiMichele et al., 2008). The typical Zechstein floras and the upper Permian floras of the Southern Alps, both of Wuchiapingian age, are the ultimate reflection of this trend during the Permian. The only well-known pteridosperm from these floras, the peltasperm *Germaropteris martinsii* (Kurtze in Germar, 1839) Kustatscher et al., 2014, is a form with small fronds and thick fleshy pinnules (Poort and Kerp, 1990; Kustatscher et al., 2014).

Four additional species were described from the Copper Shales of the Zechstein Basin, i.e. *Sphenopteris bipinnata* (Münster, 1842) Geinitz, 1862, *S. dichotoma* Althaus, 1846, *S. patens* (Althaus 1846) Geinitz, 1848 and *S. gillitzeri* Weigelt, 1931. The first three of these four species are from Richelsdorf (Hesse, Germany), and *S. gillitzeri* is from Mansfeld (Saxony Anhalt, Germany).

Sphenopteris bipinnata and *S. gillitzeri* are known as single specimens only. Also the other two species are very rare and known from very few specimens. The preservation of these Copper Shale plants is generally poor. For further details we refer to Table 1a, 1b and to Schweitzer (1960).

Although neither fructifications nor cuticles are known, it seems very unlikely that the Tregiovo sphenopterids were ferns. A pteridospermous nature is more plausible regarding the fact that they are part of an association dominated by xerophytic elements and because they also show xeric features. Although the sphenopterids have a very stiff appearance, it seems unlikely that they were primarily water-transported. Longer-distance water transport usually causes severe damage and fragmentation. Several nearly complete fronds were found in finely laminated organic-rich lacustrine sediments that reflect dysoxic, very-low-energy conditions at the bottom of the lake. The widened bases seen in some of the nearly complete fronds indicate that they were abscised as complete entities. The most plausible explanation is that fronds were abscised during storms and blown into the lake, where they probably floated on the water surface and sank to the bottom after having become waterlogged. This scenario has also been proposed for lower Permian lacustrine shales deposited under low-energy conditions, which show in particular levels an enrichment of very well-preserved conifers (Kerp et al., 1990).

The Tregiovo flora shows with five species of *Sphenopteris* the highest diversity of sphenopterids in a single Kungurian locality, even though one of the forms cannot be further identified at species level. Comprising forms that are typical for the late Permian, the Tregiovo flora fills a gap in our knowledge of the temporal range of these species and documents the major climatic change that occurred during the early Permian.

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References

Avanzini, M., Bargossi, G., Borsato, A., Castiglioni, G.B., Cucato, M., Morelli, C., Prosser, G., Sapelza, A., 2007. Note illustrative della Carta Geologica d’Italia alla scala 1:50.000, Foglio 026 Appiano. Servizio Geologico d’Italia APAT, Dipartimento Difesa del Suolo, Roma, 184 pp.

Barth, S., Mohr, B.A.R., 1994. Palynostratigraphically determined age of the Tregiovo sedimentary complex in relation to radiometric emplacement ages of the Athesian Volcanic Complex. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 192, 273–292.

Barthel, M., 2006. Die Rotliegendflora des Thüringer Waldes. Teil 4: Farnsamer und Farnlaub unbekannter taxonomischer Stellung. Veröffentlichungen des Naturhistorischen Museums Schleusingen 21, 33–72.

Barthel, M. 2016. Die Rotliegend-Flora der Döhlen-Formation. Geologica Saxonica 61(2), 105–238.

Brousmiche, C., 1983. Les fougères sphénopteridiennes du Bassin Houiller Sarro Lorrain (Systematique Stratigraphie). Societé Géologique du Nord, Publication 10, 1–477.

Cassinis, G., Doubinger, J., 1991. On the geological time of the typical Collio and Tregiovo continental beds in the Southalpine Permian (Italy), and some additional observations. Atti Ticinensi di Scienze della Terra 34, 1–20.

Cassinis, G., Doubinger, J., 1992. Artinskian to Ufimian palynomorphs assemblages from the Central Southern Alps, Italy and their regional stratigraphic implications. In: Nairn, A.E.M., Koroteev, V. (Eds.), Contributions to Eurasian Geology, Papers Presented at the International Congress Permian System of the World, Part I. University of South Carolina, Columbia, pp. 9–18.

Cassinis, G., Nicosia, U., Pittau, P., Ronchi, A., 2002. Palaeontological and radiometric data from the Permian continental deposits of the Central-Eastern Southern Alps (Italy), and their stratigraphic implications. Mémoire de l’Association des Géologues du Permien, 2, 53–69.

Conti, M.A., Mariotti, N., Nicosia, U., Pittau, P., 1997. Succession of selected bioevents in the continental Permian of the Southern Alps (Italy): improvements in intrabasinal and interregional correlations. In: Late Palaeozoic and Early Mesozoic Circum-Pacific Events and Their Global Correlation, Cambridge University Press, 51–65 pp.

Conti, M.A., Mariotti, N., Manni, R., Nicosia, U., 1999. Tetrapod footprints in the Southern Alps: an overview. In: Cassinis, G., Cortesogno, L., Gaggero, L., Massari, F., Neri, C., Nicosia, U., Pittau, P. (Eds.), Stratigraphy and Facies of the Permian Deposits between Eastern Lombardy and the Western Dolomites. Field trip guidebook (Appendix), 23–25 Sept 1999. Earth Sciences Department, Pavia University, pp. 137–138.

DiMichele, W.A., Kerp, H., Tabor, N.J., Looy, C.V., 2008. The so-called “Paleophytic-Mesophytic” transition in equatorial Pangea – Multiple biomes and vegetational tracking of climate change through geological time. Palaeogeography Palaeoclimatology Palaeoecology 286, 152–163.

DiMichele, W.A., Wagner, R.H., Bashforth, A.R., Álvarez-Vázquez, C., 2013. An update on the flora of the Kinney Quarry of central New Mexico (Upper Pennsylvanian), its preservational and environmental significance. New Mexico Museum of Natural History and Science Bulletin 59, 289–325.

DiMichele, W.A., Lucas, S.G., Looy, C.V., Kerp, H., Chaney, D.S., 2017. Plant fossil from the Pennsylvanian–Permian transition in western Pangea, Abo Pass, New Mexico. Smithsonian Contributions to Paleobiology 99(I–VIII), 1–40.

Doubinger, J., Vetter, P., Langiaux, J., Galtier, J., Broutin, J., 1995. La flore fossile du bassin houiller de Saint-Étienne. Mémoire du Muséum d’Histoire Naturelle, Paris 164, 1–355.

Forte, G., Kustatscher, E., Van Konijnenburg–van Cittert, J.H.A., Looy, C.V., Kerp., H., 2017. Conifer diversity in the Kungurian of Europe – Evidence from dwarf-shoot morphology. Review of Palaeobotany and Palynology 244, 308–315; 10.1016/j.revpalbo.2017.01.004

Geinitz, H.B., 1869. Über fossile Pflanzenreste aus der Dyas von Val Trompia. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie 1869, 456–461.

Gothan, W., Nagalhard, K., 1922. Kupferschieferpfanzen aus dem niederrheinischen Zechstein. Jahrbuch der Preußischen Geologischen Landesanstalt 42, 440–459.

Kerp, H., Poort, R.J., Swinkels, H., Verwer, R., 1990. Aspects of a Permian Palaeobotany and Palynology. IX. Conifer-dominated Rotliegend floras from the Saar-Nahe Basin (?late

Carboniferous–early Permian; SW-Germany) with special reference to the reproductive biology of early conifers. Review of Palaeobotany and Palynology 62, 205–248.

Langiaux, J., 1982. Frondes sphénopteridiennes dans le Stéphanien terminal de Blanzy Montceau. Revue périodique de la Physiophile, Société d'Études des Sciences Naturelles et Historiques de Montceau-les-Mines, Montceau-les-Mines 97, 81–100.

Lausberg, S., Kerp, H., 2000. Eine Coniferen-dominierte Flora aus dem Unterrotliegend von Alsenz, Saar-Nahe-Becken, Deutschland. Feddes Repositorium 111(7–8), 399–426.

Lucas, S.G., Nelson, W.J., DiMichele, W.A., Krainer, K., Barrick, J.A., Voigt, S., Chaney, D.S., Elrick, S., Spielmann, J.A., 2013. Field Guide to the Carboniferous – Permian transition in the Cerros de Amado and Vicinity, Socorro Country, Central New Mexico. New Mexico Museum of Natural History and Science Bulletin 59, 39–76.

Marchetti, L., Forte, G., Bernardi, M., Wappler, T., Hartkopf-Fröder, C., Krainer, K., Kustatscher, E., 2015. Reconstruction of a Late Cisuralian (Early Permian) floodplain lake environment: Palaeontology and sedimentology of the Tregiovo Basin (Trentino-Alto Adige, Northern Italy). Palaeogeography, Palaeoclimatology, Palaeoecology 440, 180–200.

Marocchi, M., Morelli, C., Mair, V., Klotzli, U., Bargossi, G.M., 2008. Evolution of large silicic magma systems: remarks new U-Pb zircon data on the NW Permian Athesian Volcanic Group (Southern Alps, Italy). Journal of Geology 116, 480–498.

Mostler, H., 1966. Sedimentäre Blei-Zink-Vererzung in den mittelpermischen "Schichten von Tregiovo" (Nonsberg, Nord-Italien). Mineralium Deposita 2, 89–103.

Neri, C., Avanzini, M., Bampi, T., Bargossi, G.M., Mair, V., Morelli, C., Pittau, P., Ronchi, A., Sapelza, A., 1999. The Tregiovo area and related volcanics in the Tregiovo section. 1.2. The Tregiovo section. In: The Continental Permian, International Congress, 15–25 Sept., 1999, Brescia, Italy – Stratigraphy and facies of the Permian deposits between Eastern Lombardy and the Western Dolomites, Field Trip Guidebook, 23–25 Sept. 1999, Earth Science Department, Pavia University, Pavia, pp. 81–82.

Poort, R.J., Kerp, J.H. F., 1990. Aspects of Permian palaeobotany and palynology. XI. On the recognition of true peltasperms in the Upper Permian of western and central Europe and a reclassification of species formerly included in *Peltaspermum* Harris. Review of Palaeobotany and Palynology 63, 197–225.

Remy, W., Remy, R., 1978. Die Flora des Perms im Trompia-Tal und die Grenze Saxon/Thuring in den Alpen. Argumenta Palaeobotanica 5, 57–90.

Roscher, M., Schneider, J.W., 2006. Permo–Carboniferous climate: Early Pennsylvanian to Late Permian climate development of central Europe in a regional and global context. In: Lucas, S.G., Cassinis, G., Schneider, J.W. (Eds.), Non-Marine Permian Biostratigraphy and Biochronology. Geological Society of London, Special Publications 265, 95–136.

Schweitzer, H. J., 1960. Die Sphenopteriden des Zechsteins. Senckenbergiana Lethaea 41, 37–57.

Schweitzer, H. J., 1962. Die Makroflora des niederrheinischen Zechsteins. Fortschritte in der Geologie von Rheinland und Westfalen 6, 331–376.

Schweitzer, H. J., 1986. The land flora of the English and German Zechstein sequences. In: Harwood, G.M., Smith, D.B. (Eds.), The English Zechstein and related topics. Geological Society Special Publication 22, 31–54.

Šimůnek, Z., Martínek, K., 2009. A study of the Late Carboniferous and Early Permian plant assemblages from the Boskovice Basin, Czech Republic. Review of Palaeobotany Palynology 155, 275–307.

Tabor, N.J., Montañez, I.P., 2002. Shift in late Paleozoic atmospheric circulation over western equatorial Pangea: Insights from pedogenic mineral δ18C compositions. Geology 30, 1127–1130.

Tabor, N.J., Montañez, I.P., 2004. Morphology and distribution of fossil soils in the Permo–Pennsylvanian Wichita and Bowie Groups, north-central Texas, USA: implications for western equatorial Pangean palaeoclimate during icehouse–greenhouse transition. Sedimentology 51, 851–884.

Van Amerom, H.W.J., 1975. Die eusphenopteridischen Pteridophyllen aus der Sammlung des Geologischen Bureaus in Heerlen, unter besonderer Berücksichtigung ihrer Stratigraphie bezüglich des südlimburger Steinkohlenreviers. Mededelingen Rijks Geologische Dienst, Serie C-III-1-No. 7, 1–208.

Visscher, H., Kerp, H., Clement-Westerhof, J.A., Looy, C.V., 2001. Permian floras of the Southern Alps. Natura Bresciana, Museo Civico di Scienze Naturali, Brescia, Monografia 25 pp. 117–123.

Weiss, C.E., 1879. Die Flora des Rothliegenden von Wünschendorf bei Lauban in Schlesien. Abhandlungen zur Geologischen Specialkarte von Preussen und den Thüringischen Staaten, Text, Atlas 3(1), 1–39.

Zeiller, R., 1888b. Études sur le terrain houiller de Commentry. 2. Flore fossile. I. In: B. Renault, and R. Zeiller (1888–1809), Bulletin de la Société de l'Industrie Minérale 2(2), 1–366.

Zeiller, R., 1892. Bassin houiller et permien de Brive. II. Flore fossile. Études des Gîtes Minéraux de la France pp. 1–132.

Zeiller, R., 1898. Contribution à l'étude de la flore ptéridologique des schistes permiens de Lodève. Bulletin du Muséum d'Histoire Naturelle de Marseille 1, 6–69.

CHAPTER 3

The Permian (Kungurian, Cisuralian) palaeoenvironment and palaeoclimate of the Tregiovo Basin, Italy: palaeobotanical, palynological and geochemical investigations

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Abstract

A transition from widespread humid to more drought tolerant floras characterized tropical terrestrial ecosystems during the Permian (Cisuralian). Tregiovo (Southern Alps, N-Italy) is one of the very few well dated Kungurian (late Cisuralian) plant localities in Euramerica. It was located in eastern palaeoequatorial Pangea. Two units bearing fossil plant assemblages occur in finely laminated sediments deposited in a playa-lake environment. In this paper, the sedimentology of the Tregiovo Basin is reviewed, and new palaeobotanical, palynological and stable isotopic data are presented, in order to reconstruct the palaeoclimatic and palaeoenvironmental conditions of the Kungurian in the Southern Alps. Both fossil plant assemblages dominated by conifers (*Hermitia*, *Feysia*, *Quadrocladus*, *Dolomitia*), together with sphenophytes (*Annularia*), ginkgophytes (*Sphenobaiera*), pteridosperms (*Peltaspermum*), taeniopterids and sphenopterids. These taxa, which occur with different abundances in the two plant assemblages, both indicate semi-arid conditions. Associated palynoflora, dominated by bisaccate pollen, and the extremely rare spore occurrences, is consistent with the xerophytic character of the macroflora, and suggests that the fossil plant record was not affected by collection or preservation bias. Stable isotopic analyses on two stratigraphic sections reveals an upward trend of increasingly negative $\delta^{13}C_{org}$ (VPDB), which may correlate with roughly coeval records from marine and continental successions such as in North China and South Africa. This isotopic shift may be attributed to a global perturbation of the atmospheric $\delta^{13}C$, although the influence of local environmental factors can not be excluded.

Keywords: Permian, lacustrine deposit, playa lake, fossil plants, organic carbon, $\delta^{13}C_{org}$

1. Introduction

The Late Palaeozoic was a time of important changes for palaeogeography, climate and terrestrial ecosystems. The supercontinent Pangea was in it's final stages of consolidation, which concluded during the Permian, with the formation of the Central Pangean Mountain chain (Ziegler et al., 1997). The Late Palaeozoic Ice Age (LPIA), the longest-lived (~ 335 to 256 Ma) ice age of the Phanerozoic (e.g., Montañez et al., 2007), reached its acme during the early Permian (Cisuralian) with the formation of widespread continental ice sheets (e.g., Frakes et al., 1992; Isbell et al., 2003; Jones and Fielding, 2004; Montañez et al., 2007; Montañez and Poulsen, 2013), whose waxing and waning produced large variations of sea level (e.g., Rankey, 1997; Olszewski and Patzkowsky, 2003; Rygel et al., 2008) and consequent palaeogeographical and palaeoenvironmental changes (Fig. 1). Data on palaeosols demonstrate how, at low latitudes, conditions changed stepwise from a humid (*sensu* Cecil, 2003) tropical climate during the Pennsylvanian, to sub-humid climates in the early Cisuralian to semi-arid and to arid climates by the late Cisuralian in central and western Pangea (e.g., Tabor and Montañez, 2004; Schneider et al., 2006; Montañez et al., 2007; DiMichele et al., 2008, 2011; Peyser and Poulsen, 2008; Horton et al., 2012; Montañez and Poulsen, 2013; Falcon-Lang et al., 2014; Michel et al., 2015).

Land plants were already an important part of the terrestrial ecosystems in the Permian, and constituted a significant carbon reservoir. With the evolution of wood in the Devonian (Rowe, 2000), terrestrial plants improved their capability to store carbon in their tissues as lignin that, being more resistant to biodegradation, was subtracting CO_2 from the atmosphere as it was permanently

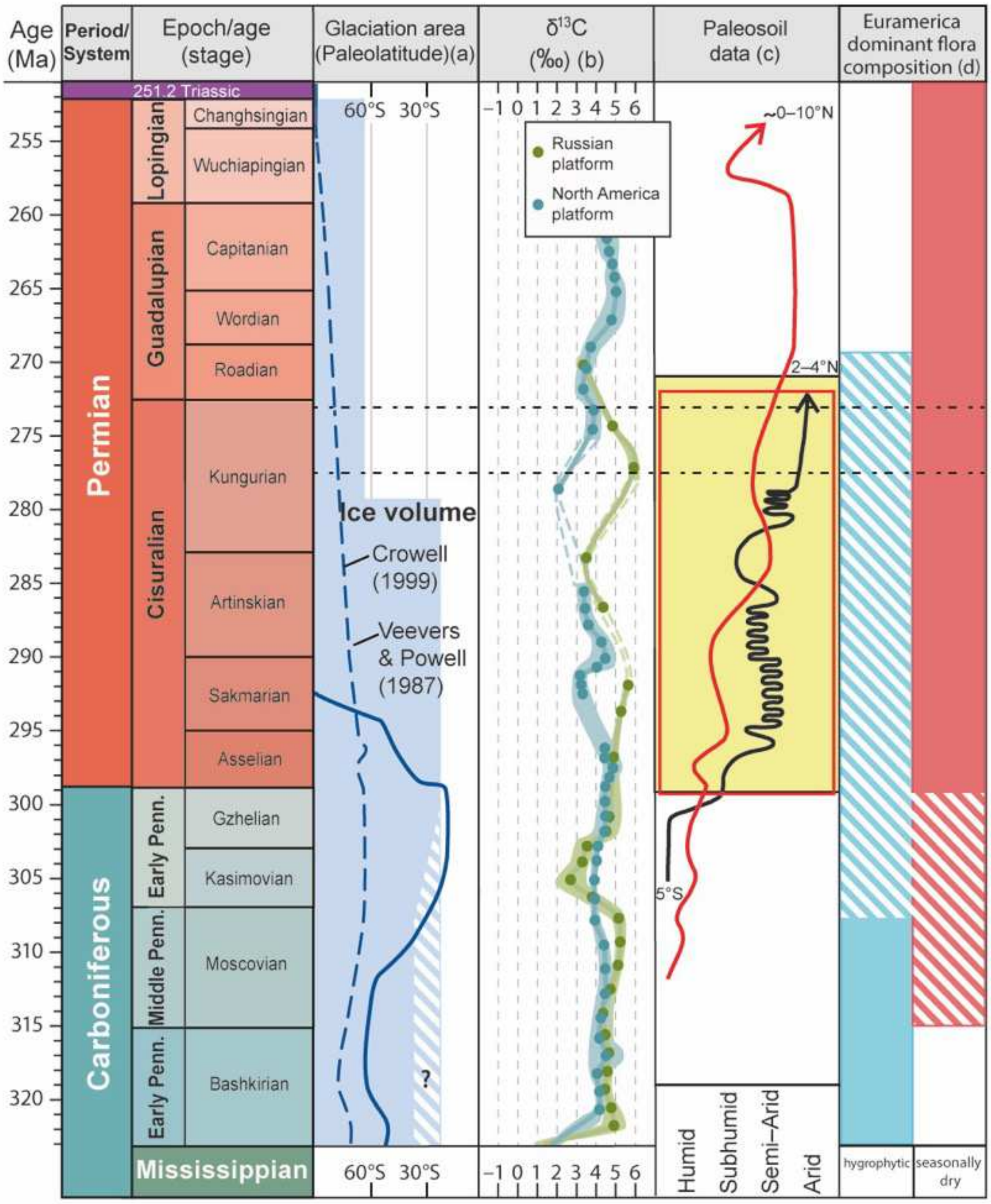


Fig. 1. Permian palaeoclimate trends, from literature. Chronostratigraphy from Cohen et al., (2013, updated) http://www.stratigraphy.org/ICSchart/ChronostratChart2017-02.jpg 28.08.2017. A) Area of glaciation adapted from Frakes & Francis (1988) and Crowley & Baum (1992); B) brachiopod δ13C from the Russian platform and from western and central North America (Grossman et al. 2008); C) Inferred palaeoclimatic trends for Equatorial Regions (black curve) and European Basins (red curve) based on climate-sensitive lithologies across tropical Pangea. “Humid” indicates humid conditions (precipitations > 1000 mm/yr) and most months (~9) with precipitation in excess of evapotranspiration, as indicated by the occurrence of coal, laterite and bauxite. “Arid” indicates dry conditions with precipitation less than ~300 mm/yr, and less than 5 months/yr with precipitation in excess of evapotranspiration, as indicated by the occurrence of palaeosol profiles with evaporite minerals (e.g., gypsum) and carbonate. The yellow area and the red square area indicate distinct seasonality, respectively for Equatorial Regions and European Basins (e.g., Tabor and Montañez, 2004) and the occurrence of fusain (Falcon-Lang, 2000); D) Main floral composition (data from DiMichele et al, 2001; 2011). The dashed horizontal lines indicate the time interval covered by the Tregiovo Formation (between 274.1 ± 1.6 Ma and 276.5 ± 1.1 Ma; Avanzini et al., 2007; Marocchi et al., 2008). A–B are modified from Montañez and Poulsen 2013; C is modified from DiMichele et al., 2008.

transferred to the lithosphere as coal. The diversification of terrestrial plants and the formation of widespread coal deposits during the Carboniferous could in fact have been responsible for the decreasing pCO_2 in the atmosphere and may have caused the transition from greenhouse conditions to the LPIA (Kump et al., 2000; Beerling and Berner, 2005). In the Permian, the terrestrial ecosystems were populated by several groups of plants, which especially in the palaeoequatorial regions, appeared to suffer from increasing aridity related to the end of the LPIA (e.g., DiMichele et al., 2001, 2008, 2009; Tabor and Montañez, 2004; Montañez et al., 2007; Peyser and Poulsen, 2008; Tabor and Poulsen, 2008; Horton et al., 2012; Montañez and Poulsen, 2013; Michel et al., 2015). This accounts for the replacement of hygrophytic floras by xerophytic communities, tolerant of seasonally dry climates. Such replacement originated in western North America and proceeded, stepwise and diachronically, towards central and eastern Pangea (e.g., Knoll, 1984; DiMichele, 2014; DiMichele et al., 2001; Looy, 2007; Looy et al., 2014; Looy and Stevenson, 2014, Falcon-Lang et al., 2017). It was during the Permian that conifers and other gymnosperms, which occupied extrabasinal areas and were better adapted to drier conditions, progressively spread, moving into the lowlands, thus increasing their preservational potential (e.g., DiMichele et al., 2011; Looy et al., 2014) and becoming a dominant element of the landscapes, till the Mesozoic.

Climate change and the turnover of terrestrial biota left a strong imprint on the stable carbon isotope composition of atmospheric CO_2 and on its concentration (e.g., Arens, et al., 2000; Beerling et al., 2002; Berner, 2003; Peter-Kottig et al., 2006; Montañez et al., 2007; Tabor and Poulsen, 2008; Montañez et al., 2016), as recorded by marine carbonates (e.g., Hayes et al., 1999; Veizer et al., 1999; Liu et al., 2017a) and organic matter preserved in sediments (e.g., Faure et al., 1995; Zhang et al., 1999; Peter-Kottig et al., 2006). Generally, the Palaeozoic is strongly characterized by a C3 plant signal (Bocherens et al., 1993). The $\delta^{13}C_{org}$ (carbon stable isotopic composition of organic matter) of Permian terrestrial organic matter ranges between –25.5‰ and –22.9‰, which is comparable to modern C3 plants (from –34‰ to –20‰; O'Leary, 1988). $\delta^{13}C_{org}$ values (organic matter) increased during the Cisuralian, and later started to decrease during the Guadalupian, reaching mean values of –24 ‰ (e.g., Peters-Kottig et al., 2006). The increase of $\delta^{13}C_{org}$ could have been caused by the sequestration of organic matter, and started during the Carboniferous, with the formation of widespread coal deposits (e.g., Berner, 2003; Peters-Kottig et al., 2006). The subtraction of ^{12}C from the exchangeable carbon reservoirs caused an increase of $\delta^{13}C_{org}$ beginning in the early Permian, whereas the subsequent decrease of $\delta^{13}C_{org}$ could be related to several factors, such as the decrease of organic matter burial in terrestrial sediments (Berner et al., 2003), tectonic and climatic processes

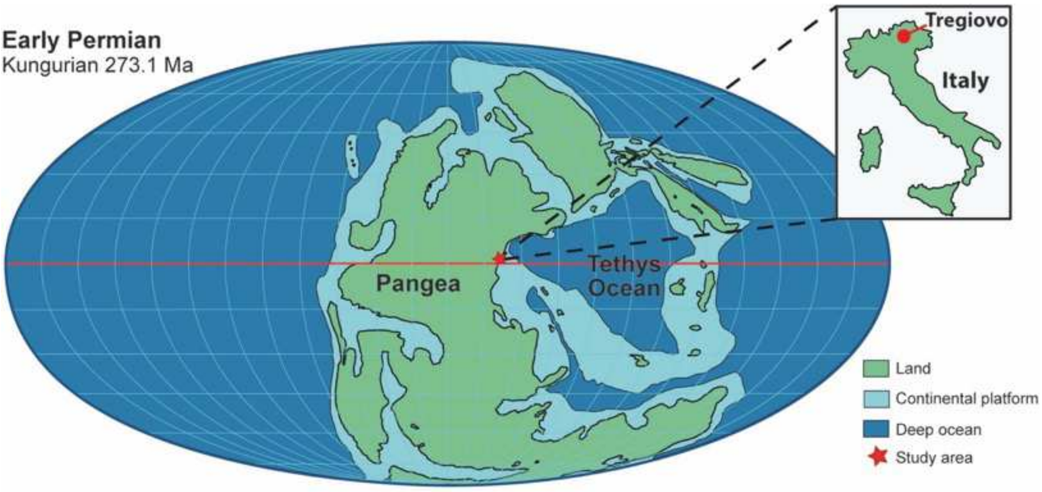


Fig. 2. Kungurian palaeogeography and location of Italy and Tregiovo Basin. Modified from the PALEOMAP PaleoAtlas for ArcGIS (Scotese, 2014).

linked to the consolidation of Pangea (e.g., Faure et al., 1995; Kerp, 1996; Kidder and Worsley, 2004), the increase of weathering (Peters-Kottig et al., 2006) and episodes of release of CH_4 from clathrate deposits (de Wit et al., 2002).

Late Cisuralian floras are scarce, especially in the Euramerican Province. Well described plant assemblages are those from western Euramerica from Lower Pease River (DiMichele et al., 2001; Looy, 2007; Looy and Stevenson, 2014) and from South Ash Pasture (DiMichele et al., 2004). A well-dated Kungurian (late Cisuralian) fossil plant assemblage has been found in the small Tregiovo Basin (northeastern Italy), located during the Permian in eastern palaeoequatorial Pangea (Fig. 2), close to the coast of the Tethys Ocean. The "Le Fraine" section in the Tregiovo Basin (Marchetti et al., 2015) yielded a uniquely abundant and diverse fossil plant assemblage (e.g., Forte et al., 2017). In this work, we further investigate the Tregiovo Basin with the aims of: (1) improving the knowledge about the timing and mode of the hygrophytic – xerophytic transition in eastern Pangea, (2) recovering a continental $\delta^{13}C_{org}$ record of a well dated portion the Kungurian, and (3) suggesting possible relationships between the floral composition and potential local environmental factors versus global climatic forcing.

2. Geological setting

The Tregiovo Formation was deposited in a small (about 2 km wide) sedimentary basin (Tregiovo Basin) of the Athesian Volcanic District (Marchetti et al., 2015 and references therein). The volcanic rocks of the Athesian Volcanic Group (AVG) extend over 2000 km^2 and represent the largest and

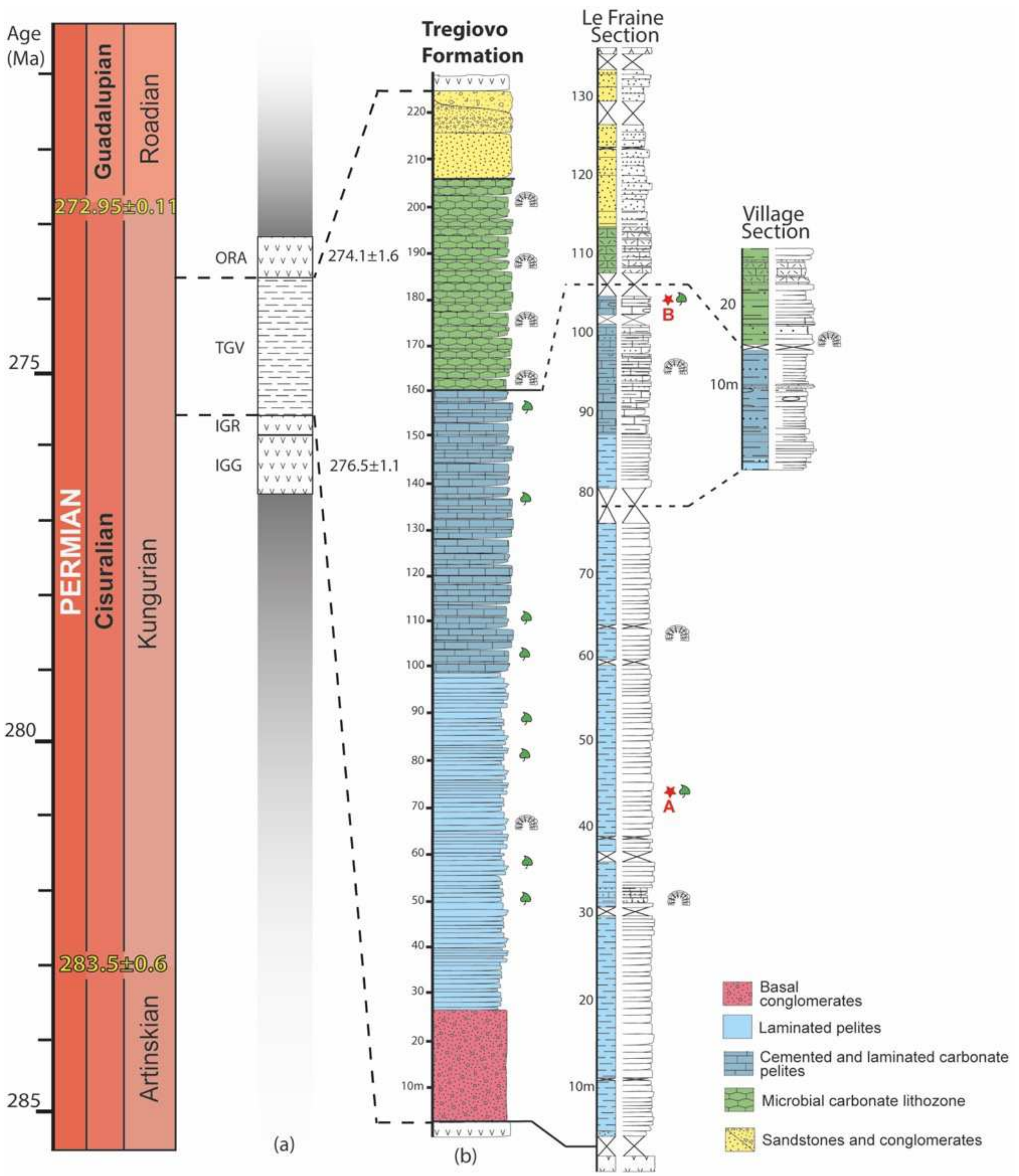


Fig. 3. A. Correlations are based on lithostratigraphy. Chronostratigraphy from Cohen et al., (2013, updated) http://www.stratigraphy.org/ICSchart/ChronostratChart2017-02.jpg 28.08.2017. In column (a) the simplified stratigraphy of the Tregiovo Formation, which overlies on the Gargazzon/Gargazzone and Gries Formations (IGR and IGG) and underies the Ora Formation; B. in column b the lithozones of the Tregiovo Formation described by Klaus and Mostler, 1983; C) "Le Fraine" section, simplified from Marchetti et al. (2015), with a reinterpretation of lithozones; D) the portion of Tregiovo Village section logged for this study.

best-exposed Permian volcanic succession in Europe (e.g., Morelli et al., 2007; Marocchi et al., 2008). Stratigraphically, the Tregiovo Formation is enclosed between the Ora/Auer Formation and Gargazzone/Gargazzon and Gries Formation, volcanic units that were dated radiometrically respectively at 274.1 ± 1.6 Ma and 276.5 ± 1.1 Ma (e.g., Avanzini et al., 2007; Marocchi et al., 2008), thus attributing the Tregiovo Formation to the middle Kungurian. It is subdivided into two sub-units (Avanzini et al., 2007): a lower lithozone of poorly sorted conglomerates and an upper lithozone, up to 200 m thick, yielding plant fossils, in which laminated pelites prevail. Klaus and Mostler (1983) and Marchetti et al. (2015) identify two more lithozones above the laminated pelites: a third lithozone with lacustrine microbial carbonates and a fourth lithozone with sandstones and conglomerates (Fig. 3). The variable thickness (0–200 m) of the formation suggests that its depositional basin may have been limited by tectonic thresholds (e.g., Neri et al., 1999; Marchetti et al., 2015). The type section of the Tregiovo Formation cropped out along the Tregiovo–Lauregno provincial road, but is unfortunately no longer accessible, being covered by concrete walls and a wire-netting fence. The area is well-known for its plant fossils, vertebrate footprints and palynomorphs (e.g., Klaus, 1963; Remy and Remy, 1978; Cassinis and Doubinger, 1991, 1992; Cassinis and Neri, 1992; Barth and Mohr, 1994; Conti et al., 1997, 1999; Neri et al., 1999; Visscher et al., 2001).

The present paper considers the “Le Fraine” section (Fig. 4) and the Tregiovo village section (Fig. 5). The “Le Fraine” section crops out near the small village of Tregiovo in the Upper Val di Non, Trento province (NE Italy; Fig. 2), between 46°26.230′N 011°02.623′E and 46°26.178′N 011°02.873′E (UTM 32N, WGS 84), and is ca. 135 m thick. The lower part is mainly composed of very thinly laminated, dark, siliceous argillites and shales, deposited in a playa-lake to lacustrine environment (Avanzini et al., 2007; Marchetti et al., 2015). Plant remains, vertebrate and invertebrate footprints, conchostracan shells and palynomorphs mainly occur in this part of the section. Some levels contain abundant pyrite. Along with the scarcity of bottom-dwelling fauna, the absence of bioturbation and the preservation of depositional laminae throughout the section indicate suboxic or anoxic conditions at the bottom of the lake (Marchetti et al., 2015). The upper part is made of massive pelites, conglomerates and sandstones, the latter interpreted as alluvial sediments. The second outcrop, located near the village of Tregiovo (Fig. 5; 46° 26.393′N 11° 3.033′E), corresponds to the uppermost part of the Tregiovo Formation (Neri et al., 1999). The horizons rich in plant remains fall within the laminated pelitic lithozone; undetermined plant fragments were also observed in the third lithozone, with microbial carbonates, of the Tregiovo village section. This latter section was only studied for its more diverse facies associations and was sampled for palynology and geochemical analyses on a selected best preserved tract (ca. 27 m thick) that is not dissected by faults.

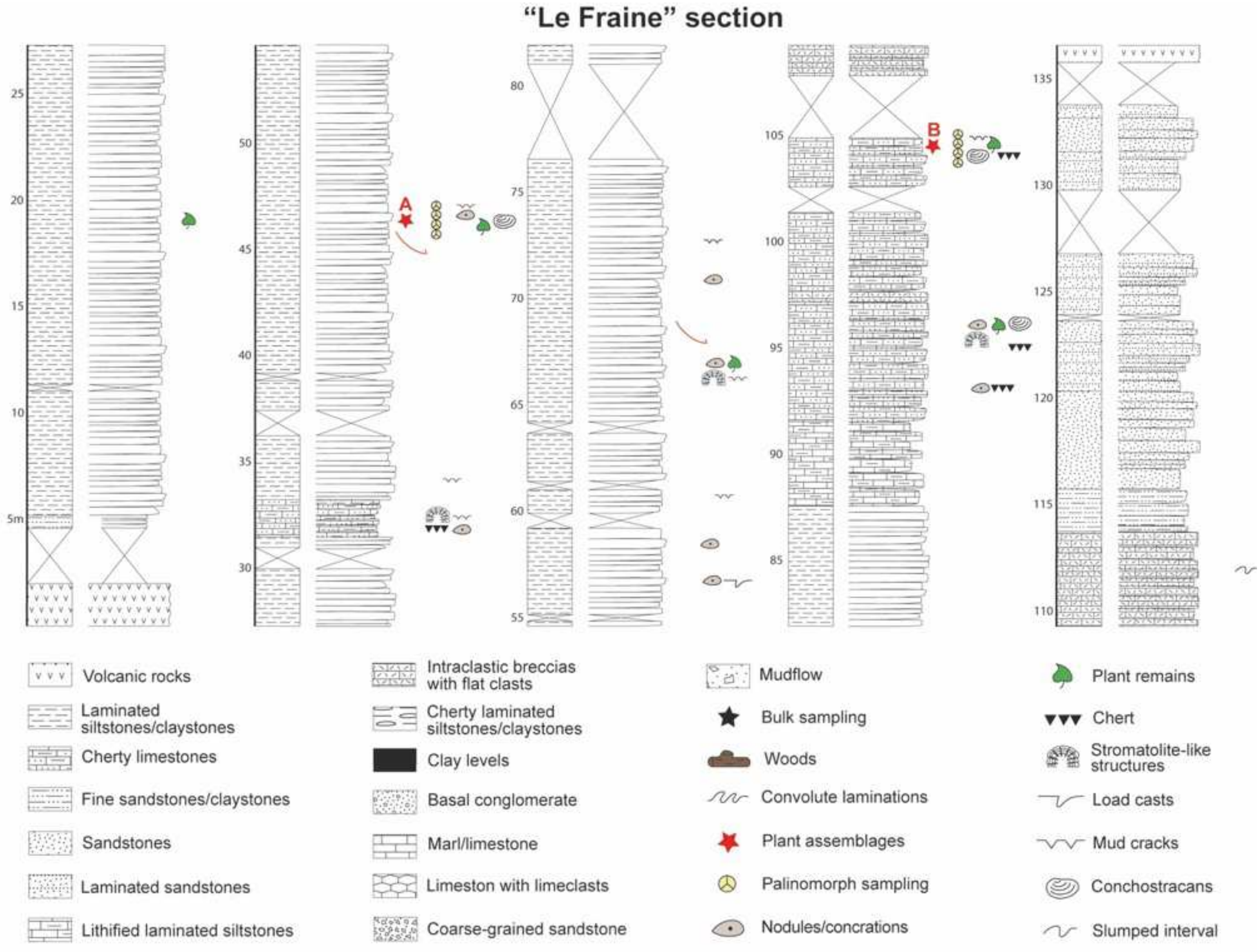


Fig. 4. Detailed log of "Le Fraine" section (Modified from Marchetti et al., 2015).

3. Material and methods

The plant remains come from two main sections: the type section near the village of Tregiovo (Remy and Remy, 1978; Neri et al., 1999; Visscher et al., 2001), and the "Le Fraine" section (Marchetti et al., 2015; Forte et al., 2017). Plants from "Le Fraine" come from two levels of the laminated part of the section (Marchetti et al., 2015; Forte et al., 2017), a lower one at ca. 45 m, and an upper one at ca. 105 m from the base of section (Fig. 4). About 1100 slabs with plant remains were studied, ca. 700 from the lower level (assemblage A) and ca. 400 from the upper one (assemblage B; Fig. 4).

Plant fossils consist of impressions and compressions. Some specimens are partly pyritized or covered by a thin layer of mud (Marchetti et al., 2015). Part of the material from assemblage A was studied in Marchetti et al. (2015) and is temporarily stored at MUSE, Museo delle Scienze of Trento (Italy); these specimens are labeled with the prefix "MUSE PAG", followed by progressive numbers (from 7089 to 7427). Most plant remains are preserved on blackish siliceous argillite. They occur together with footprints, whereas plant-animal interaction traces are rare (Marchetti et al., 2015; Labandeira et al., 2016). The remaining slabs are deposited in the private collection of Mr. Ferruccio Valentini (Tuenno, Trento Province), who collected almost all the material from "Le Fraine". This new material, Collezione Valentini, is temporarily stored with the private collector. The studied material from the type section consists of ca. 12 specimens, stored at the Museo Civico di Storia Naturale of Brescia (Brescia Province, Lombardy Region, N-Italy). This material was collected by private collectors, has been studied by Remy and Remy (1978) and Visscher et al. (2001) and is labelled with the prefix "PA" followed by progressive but not consecutive numbers (00058–91).

All the material has been photographed with a digital reflex camera (Canon EOS 550D) and studied under a dissecting stereomicroscope (Olympus SZ40). The macrofossils were measured with callipers and on digital photographs by using the free software ImageJ64. This method of census is more appropriate for Palaeozoic floras, in which leaf counting is more complicated because fern fronds, seed fern leaves and conifer branching systems may be easily fragmented due to decay or mechanical stress (e.g., Pfefferkorn et al., 1975; Wing and DiMichele, 1995). This increases the risk of over-representation for those groups (Wing and DiMichele, 1995; Uhl and Lausberg, 2008).

Eight palynological samples have been collected from the two horizons with plants of the "Le Fraine" section (Fig. 4) whereas six have been collected along the Tregiovo village section (Fig. 5), from different facies. The palynological samples have been prepared at the Laboratory of Palynology of the Geosciences Department of Padova. All the samples were manually crushed with an agate mortar and treated with HCl (37%), HF (37%) and HNO_3 (40%). The residue was centrifuged and neutralized using deionized water, and sieved (15 µm). Slides were sealed with special glue (Eukitt®) and are stored at the Geosciences Department at Padova. Sporomorphs are very abundant in both levels, and organic matter and phytoclasts are abundant as well.

Stable carbon isotope and TOC (Total Organic Carbon) analyses were carried out on 70 bulk rock samples collected along the "Le Fraine" and the Tregiovo village sections. In particular, the samples were collected approximately every five meters, with a denser sampling interval (every 0.5–1 m) in the "Le Fraine" section, in corresponding to the two levels yielding plants remains (Fig. 4). The samples from the Tregiovo village section were collected at intervals of ca. 30 cm. All samples were crushed with an agate mortar grinder at the labs of IGG-CNR in Padova. The powders were treated with HCl 10% in polyethylene Falcon tubes overnight, in order to remove carbonates. They were rinsed with deionized water until neutrality and dried at 40°C. Ca. 2 mg of treated sample were weighted in tin capsules, which were successively analysed at the stable isotope Laboratory of the Department of Geosciences (University of Padova) with a Thermo Flash 2000 Elemental Analyzer connected to a Thermo Delta V Advance Isotope Ratio Mass Spectrometer. Results were normalized with two international standards i.e. CH-6 (-10.449‰) and CH-7 (-32.151‰). A quality assurance standard (ZER, C3 plant sucrose) was run along the samples and yielded an internal reproducibility of 0.16 ‰ (standard deviation based on >20 repetitions). For the TOC analyses, 2 mg of powder were weighted directly in silver cups. Successively, samples were etched three times with 20 µl of HCl 10% on a heating plate at 70°C. Silver cups were then wrapped and analysed at the Geochemical Laboratory of the Department of Geosciences (University of Padova) with the Thermo Flash 2000 Elemental Analyzer.

4. Results

4.1. Sedimentology

The previous work of Marchetti et al., (2015) identified three facies associations (A–C) here briefly reported. Facies association A is characterized by thin laminated layers of dark siltstones/claystones, rarely separated by marly limestones. This facies association characterizes the first ca. 85 m of the "Le Fraine" section (Fig. 4), and contains abundant plant remains (assemblage A and B), vertebrates and invertebrate tracks, conchostracans and mud cracks. Facies association B characterizes the upper part of the section (from ca. 85 to 115 m) and consists of thin brownish marly limestones, organized in thicker compact beds. Light-gray limestone layers alternate with dark grey laminated mudstone layers. Limestones are interpreted as being formed from microbial or micritic carbonates. Thin silica beds occur, intercalated with mudstones and limestones. Facies association C consists of grey and brownish conglomerates, fine-grained sandstones, with local erosion traces and crossed-stratification, and constitutes the last 20 m of the "Le Fraine" section (see more in Marchetti et al., 2015).

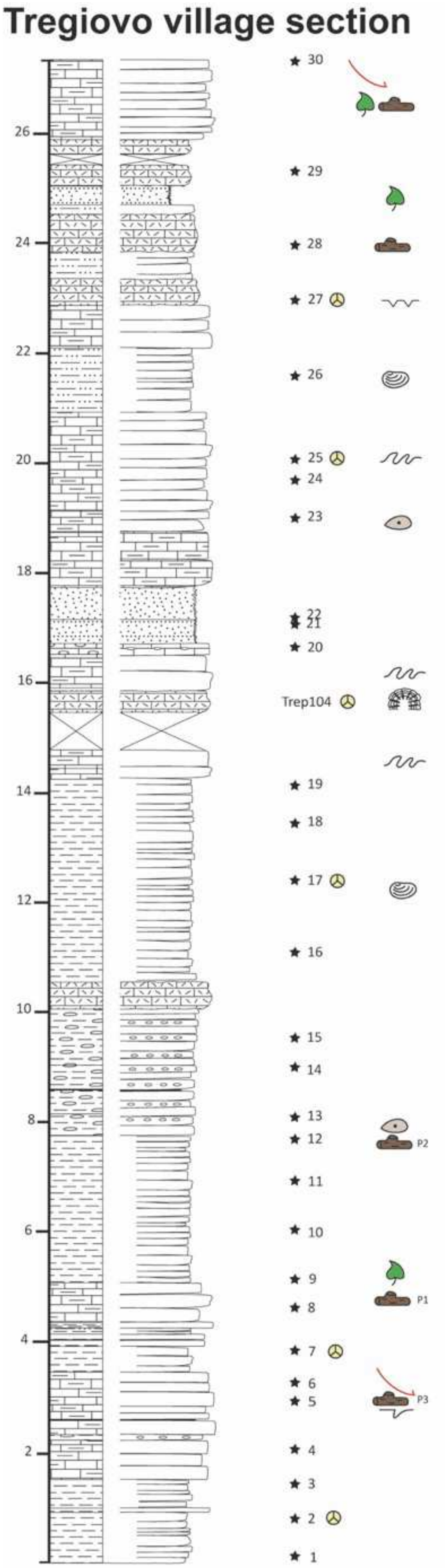


Fig. 4. Detailed portion of the Tregiovo Village section logged in this study. Symbols as in figure 4.

A ca. 27 m long, undisturbed portion of the Tregiovo village section has been selected at the transition from the laminated pelitic lithozone and a microbial carbonate-bearing lithozone, and has been logged and sampled in detail (Fig. 5). Furthermore, the facies of the "Le Fraine" section were in part reinterpreted based on field observations and samples from previous work (Marchetti et al., 2015).

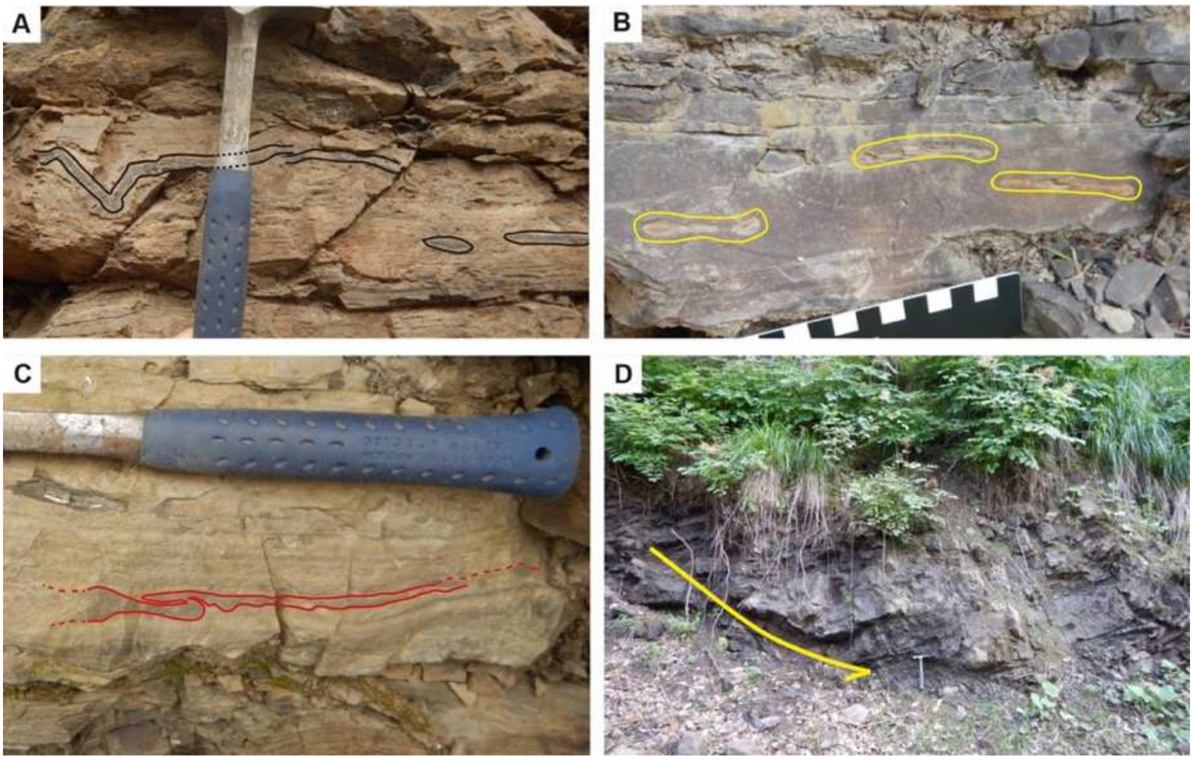


Fig. 6. Sedimentary structures from the Tregiovo village section that occur at ca. 15–25 m. A. deformed chert levels and nodules within laminated siltstone; B. carbonate flat pebbles within siltstone; C. plastic deformation of silt laminae; D. siltstone and laminated siltstone layers involved in a m-scale slump from the middle part of the Tregiovo village section.

4.1.1. Laminated pelites lithozone

This lithozone corresponds to Facies association A of Marchetti et al. (2015). The most common facies in this interval is made of gray laminated pelites. Laminae are typically from less than 1 mm to few mm thick and sometimes exhibit, in the field or in thin section, normal grading. Mud cracks and small plant fragments are common. Articulated plant fronds or branches, and accumulations of conchostracan shells, occur less commonly. These laminated pelites appear more or less erodible in the field, depending on their degree of cementation. X-ray powder diffraction analyses

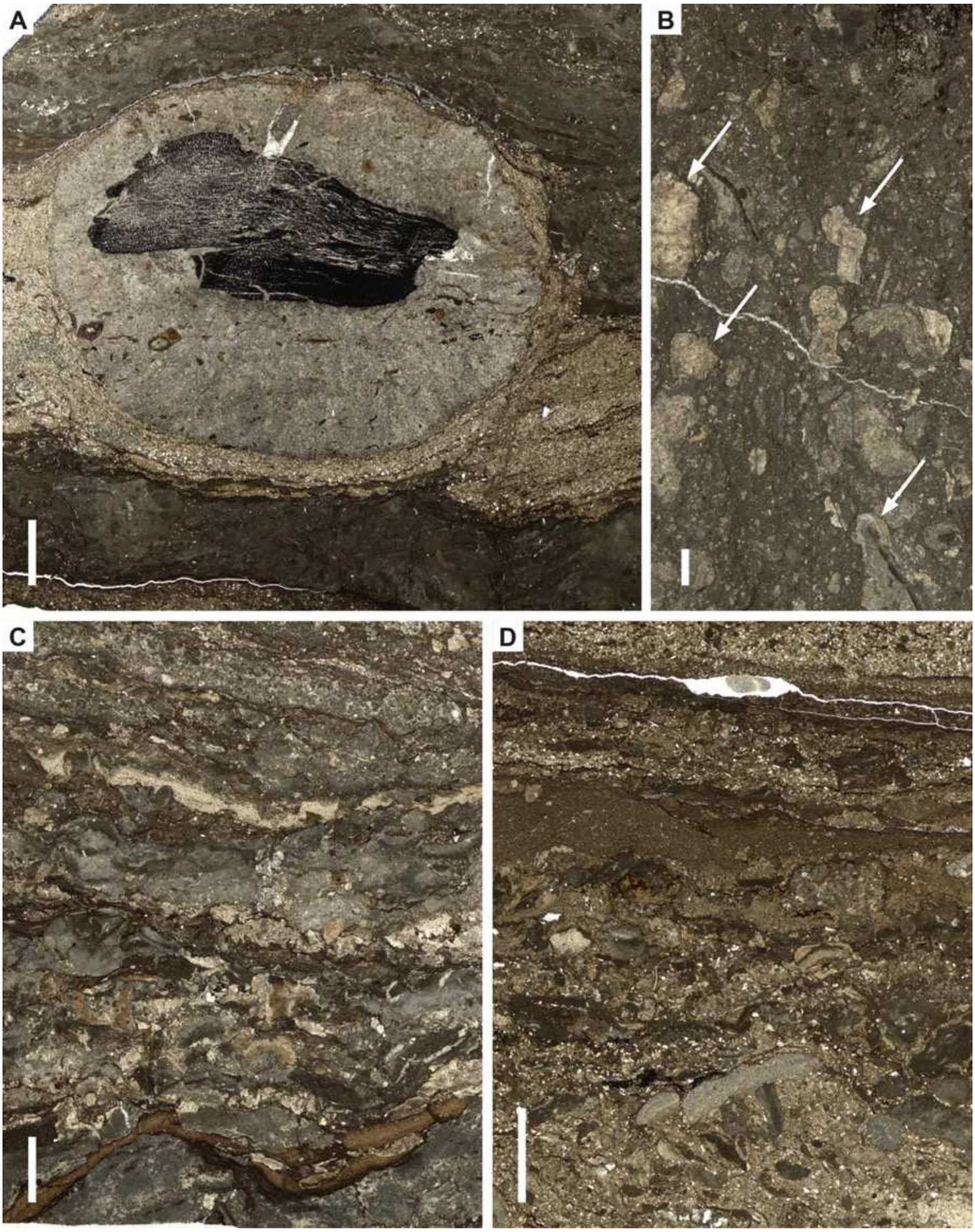


Fig. 7. Microfacies from the Tregiovo village section, microbial carbonate lithozone, under plain polarized light. A. coalified wood fragment with visible tracheids, enclosed in a calcareous nodule and embedded in an arenaceous siltstone lamina. Deformation of this lamina around the nodule implies that nodule formation occurred before and during sediment compaction. Sample form the top of the section; B. intraclastic breccia, ca. 17 m. Most elements of this breccia, like the ones indicated by the white arrows, are carbonates with clotted peloidal fabric, interpreted as lacustrine microbial carbonates; C. laminated intraclastic rudstone-breccia, ca. 14 m with fragments of clotted peloidal micrite, interpreted as microbialite, alternating with silicified arenaceous levels; D. silicified arenaceous siltstone and intraclastic breccia from the top of the section, with clasts with clotted peloidal fabric. Some are flat laminated carbonate pebbles, i.e. fragments of stromatolite. Scale bars 2 mm.

revealed, along with quartz, feldspars and white mica, which have a detrital origin, and the common occurrence of a Fe-bearing mineral of the chlorite group. This Fe mineral probably derives from the alteration of mafic minerals or lithic grains of volcanic origin. Furthermore, the carbonate mineral calcite is present at all stratigraphic levels in the “Le Fraine” section. Calcite is observed as a cement in interstitial position in thin sections of the coarser (silt-sized) pelite samples. In the upper part of the laminated pelite lithozone, nodules and layers of secondary calcite and chert are more commonly observed and cementation is widespread. These better cemented laminated pelites span the interval between 90 m and 105 m above the base of the “Le Fraine” section, and were included in Marchetti et al. (2015) in facies association B (Fig. 4), together with flat pebble breccia, which are carbonate rocks in which the main constituent are large flat carbonate intraclasts, often derived from the reworking of partially cemented stromatolite (e.g., Demicco and Hardie, 1994; peloidals stromatolites, Fig. 7A–D).

4.1.2. Microbial carbonates lithozone

This interval lies on the laminated pelites lithozone with a sharp contact in the Tregiovo village section, whereas the contact is poorly exposed at “Le Fraine” (Fig. 4). At “Le Fraine”, only two facies were observed: m-scale layers of massive pelite with rare mud pebbles, and a breccia with cm-scale carbonate flat pebbles (Fig. 6, B; Fig. 7 B–D), in a sandstone matrix. The flat pebbles are made of fragmented laminae of carbonate with clotted peloidal fabric, whereas quartz grains are the main components of the sandy matrix (Fig. 8A–D).

At the Tregiovo village section, this lithozone is more differentiated and better exposed. It is made of an alternation of poorly sorted breccia beds with irregular, erosive bases intercalated with intervals of laminated pelites and thin poorly cemented beds of laminated fine sandstone. Laminated pelites are similar to those of the underlying lithozone, but are pervasively affected by soft-sediment deformation as convoluted lamination (Fig. 6C) and autoclastic breccia, which involves also silicified or cemented layers (Fig. 6A). Fine grained sandstones form beds a few cm thick, with poorly preserved plant fragments, that have a poorly defined plane bed lamination.

Breccias occur in m-scale intervals of amalgamated beds, each 10–30 cm thick, made of carbonate intraclasts in which a clotted peloidal fabric is often preserved. Intraclasts are from 1 mm to few centimeters in diameter and angular. Flat pebbles of laminated clotted peloidal micrite also

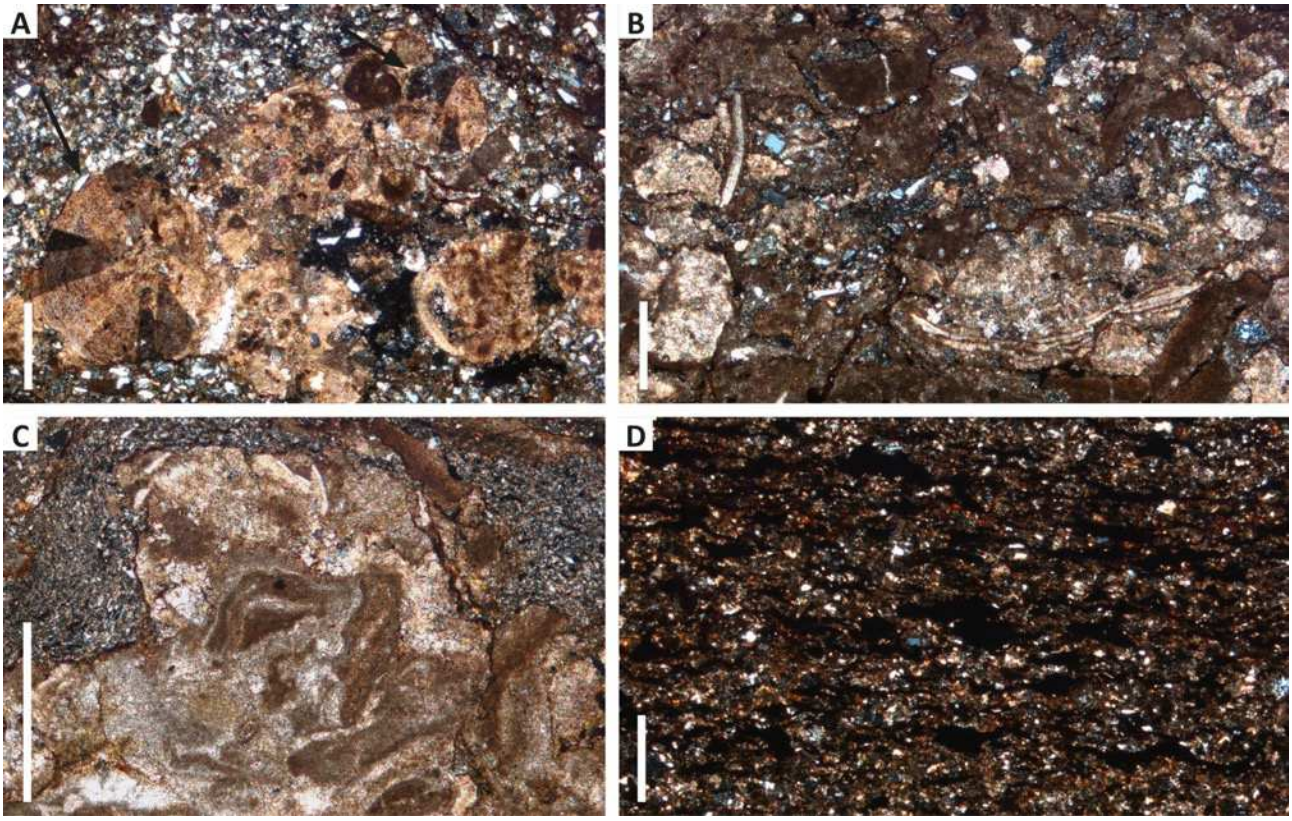


Fig. 8. Microfacies from the Tregiovo Village section as seen with crossed polarizers; A–C from the top of the microbial carbonate lithozone, and D from ca. 15 m (cemented and laminated carbonate pelites lithozone). A. Spherulites and microbial carbonate intraclasts within a fine arenite mainly composed of quartz granules; B. Conchostracans and carbonate intraclasts with clotted peloidal fabric, within arenaceous matrix; C. a relatively large carbonate intraclast with visible peloidal fabric and convoluted lamination (peloidal stromatolite), in a siltstone matrix; D. fine laminated arenite rich in organic matter grains, probably leaf and wood fragments. Scale bars 400 μm.

occur, as well as sporadic calcitic spheroids (Fig. 8A). Clotted peloidal carbonates, sometimes laminated, and carbonate spheroids are typical fabrics of microbial carbonates in continental environments (e.g., Della Porta, 2015). Carbonate clasts are embedded in a fine sandstone matrix (Fig. 7A–D) with mainly quartz, lithics of a possible volcanic origin, biotite, white mica and feldspar (Fig. 8A–D).

At the village section, this facies association is involved in large slumps, several meters thick, bounded at their base by sharp discordant planes with slickensides. Laminated pelites below the slump plane may have convoluted lamination (Fig. 6C).

4.2. Palaeobotany

The Tregiovo plant assemblages are dominated by diverse conifers, represented by four genera (*Dolomitia*, *Hermitia*, *Feysia*, *Quadrocladus*). Other groups are sphenophytes (*Annularia*), ferns and/or seed ferns (e.g., *Peltaspermum*, *Lodevia* and *Sphenopteris*), ginkgophytes (*Sphenobaiera*), and at least three *incertae sedis* taxa (*Taeniopteris*, Morphotype 1 and Morphotype 2; Figs. 9, 10). All plant groups occur in both assemblages (A and B), but with different abundances. In particular, the abundances of conifers and ferns and/or seed ferns change significantly between the two assemblages (Fig. 11; Table 1).

4.2.1. Sphenophytes

Only two specimens can be assigned to a genus within this group; one comes from assemblage A and one from assemblage B. They are represented by axis fragments, with whorls of lanceolate leaves, typical for the genus *Annularia* Sternberg, 1821 (Fig. 9A), an ubiquitous genus during the Carboniferous–Cisuralian (e.g., Taylor et al., 2009). This is so far the only occurrence of *Annularia* sp. for the Cisuralian of the Southern Alps (Marchetti et al., 2015). Several more remains possibli attributable to sphenophytes were discovered in the flora, including a diaphragm of elliptic shape, partially deformed (Fig. 9B). The structure is formed externally by a ring (3–5 mm thick) that has an indented external margin resembling the cross-section view of the vascular bundles of a stem of a sphenophyte. On the inside, the disk-like surface shows a series of concentric rings delineated by small holes. Additionally, there are small external impressions of sphenophyte stem fragments (up to 90 mm long and 30 mm wide) with longitudinal impressions of vascular bundles interrupted by a nodal structure (Fig. 9C), attributable to sphenophytes have been found.

4.2.2. Ferns and/or seed ferns

This heterogeneous group includes several fronds, frond fragments, pinnae fragments, pinnules and ovuliferous organs, which belong either to ferns or seed ferns. Several umbrella-shaped, lobed ovuliferous discs are assigned to the genus *Peltaspermum* Harris, 1937 (e.g., Fig. 9D), a peltaspermalean female reproductive organ. *Peltaspermum* is less abundant in assemblage A (ca. 2%) than in assemblage B (ca. 10%). The genus *Sphenopteris* (Brongniart) Sternberg, 1825 (Fig. 9E) is well represented in the Tregiovo flora. Fragmented and almost complete fronds have been attributed to *Sphenopteris* sp., *S. kukukiana* Gothan et Nagalhard, 1921, *S. patens* (Althaus) Geinitz,

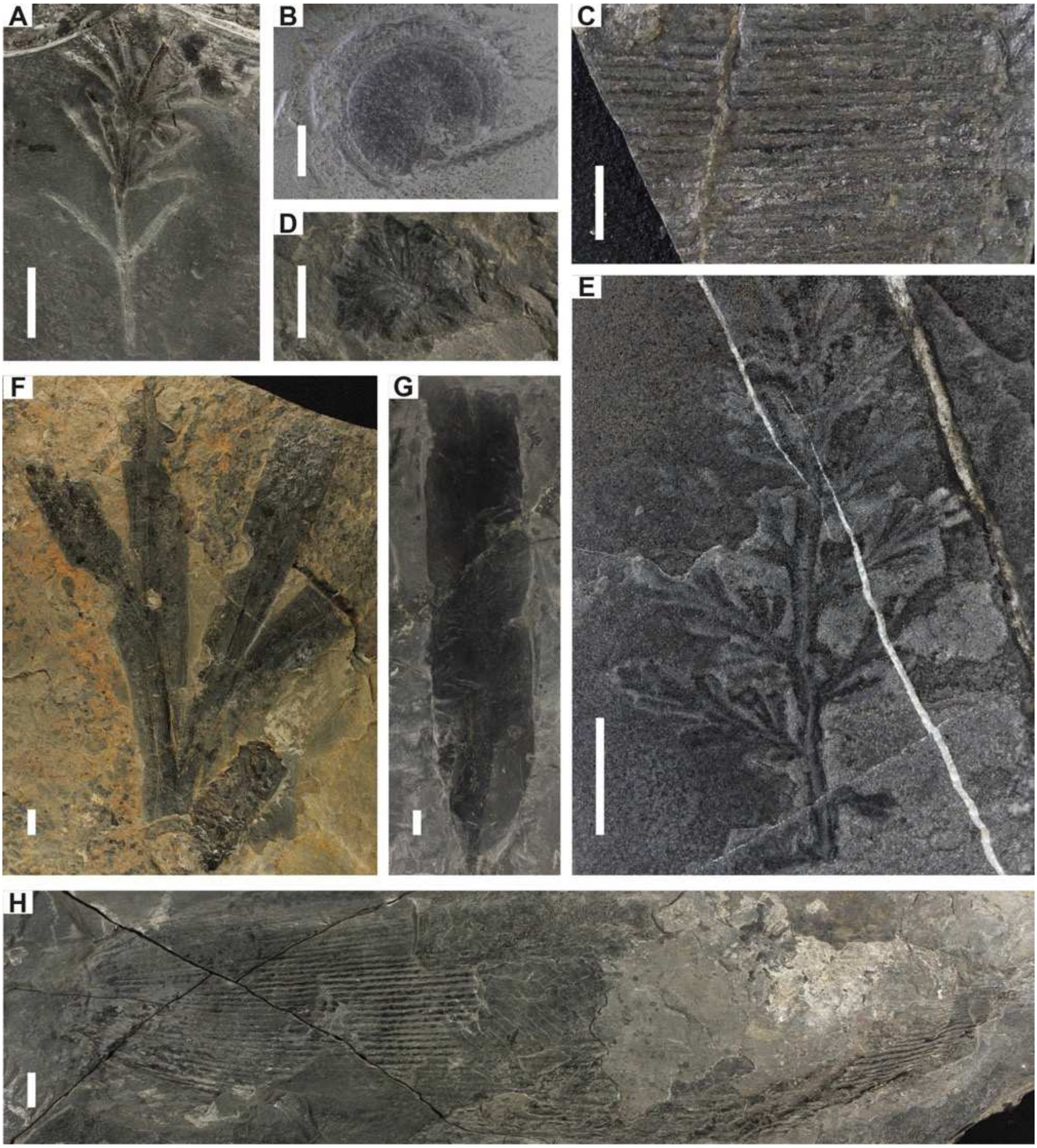


Fig. 9. Plant remains form the “Le Fraine” section plant assemblages. A. *Annularia* sp.; B. Sphenophyte diaphragm; C. external impression of sphenophyte stem with vascular visible bundles; D. ovuliferous disc of *Peltaspermum* sp.; E. frond fragment of *Sphenopteris* sp.; F. Morphotype 1 foliage; G. leaf fragment of *Taeniopteris* sp.; H. leaf of Morphotype 2. Scale bar 10 mm.

1848, *S. suessii* Geinitz 1869 and *Sphenopteris* sp. cf. *S. geinitzii* (Geinitz) Göppert 1864, showing a noteworthy diversity (Forte et al., submitted).

4.2.3. Ginkgophytes

Ginkgophytes are poorly represented in the "Le Fraine" assemblages (2%; Table. 1). Leaves with wedge-shaped laminae, deeply incised and forming two narrow lobes with rounded apex, are putatively attributed to the genus *Sphenobaiera* Florin, 1936 (Fig. 10A). They were found only in assemblage A.

4.2.4. Conifers

Conifers dominate in both assemblages, especially in assemblage A, where they reach over 85%, whereas in assemblage B, ca. 60% of the specimens are conifers (Table 1). Foliate shoots are very abundant, but leaves, cones and dwarf-shoots were also found. Among the latter, at least five different taxa occur: *Dolomitia* (Fig. 10B), putative *Pseudovoltzia*-like dwarf shoots and three more morphotypes (i.e., Types A, B, C; Fig. 10C) with uncertain affinity (Forte et al., 2017). These dwarf-shoots range from forms with very connate and ovate scales closely related to voltzian Voltziales, to forms with many free sterile scales, similar to the walchian Voltziales (Forte et al., 2017). None of the dispersed conifer cones (Fig. 10E) has been found anatomically connected to foliate shoots fragments. Moreover, their poor preservation (cones are highly coalified) did not allow species identification.

Several foliate shoots, characterized by falcate needle-like leaves, helically arranged around the axis have been attributed to the genus *Hermitia* Kerp et Clement–Westerhof, 1986 (e.g., Fig. 10G). Several foliate shoots, with rounded and short squamose leaves, have been found as well and attributed to the species *Hermitia geinitzii* Kerp et Clement-Westerhof, 1986, known so far only from the Cisuralian Collio Basin (North-western Italy, Lombardy region; Cassinis, 1966; Remy and Remy, 1978; Visscher et al., 2001), and Tregiovo (Marchetti et al., 2015). Branches belonging to voltzian conifers (voltzian Voltziales) have been found as well. The most abundant taxon of the two assemblages is *Feysia* Broutin et Kerp, 1994 (e.g., Fig. 10F), which is a broad-leaved conifer, with non- or hardly decurrent, spirally arranged leaves, triangular to obovate, with the apex slightly recurved towards the axis. Other foliate shoot fragments with spirally arranged spatulate leaves belong to the genus *Quadrocladus* Mädler, 1957. The leaves have a rounded apex and arise at an angle of ca. 30–60° from the axis (e.g., Fig. 10D). Before the discovery in the Tregiovo flora (i.e., Remy and Remy, 1978; Visscher et al., 2001; Marchetti et al., 2015), this genus was only known from the Lopingian of Germany (Mädler, 1992; Uhl and Kerp, 2002a; Uhl and Kerp, 2005) and Italy (Bletterbach, Uhl and Kerp, 2005b; Kustatscher et al., 2012).

Fig. 10. Ginkgophyte and conifers from the "Le Fraine" section plant assemblages. A. *Sphenobaiera* sp. Florin, 1936; B. dwarf-shoot of *Dolomitia* sp.; C. dwarf-shoot type A; D. shoot fragment of *Quadrocladus* sp.; E. undetermined conifer cone; F. shoot fragment of *Feysia* sp.; G. Shoots of *Hermitia* sp.; scale bar 10 mm.

Table 1. Fossil plant taxa from the "Le Fraine" section.

Taxon (Genus/Species)	Group	References	Assemblage A/B	Number of specimens
Annularia sp.	Sphenophytes	Sternberg, 1821	A, B	4
Peltaspermum sp.	Seed Ferns	Harris, 1937	A, B	40
Sphenopteris sp.	Ferns and/or Seed Ferns	Sternberg, 1825	A, B	93
Sphenopteris kukukiana	Ferns and/or Seed Ferns	Gothan and Nagalhard, 1921	A, B	9
Sphenobaiera sp.	Ginkgophytes	Florin, 1936	A	7
Feysia sp.	Conifers	Broutin and Kerp, 1994	A, B	275
Quadrocladus sp.	Conifers	Mädler, 1957	A, B	86
Hermitia sp. and *Hermitia geinitzii*	Conifers	Kerp and Clement–Westerhof, 1986	A, B	143
Dolomitia sp.	Conifers	Clement–Westerhof, 1987	A, B	7
cf. *Pseudovoltzia* sp.	Conifers	Florin, 1927	A, B	3
Dwarf-shoot type A	Conifers	Forte et al., 2017	B	1
Dwarf-shoot type B	Conifers	Forte et al., 2017	B	1
Dwarf-shoot type C	Conifers	Forte et al., 2017	B	1
Taeniopteris sp.	Uncertain affinity	Brogniart, 1828	A, B	12
Morphotype 1	Uncertain affinity	Marchetti et al., 2015	A, B	25
Morphotype 2	Uncertain affinity	Marchetti et al., 2015	A	18

Table. 1. Fossil plant taxa from the assemblages A and B of "Le Fraine" section of Tregiovo, and number of specimens of each taxon. Position of assemblages A and B as in figure 4.

4.2.5. Foliage with uncertain affinities

Leaves with lanceolate laminae, a marked midrib and parallel, undivided veins arising from the midrib at an almost perpendicular angle, occur in assemblage A. These types of leaves (Fig. 9G), assigned generally to the genus *Taeniopteris* Brogniart, 1828, have been produced by several plant groups including cycads, ferns and seed ferns (e.g., Taylor et al., 2009).

Two different morphotypes have been identified from the material from "Le Fraine". Morphotype 1 (Fig. 9F) is represented by leaves with a lamina that bifurcates symmetrically at least once, more rarely twice, forming ribbon-like segments, with a regular margin. Each segment is characterized by a central, wide midvein (or rachis) covered by some parallel wrinkles. No secondary veins are visible on the lamina. Because of its insufficient elements, a clear botanical attribution is impossible. Morphotype 2 is represented by big elongate leaves with distinct longitudinal, parallel veins (e.g., Fig. 9H). The basal area of the leave is thicker, the distal margin of the lamina appears serrated. Morphotype 2 occurs only in the assemblage A, with about 2%. Also in this case, a clear taxonomical attribution is not possible.

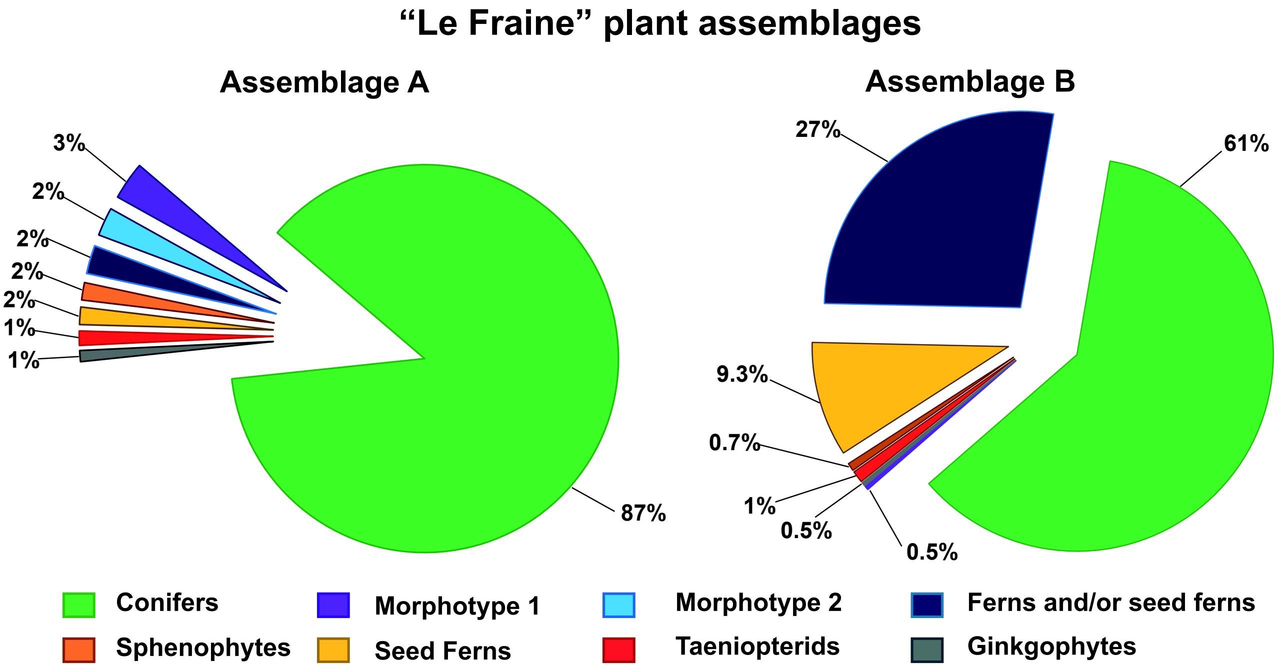


Fig. 11. Quantitative diagrams that illustrate the abundance of the different groups of plants for the two different assemblages (A and B) of the "Le Fraine" section.

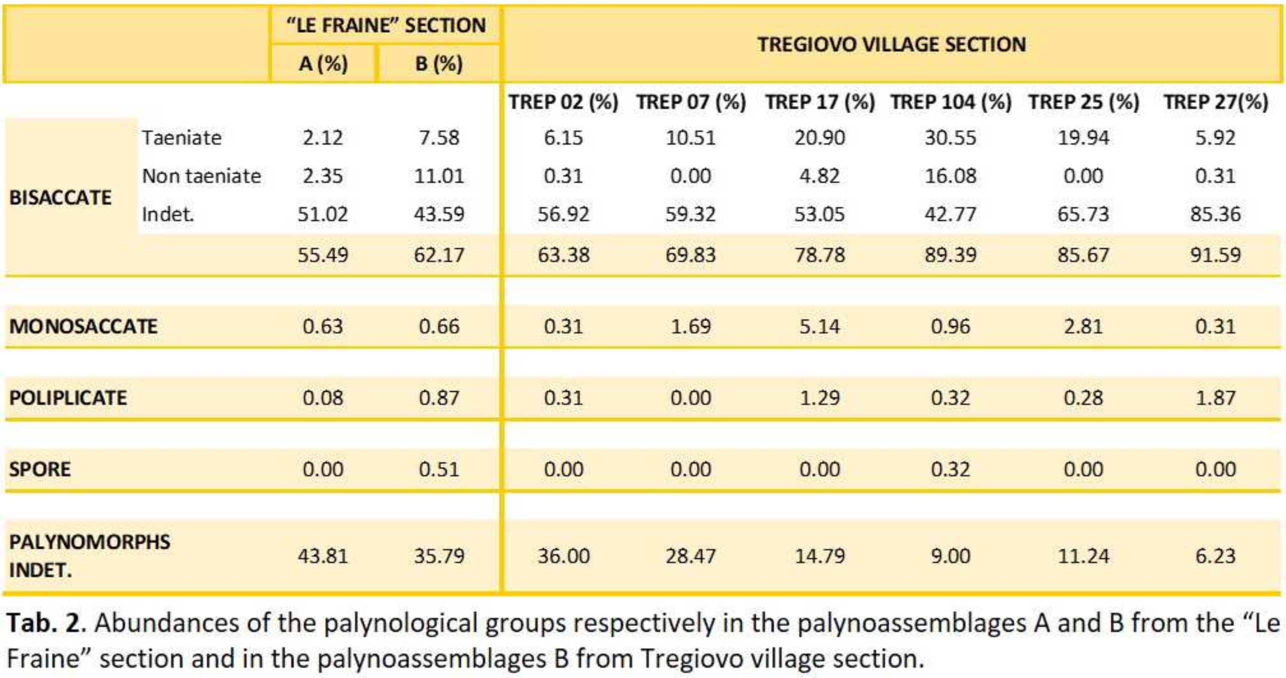
4.3. Palynology

Palynological samples from "Le Fraine" are dominated by dispersed amorphous organic matter (<70–90% of all the organic matter). Most of the amorphous kerogen has an undefined origin, although it originated probably from vegetal matter. A smaller portion can clearly be attributed to phytoclasts, composed of altered wood fragments (very dark brown to black in color), fragments of cuticles (yellowish in color), and conifer pitted tracheids (dark brown in color). Some fungal hyphae and spores occur as well, although exclusively in the lower assemblage. The sporomorphs are poorly preserved, dark brown in color, often broken and with a "bubbly" appearance, which made the observation of many morphological characters difficult (Fig. 12A–U). The poor preservation is likely attributable to diagenesis. Nonetheless, one sample collected from the Tregiovo village section (ca. 16 m from the base of the section, Trep 104), is better preserved (Fig. 13A–J). Apertures, taeniae, ornamentation and the reticulate structures of sacci are clearly visible (Fig. 13A–J). This sample gave us better insights in the diversity of the Kungurian microflora from Tregiovo.

4.3.1. Palynoassemblage A ("Le Fraine" section)

The degree of preservation of palynoassemblage A is low, since most sporomorphs are mainly dark brown in color, degraded and broken. The number of undetermined sporomorphs in the lower assemblage is, thus, around 43% (Table 2). Bisaccate pollen are the most abundant group, ranging from 45% to 60%. For many of them it is not even possible to determine whether they were taeniate or non taeniate, because of their poor preservation. Recognizable taeniate pollen range in abundance from 2.4% to 3.4% and include mainly *Lueckisporites* Potonié et Klaus, 1954 (e.g., Figs. 12F, 12L–M), *Protohaploxypinus* Samoilovitch, 1953, *Protodiploxypinus* Samoilovitch, 1953 and cf. *Striatopodocarpites* sp. (e.g., Figs. 12K, 12O). Recognizable non taeniate pollen are slightly more abundant, ranging from 0.63% to 5.8% and including *Illinites* Kosanke, 1950*, Gardenasporites* Klaus, 1963 (e.g., Figs. 12H, 12J)*, Limitisporites* Leschik, 1956, *Alisporites* sp. (e.g., Fig. 12E), *Platysaccus* sp. (e.g., Figs. 12I, 12R) and *Falcisporites* Leschik, 1956. Monosaccate pollen reach less than 1% and are represented by *Potonieisporites* Bhardwaj, 1955 and *Nuskoisporites* Potonié et Klaus, 1954 (Fig. 12S–U), Poliplicate pollen are extremely rare (<0.1%). No spores have been found (Table 2).

Table 2. Abundance of the palynological groups form the two Tregiovo sections.



		"LE FRAINE" SECTION		TREGIOVO VILLAGE SECTION					
		A (%)	B (%)	TREP 02 (%)	TREP 07 (%)	TREP 17 (%)	TREP 104 (%)	TREP 25 (%)	TREP 27(%)
BISACCATE	Taeniate	2.12	7.58	6.15	10.51	20.90	30.55	19.94	5.92
	Non taeniate	2.35	11.01	0.31	0.00	4.82	16.08	0.00	0.31
	Indet.	51.02	43.59	56.92	59.32	53.05	42.77	65.73	85.36
		55.49	62.17	63.38	69.83	78.78	89.39	85.67	91.59
MONOSACCATE		0.63	0.66	0.31	1.69	5.14	0.96	2.81	0.31
POLIPLICATE		0.08	0.87	0.31	0.00	1.29	0.32	0.28	1.87
SPORE		0.00	0.51	0.00	0.00	0.00	0.32	0.00	0.00
PALYNOMORPHS INDET.		43.81	35.79	36.00	28.47	14.79	9.00	11.24	6.23

Tab. 2. Abundances of the palynological groups respectively in the palynoassemblages A and B from the "Le Fraine" section and in the palynoassemblages B from Tregiovo village section.

4.3.2. Palynoassemblage B ("Le Fraine" section)

In the upper assemblage (assemblage B), the number of undetermined sporomorphs is lower than in assemblage A, around 35% (Table 2). Undetermined bisaccate pollen grains are the most abundant group, ranging from 41 to 45%. The second most abundant group is represented by non taeniate bisaccate pollen, which range from 6 to 16%, including basically the same genera that occur in assemblage A, such as: *Illinites*, *Gardenasporites*, *Falcisporites* and *Limitisporites*. Taeniate bisaccate pollen are less represented in assemblage B, ranging from 6 to 9%, and including *Lunatisporites, Lueckisporites*, *Protohaploxypinus* and *Protodiploxypinus.* Poliplicate pollen are represented only by *Vittatina* Wilson, 1962 (Fig. 12P), with less than 2.5%. Similarly, monosaccate pollen grains are rare (Table 2) and basically represented by the genus *Nuskoisporites*. Spores are extremely rare, and never exceed 1% (Table 2; Fig. 12A–C).

4.3.3. Palynoassemblage B (Tregiovo village section)

The state of preservation at Tregiovo village is slightly better compared to the two palynoassemblages of the "Le Fraine" section, as indicated by the lower percentages of indeterminable palynomorphs (Table 2). In particular, sample Trep 104 yielded well preserved sporomorphs (Fig. 13A–J). The damage ("bubbly") appearance of the pollen surface is more rare and characterizes only few pollen grains. The color ranges from yellow to light brown. In the Tregiovo village section bisaccate pollen are again dominant (ca. 55 to 90%, Table 2; Fig. 14) with respect to other groups, and include non taeniante forms such as *Falcisporites* (Fig. 13B) and *Gardenasporites* (Fig. 13C), and taeniate *Striatoabieites* (Fig. 13D–E), *Lueckisporites* (Fig. 13F). Monosaccate pollen, represented by the genus *Nuskoisporites* (Fig. 13H–J) and poliplicate pollen are, on average, more abundant in the Tregiovo village section than in samples from the "Le Fraine", whereas spores are very rare (Table 2; Fig. 14).

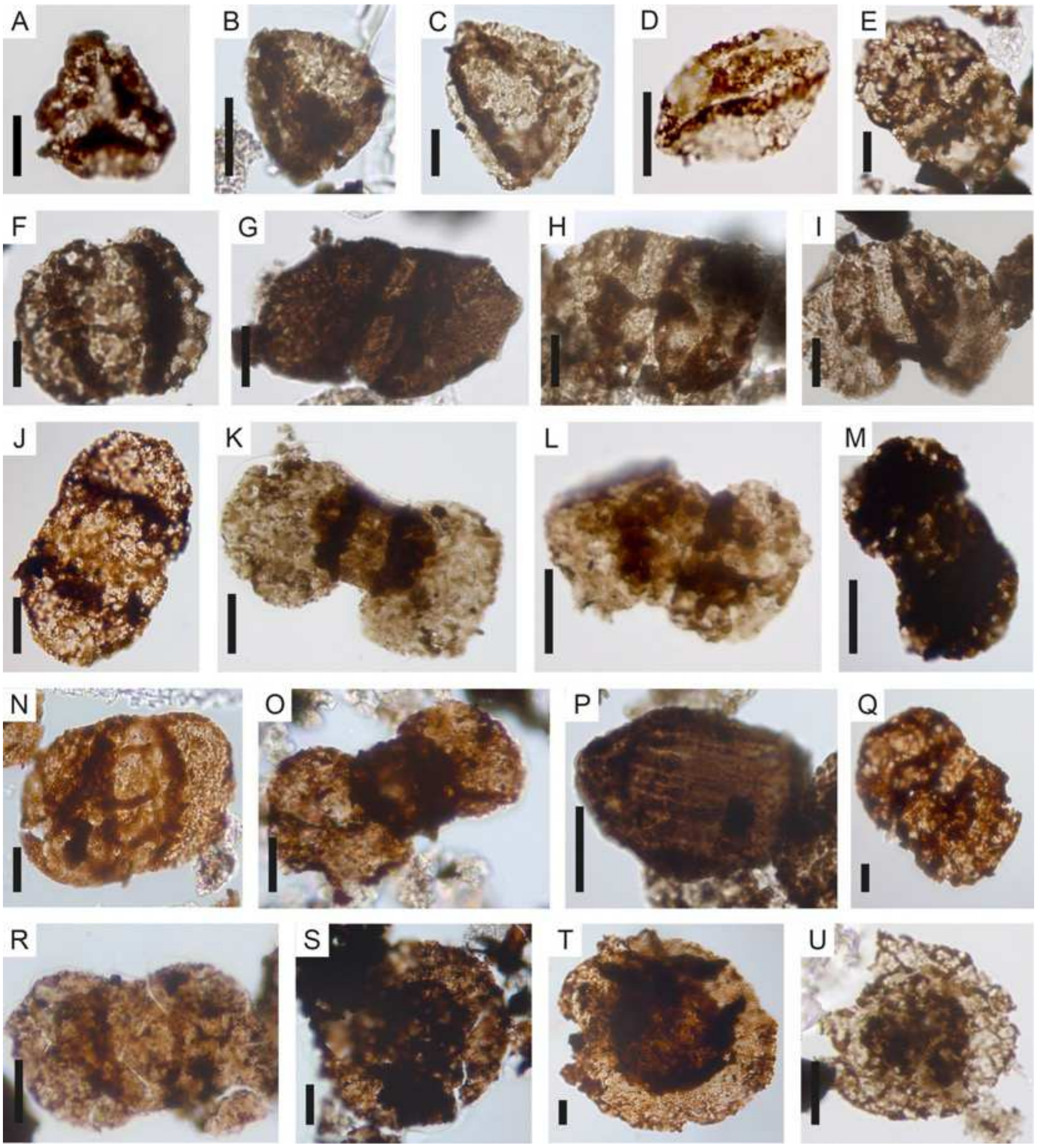


Fig. 12. Palynomorphs from the "Le Fraine" section plant assemblages. A–C. undetermined spores; D. cf. *Cycadopites* sp.; E. *Alisporites* sp.; F. *Lueckisportites* sp.; G. *Alisporites* sp.; H. *Gardenasporites* sp.; I. cf. *Platysaccus* sp.; J. cf. *Gardenasporites* sp.; K. *Striatopodocarpites* sp.; L–M. *Lueckisportites* sp; N. *Lunatisporites* sp.; O. *Striatopodocarpites* sp.; P. *Vittatina* sp.; Q–R. cf. *Alisporites* sp.; S–U. *Nuskoisporites* sp.; scale bars 20 µm.

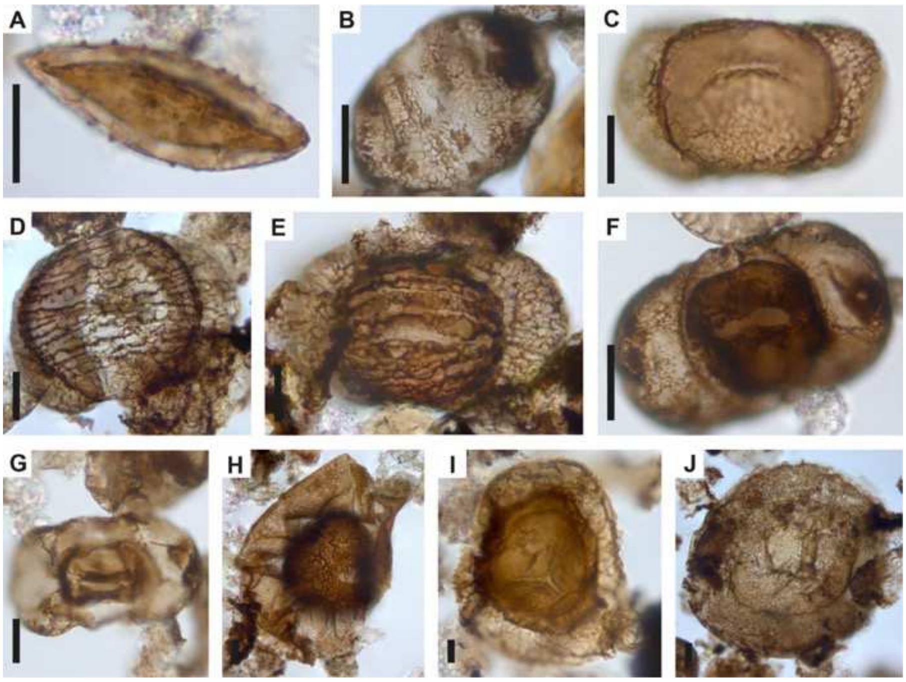


Fig. 13. Palynomorphs from the Tregiovo village section, sample Trep104. A. undetermined spinate sporomorph; B. cf. *Falcisporites* sp.; C. *Gardenasporites* sp.; D–E. *Striatoabieites* sp.; F–G. *Lueckisporites* sp.; H–J. *Nuskoisporites* sp.; scale bars 20 µm.

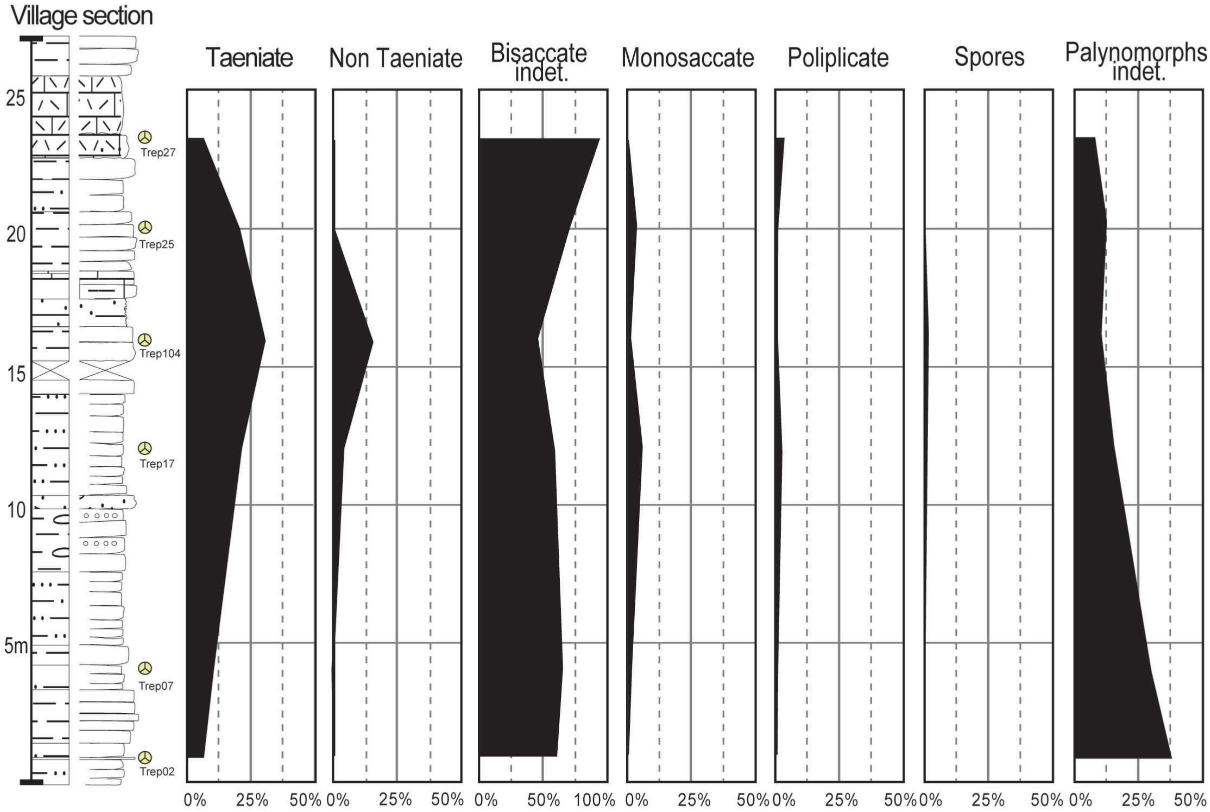


Fig. 14. Relative abundance of main palynological groups from the Tregiovo Village section. Sample Trep 104 is exceptionally well preserved and this explains the lower abundance of indeterminate bisaccate pollen, which are replaced by taeniate and non taeniate bisaccate pollen. This is however the only apparent effect of preservation in palynological abundances.

4.4. Geochemistry

The “Le Fraine” rocks are rich in organic matter, with a mean TOC of 1.1% (± 0.4 standard deviation). In the first 20 m of the section, high values (1.5–2% TOC) are observed (Fig. 15). The $\delta^{13}C_{org}$ values obtained from the bulk organic matter of the “Le Fraine” section range from ca. –23.4‰ to –20.1‰ VPDB. The isotopic values are higher in the lower part. An upward trend to more negative $\delta^{13}C_{org}$ values is observed (Fig. 15). The most negative $\delta^{13}C_{org}$ values are recorded in the upper plant horizon, with a difference in $\delta^{13}C_{org}$ between the two plant horizons of about 1.7‰. The $\delta^{13}C_{org}$ values obtained from the Tregiovo village section, are more negative than those from the “Le Fraine” section, ranging from –26.5‰ to –21.2‰, and decrease along the section. The average values of the Tregiovo village section (–22‰ VPDB) are very close to the average $\delta^{13}C_{org}$ values of the upper part of “Le Fraine” (–21.7‰ VPDB), confirming that the Tregiovo village section corresponds to the uppermost part of the Tregiovo Formation, as suggested by Neri et al. (1999).

5. Discussion

5.1. Sedimentology

The laminated pelites of the Tregiovo Formation bear evidence for a subaqueous depositional environment: laminae are normally graded suggesting settling from still water, and freshwater fossils (conchostracans) are common. Laminated pelites were however frequently exposed, as testified by common mud-crack structures and tetrapod footprints. Marchetti et al. (2015) interpreted this facies association as representing ephemeral lakes that dried up frequently, possibly seasonally, corresponding thus to a playa-lake depositional system. The carbonate and chert components in this first lithozone are of diagenetic origin. In particular, chert forms nodules or nodular laminae and beds that parlially replace laminated sediments. Marchetti et al. (2015) suggest that silica derives from the circulation of volcanic fluids. The carbonate intraclasts, flat pebbles and spheroids of the overlying lithozone are instead microbial carbonates. Their fabric cannot be used to discriminate between different continental carbonate depositional environments (Della Porta, 2015), however, being intercalated with laminated pelites, these carbonates are interpreted as lacustrine.

Fresh water limestones with cyanobacterial laminites were already reported by Neri et al. (1999) from the Tregiovo Formation. Moreover, centimeter-thick oncoid-like algal crusts and laminae have been observed by Fritz and Krainer (2006) in the nearby Kungurian Sinnich/Sinigo outcrop (Bozen/Bolzano Province, Athesian Volcanic Complex). Consistent with this interpretation, the lithozone with microbial carbonates contains little or no evidence of subaerial exposure, and neither tetrapod footprints nor mud-cracks were found in this interval. The common occurrence of microbial carbonates supports a stable lacustrine environment rather than a playa lake in this phase. Slump structures, flat pebble (intraformational) breccia deposits, autoclastic breccia and convoluted laminations are the products of soft-sediment deformation.

The Orobic Basin, cropping out some 50 km to the West in the Lombardian Alps, was filled by two depositional cycles and has a poorly constrained, possibly Kungurian age (e.g., Berra et al., 2016). The first depositional cycle displays a sedimentary evolution similar to the one discussed in this paper. Coarse siliciclastic deposits cover an erosional surface and pass gradually, through a heterolithic unit, to dark laminated mudstones similar to the laminated pelite lithozone of the Tregiovo Formation (Berra et al., 2016). In the Orobic Basin, the upper part of the laminated mudstones contains microbial carbonates and structures related to syndepositional, soft-sediment deformation (Berra and Felletti, 2011; Berra et al., 2016). The carbonate-bearing unit of the Orobic Basin is analogous to the microbial carbonate lithozone of the Tregiovo Formation. Berra et al. (2016) interpreted the laminated dark mudstones of the Orobic Basin as playa-lake deposits, and the microbial carbonates in its upper part as formed in permanent lakes, a succession of depositional environments identical to that inferred for the Tregiovo Basin. Soft-sediment deformation is common, in both basins, along with the appearance of lacustrine microbial carbonates. It would be tempting to correlate these similar sedimentary successions of the Orobic and Tregiovo basins. Lacustrine carbonates would then occur because of a common shift to more humid climatic conditions, and soft-sediment deformation may have been triggered by earthquakes of the same tectonic phase affecting a wide region of the Southern Alps. Unfortunately, however, given the loose geochronological constraints, it is impossible at present to prove the synchronicity of these two analogous successions.

5.2. Palaeobotany

The increasing aridity recorded during the Permian at low latitudes (Montañez et al., 2007; DiMichele et al., 2008, 2009; Tabor and Poulsen, 2008; Horton et al., 2012; Montañez and Poulsen, 2013; Michel et al., 2015) favored the spread of conifers and other gymnosperms, such as certain groups of seed ferns, due to their more drought-tolerant character with respect to other groups of Pennsylvanian–Cisuralian plant communities (e.g., DiMichele et al., 2006; 2011). The walchian conifers originated during the Pennsylvanian in extrabasinal environments, where conditions were drier (e.g., Hernandez-Castillo et al., 2003; Looy et al., 2014). The voltzian conifers appeared later, and became widespread from the late Cisuralian onwards, colonizing also the lowlands (e.g. DiMichele et al., 2008; Looy et al., 2014). The plant assemblages of Tregiovo reflect very well the result of this aridification process in the Cisuralian palaeotropics (e.g., Montañez et al., 2007; Tabor and Poulsen, 2008). Walchian conifers (walchian Voltziales), typically small trees with plagiotropic branching and needle-like leaves, and voltzian conifers (voltzian Voltziales), mainly characterized by spirally arranged, broad leaves and orthotropic branching (e.g., Hernandez-Castillo et al., 2003) occur together in both assemblages (A and B) at Tregiovo. This is of particular interest, because broad-leaved conifer branching systems are generally rare in the Cisuralian (e.g., Broutin and Kerp, 1994) but are abundant/common in Tregiovo (more than 50%; Table 1). Broad-leaved conifers such as *Ullmannia* Göppert 1850 have been found in the Lower Pease River Flora (Kungurian-Roadian), from western Pangea (DiMichele et al., 2001), showing how broad-leaved conifers were very widespread durin the lower Permian. Moreover, the occurrences of *Dolomitia* and *Pseudovoltzia*-like dwarf-shoots in the Tregiovo plant assemblages date the appearance of these two genera back to the middle Kungurian, adding important information on the evolution of conifers and on the transition from walchian to voltzian conifers in Euramerica (Forte et al., 2017).

The large number of plant fossils from the “Le Fraine” section (more than one thousand), together with material from the type section (20 specimens), represents one of the largest and well-dated plant assemblages from the Kungurian of the eastern Pangea palaeotropics. Although part of assemblage A has been described by Marchetti et al. (2015), the specimens from assemblage B and additional material from assemblage A give deeper insights into the composition and diversity of certain plant groups (Forte et al., 2017) within each assemblage and permit a comparison between the two assemblages (Fig. 11; Table 1). Conifers are more abundant in assemblage A, where they represent 86% of the plant fossil remains. They decrease in assemblage B parallel to the increase in abundance of the “ferns and/or seed ferns” group from 6% in assemblage A to more than 30% in assemblage B (Fig. 11; Table 1). This group includes *Peltaspermum* sp., the reproductive organ of peltaspermalean seed ferns, and fronds of *Sphenopteris*. The latter is a fossil genus that includes many species of uncertain botanical affinity, characterized by pteridophyllous foliages with strongly lobed and dissected pinnules. However, their very stiff and rigid appearance suggests a putative adaptation to drier conditions (Forte et al., submitted). Even though there is a clear change in floral composition, the character of both assemblages is xerophytic. This suggests the persistence of a generally semi-arid/arid climate (*sensu* Cecil 2003), and reflect a stepwise change towards more arid conditions that took place at a global scale from the Pennsylvanian to the late Cisuralian (e.g., Tabor and Montañez, 2004; Schneider et al., 2006; Montañez et al., 2007; DiMichele et al., 2008, 2011; Peyser and Poulsen, 2008; Horton et al., 2012; Montañez and Poulsen, 2013; Michel et al., 2015).

5.3. Palynology

Previous palynological studies of the Tregiovo Basin have so far been focused on biostratigraphy (i.e., Klaus, 1963; Cassinis and Doubinger, 1991, 1992; Neri et al., 1999; Barth and Mohr, 1994). Three different palynological assemblages (I, II and III) were distinguished by Neri et al. (1999); assemblages I and II where found in the type section, whereas assemblage III comes from the Tregiovo village section. Assemblage III was considered more indicative of late Permian age than early Permian age, based on its similarity with pollen from the overlying Gröden/Val Gardena Sandstones, such as the abundance of *Nuskoisporites dulhnuntyi* Potonié et Klaus, 1954 (Neri et al., 1999; Cassinis et al., 2002).

The sporomorphs are poorly preserved, looking yellowish to very dark brown in color, often broken and with a degradation defined by their “bubbly” appearance. The cause of these degradation features could be the growth of pyrite cubes as result of sulphate-reducing bacterial activity (Barth and Mohr, 1994), as suggested by the common formation of pyrite around the plant fossils, or could be related to other diagenetic factors such as high pressures and temperatures, although the preservation of sporomorphs from the Tregiovo village section is slightly better. In particular, sample Trep 104 is well preserved and its analysis allowed assessment of preservational biases in all other samples. In sample Trep 104, the percentage of bisaccate indet. decreases to around 40% (Table 2), parallel to the increase of taeniate and non taeniate bisaccate pollen. The total amount of bisaccate pollen however is similar to other samples of the section, suggesting that there are no biases of preservation except for that permitting better discrimination of taeniate and non taeniate pollen in Trep 104.

Local environmental conditions influence the composition of the local vegetation, and thus also the composition of the megafossil assemblage, although pollen, especially bisaccate pollen, represent regional to supraregional areas and reflect environmental/climate conditions since they are distributed by wind over longer distances. Thus, sporomorphs and macrofossils are subjected to different taphonomic processes and a comparison between both datasets permits a more complete understanding of the fossil flora. In the case of Tregiovo the composition of the palynoflora confirms the results from the macroremains. The almost absence of spores is one of the problems that we faced during the palynological analyses. In the “Le Fraine” section, the spores never reach 1% in Palynoassemblage B and no spores have been detected in Palynoassemblage A. Also in the Tregiovo village section, spores are very rare, included in the best preserved specimen TRE 104. The scarce occurrence of spore-producing plants (e.g., Annularia sp.) in the macroflora could be one of the possible explanation of the rarity of spores in the palynoflora, and indicate the xerophytic character of the assemblage. Nonetheless, we cannot exclude a selective degradation of spores.

Nearly all determined palynomorphs are bisaccate pollen (around 90%; Table 2), which belong to gymnosperms such as conifers, ginkgophytes, cycadophytes and certain groups of seed ferns (e.g., Balme, 1995; Looy and Hotton, 2014). The monosaccate pollen *Nuskoisporites* was previously found in situ in male cones of *Ortiseia* Florin, 1964 (Clement-Westerhof, 1984; Clement-Westerhof, 1988), suggesting thus an attribution to broad-leaved conifers. Striate pollen such as *Vittatina*, on the other hand, was produced mainly by ginkgophytes and cycadophytes. The palynological analysis shows, thus, a strong correlation between both micro- and macroflora, testifying how the fossil plant record was not affected by collection or preservation bias. The xerophytic character of both assemblages is thus confirmed.

Previous authors (e.g., Neri et al., 1999), suggested, based on the presence of *Nuskoisporites* in the upper part of the section, assignment of the latter to the late Permian (Lopingian). The radiometric analyses, carried out in the last few years (e.g., Avanzini et al., 2007; Marocchi et al., 2008), assign the entire section, however, to the middle Kungurian. This makes the occurrence of *Nuskoisporites* at the “Le Fraine” section the oldest occurrence so far for this genus, dating it back at least to the Middle Kungurian.

5.4. Geochemistry

We can assume that nearly all organic matter at Tregiovo was terrestrial, and mostly originated from land plants. Thus, we considered the δ^{13}C of the finely dispersed organic matter contained in the bulk rock samples ($\delta^{13}C_{org}$) as representative of the δ^{13}C of plants. The $\delta^{13}C_{org}$ (terrestrial organic matter) of the Permian ranges between –22.9‰ and –25.5‰ and, in particular, in the Cisuralian the mean $\delta^{13}C_{org}$ is –22,9‰ VPDB (Strauss and Peter-Kottig, 2003). This range is within that of modern C3 plants (from –34‰ to –20‰; O'Leary, 1988), and more in general, the Palaeozoic was characterized by a strong signal of C3 photosynthetic plants (Bocherens et al., 1993). The values of $\delta^{13}C_{org}$ obtained from the "Le Fraine" section and from the Tregiovo village section, which range from –20.1‰ to –26.5‰ VPDB, are also within the interval of C3 plants, and compare well with other Permian continental deposits, such as the North China Coal platform (Zhang et al., 1999) and South Africa coalfields (Faure et al., 1995). Along the section, the $\delta^{13}C_{org}$ shifts towards more negative values (Fig. 15). This isotopic trend may reflect the global Palaeozoic δ^{13}C curve. In fact, $\delta^{13}C_{org}$ increased during the Cisuralian and later decreased in the Guadalupian and Lopingian, reaching mean values of –24 ‰ (e.g., Peters-Kottig et al., 2006). The phase of $\delta^{13}C_{org}$ increase could reflect the sequestration of organic matter that started during the Carboniferous and that gave origin to the Permian-Carboniferous coal deposits (Berner 2003). This subtracted ^{12}C from the exchangeable carbon reservoirs, causing a proportional increase in the δ^{13}C of the early Permian atmospheric CO_2. The subsequent decrease of $\delta^{13}C_{org}$, from Guadalupian onward, could instead correspond to a decrease of organic matter burial in terrestrial sediments (Berner et al., 2003; Peters-Kottig et al., 2006). Other causes have been suggested for the late Permian decrease of $\delta^{13}C_{org}$, such as: tectonic and climatic processes linked to the consolidation of Pangea, that could have reduced the organic carbon burial (e.g., Faure et al., 1995; Kerp, 1996; Kidder and Worsley, 2004); an increase of weathering, which could have increased the erosion of coal beds resulting in the release of ^{12}C (Peters-Kottig, et al., 2006); release of CH_4 from clathrate deposits (de Wit et al., 2002), which have very negative δ^{13}C values (~ –60‰). In sight of this, the negative trend recorded at the "Le Fraine" and the Tregiovo village sections could signify that the global negative trend, which lasted until the Permian–Triassic boundary (Peters-Kottig et al., 2006), had started already during the late Cisuralian (Kungurian).

Nonetheless, we cannot exclude a taxonomical cause for the isotopic shift. The change in floral composition could have influenced the mean of bulk $\delta^{13}C_{org}$, which has been assumed to be mostly composed of C3 plants. Several authors demonstrated how plant material (e.g., woods, cuticles, amber, coalified tissues) of different taxa may show significant differences of $\delta^{13}C_{org}$ values (e.g., Peters-Kottig, et al., 2006; Dal Corso et al., 2011, 2017). Local environmental factors as water stress may have played a role as well. Arens et al., (2000) calculated that on extant plants, the water stress/low relative humidity can affect the $\delta\ ^{13}C$ of plants causing a general increase of 3–6‰, because of the lower fractionation due to the ecological adaptation of the plants, which tend to close the stomata, in order to reduce the loss of water in drier conditions. The isotopic shift at Tregiovo may thus simply reflect a change in the taxonomical composition of plants contributing to the bulk organic matter, such as the decrease of conifers and the parallel increase in ferns and/or seed ferns in the assemblages B, or local environmental factors.

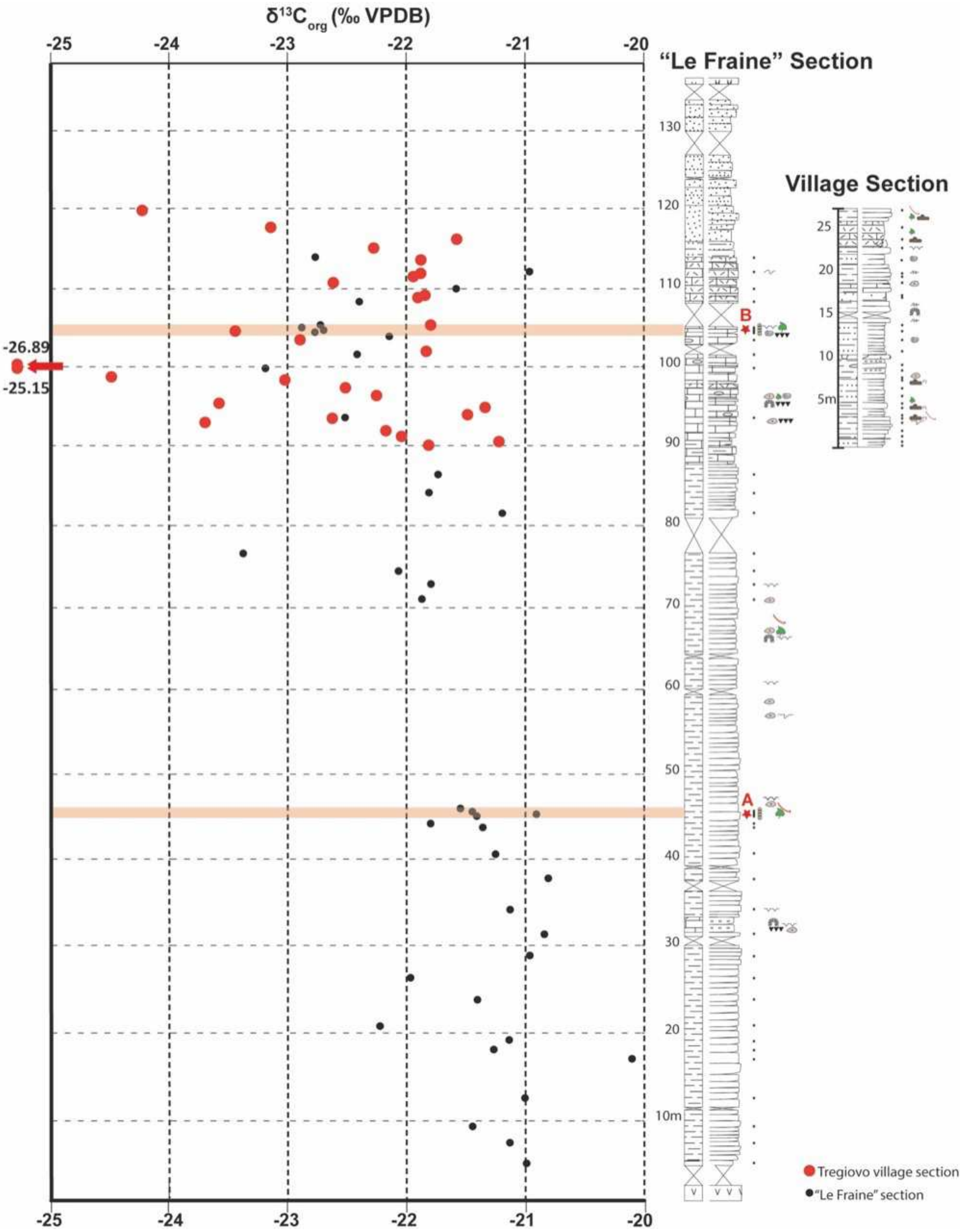


Fig. 15. $\delta^{13}C_{org}$ isotopic values measured at different levels along the "Le Fraine" and the Tregiovo Village sections. The larger red dots indicate the $\delta^{13}C_{org}$ isotopic values from the Tregiovo village section. The light orange bands indicate respectively the palaeobotanical assemblages A and B. The proposed correlation is based on lithostratigraphy, as indicated in figure 3. Symbols as in figure 4.

6. Conclusions

A multidisciplinary study in the “Le Fraine” and Tregiovo village sections allowed us to improve our understanding of the palaeoenvironmental and palaeoclimatic conditions of the Tregiovo Basin in the framework of a more global context. Plant material collected from the “Le Fraine” section showed how the floral composition changed through time, with a decrease in conifers and parallel increase in ferns and/or seed ferns from the lower assemblage A to the upper assemblage B. Nonetheless, this change is not necessarily linked to any palaeoclimatic change. The group of ferns and/or seed ferns is mainly composed of the peltasperm seed fern *Peltaspermum*, and the genus *Sphenopteris*, which includes pteridophyllous foliages with strongly lobed and dissected pinnules. The coriaceous nature of the reproductive organ and the fronds would rather suggest a xerophytic affinity for these plants. The overall scarce occurrence of spore-producing plants, such as sphenophytes (e.g., *Annularia* sp.) and undoubted ferns, in both assemblages, is paralleled by the extremely rare spores found in the palynofloras, and suggests a xerophytic character for the flora throughout the development of the Tregiovo Basin.

The palaeoenvironmental conditions may rather be related to the increasing aridity in palaeoequatorial Pangea during the Cisuralian. A stepwise change from humid to semi-arid, arid climates that took place from Pennsylvanian to the late Cisuralian has been identified at the global scale.

The $\delta^{13}C_{org}$ of the two Tregiovo sections are perfectly comparable with other coeval deposits that are roughly coeval from North China and South Africa. We recorded a clear trend towards more negative $\delta^{13}C_{org}$ values, with an amplitude of more than 1‰. Although local ecological factors, such as water-stress, or a change in floral composition may have affected the $\delta^{13}C_{org}$ of Tregiovo, a similar trend is visible also in the Kungurian $\delta^{13}C$ terrestrial organic carbon, as well as in marine carbonates. Therefore, the negative trend $\delta^{13}C$ recorded at Tregiovo may reflect a global decrease of $\delta^{13}C$ in the Kungurian.

On the other hand, we cannot exclude that a local ecological factor, such as water availability, could have influenced also the $\delta^{13}C$ of the plants. Nonetheless, the modulation of this general behavior is quite different for each taxonomical group. For these reasons, only through further taxon-specific geochemical investigations could the correlation of the carbon isotopic shift observed at Tregiovo to the Permian global $\delta^{13}C$ trend be confirmed.

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References

Arens, N.C., Jahren, A.H., Amundson, R., 2000. Can C3 plants faithfully record the carbon isotopic composition of atmospherico carbon dioxide? Paleobiology 26(1), 137–164.

Avanzini, M., Bargossi, G., Borsato, A., Castiglioni, G.B., Cucato, M., Morelli, C., Prosser, G., Sapelza, A., 2007. Note illustrative della Carta Geologica d'Italia alla scala 1:50.000, Foglio 026 Appiano. Servizio Geologico d'Italia APAT, Dipartimento Difesa del Suolo, Roma (184 pp).

Balme, 1995. Fossil in situ spores and pollen grains: an annotated catalogue. Review of Palaeobotany and Palynology 87, 81–323.

Barth, S., Mohr, B.A.R., 1994. Palynostratigraphically determined age of the Tregiovo sedimentary complex in relation to radiometric emplacement ages of the Athesian Volcanic Complex. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 192, 273–292.

Bauer, K., Kustatscher, E., Butzmann, R., Fischer, T.C., 2014. Ginkgophytes from the upper Permian of the Bletterbach Gorge (Northern Italy). Rivista Italiana di Paleontologia e Stratigrafia 120, 271–279.

Beerling, D.J., Berner, R.A., 2005. Feedbacks and the coevolution of plants and atmospheric CO_2. Proceedings of the National Academy of Sciences 102, 1302–1305.

Beerling, D.J., Royer, D.L., 2002. Fossil plants as indicators of the Phanerozoic global carbon cycle. Annual Review of Earth and Planetary Sciences 30, 527–556.

Beerling, D.J., Lake, J.A., Berner, L., Hickey, J.D., Taylor, W., Royer, D.L., 2002. Carbon isotope evidence implying high O_2/CO_2 ratios in the Permo–Carboniferous atmosphere. Geochimica et Cosmochimica Acta 66(21), 3757–3767.

Berner, R.A., 2003. The long-term carbon cycle, fossil fuels and atmospheric composition. Nature 426, 323–326.

Berner, R.A., 2004. The Phanerozoic carbon cycle: CO_2 and O_2. Oxford University Press, Oxford.

Berner, R.A., Beerling, D.J., Dudley, R., Robinson, J.M., Wildman, R.A., 2003. Phanerozoic atmospheric oxygen. Annual Review of Earth and Planetary Geosciences 31, 105–134.

Berner, R.A., Petsch, S.T., Lake, J.A., Beerling, D.J., Popp, B.N., Lane, R.S., Laws, E.A., Westley, M.B., Cassar, N., Woodward, F.I., Quick, W.P., 2000. Isotope fractionation and atmospheric oxygen: implications for Phanerozoic O_2 evolution. Sciences 287, 1630–1633.

Berra, F., Felletti, F., 2011. Syndepositional tectonics recorded by soft-sediment deformation and liquefaction structures (continental Lower Permian sediments, Southern Alps, Northern Italy): stratigraphic significance. Sedimentary Geology 235, 249–263.

Berra, F., Felletti, F., Tessarollo, A., 2016. Stratigraphic architecture of a transtensional continental basin in low-latitude semiarid conditions: The Permian succession of the central Orobic Basin (Southern Alps, Italy). Journal of Sedimentary Research 86, 408–429.

Bocherens, H., Friis, E.M., Mariotti, A., Pedersen, K.R., 1993. Carbon isotopic abundances in Mesozoic and Cenozoic fossil plants: palaeoecological implications. Lethaia 26, 347–358.

Broutin, J., Kerp, H., 1994. Aspects of Permian palaeobotany and palynology. XIV. A new form-genus of broad-leaved Late Carboniferous and Early Permian Northern Hemisphere conifers. Review of Palaeobotany and Palynology 83, 241–251.

Buggisch, W., Krainer, K., Schaffhauser, M., Joachimski, M., Korte, C., 2015. Later Carboniferous to Late Permian carbon isotope stratigraphy: A new record from post-Variscan carbonates from the Southern Alps (Austria and Italy). Palaeogeography, Palaeoclimatology, Palaeoecology 433, 174–190.

Buggisch, W., Wang, X, Alekseev, A.S., Joachimski, M.M., 2011. Carboniferous–Permian carbon isotope stratigraphy of successions from China (Yangtze platform), USA (Kansas) and Russia (Moscow Basins and Urals). Palaeogeography, Palaeoclimatology, Palaeoecology 301, 18–38.

Cassinis, G., 1966. La Formazione di Collio nell'area-tipo dell'alta Val Trompia (Permiano inferiore bresciano). Rivista Italiana di Paleontologia e Stratigrafia 72, 567–590.

Cassinis, G., Doubinger, J., 1991. On the geological time of the typical Collio and Tregiovo continental beds in the Southalpine Permian (Italy), and some additional observations. Atti Ticinesi di Scienze della Terra 34 pp. 1–20.

Cassinis, G., Doubinger, J., 1992. Artinskian to Ufimian palynomorphs assemblages from the Central Southern Alps, Italy and their regional stratigraphic implications. In: Nairn, A.E.M., Koroteev, V., (Eds.), Contributions to Eurasian Geology, Papers Presented at the International Congress Permian System of the World, Part I. University of South Carolina, Columbia, pp. 9–18.

Cassinis, G., Neri, C., 1992. Sedimentary and palaeotectonic evolution of some Permian continental basins in central Southern Alps, Italy. Cuad. Geol. Iber. 16, 145–176.

Cassinis, G., Nicosia, U., Pittau, P., Ronchi, A., 2002. Palaeontological and radiometric data from the Permian continental deposits of the Central-Eastern Southern Alps (Italy), and their stratigraphic implications. In: Deroin J.-P. (Ed.), Entre Laurussia et Gondwana. Le Permien d'Europe et d'Afrique du Nord. Mémoire de l'Association des Géologues du Permien, 2, Septembre, 53–74.

Cecil, C.B., 2003. The concept of autocyclic and allocyclic controls on sedimentation and stratigraphy, emphasizing the climatic variable. SEPM Special Publication 77, 13–20.

Clement-Westerhof, 1984. Aspects of Permian palaeobotany and palynology. IV. The conifer *Ortiseia* Florin from the Val Garderna Formation of the Dolomites and the Vicentinian Alps (Italy) with special reference to a revised concept of the Walchiaceae (Goppert) Schimper. Review of Palaeobotany and Palynology 41, 51–66.

Clement-Westerhof, J.A., 1987. Aspects of Permian palaeobotany and palynology. VII. The Majonicaceae, a new family of Late Permian conifers. Review of Palaeobotany and Palynology 52, 375–402.

Clement-Westerhof, 1988. Morphology and phylogeny of Paleozoic conifers. In: Beck, C. (Eds.), Origin and Evolution of Gymnosperms. Columbia University Press, New York, pp. 298–337.

Cohen, K.M., Finney, S.C., Gibbard, P.L., Fan, J.-X. 2013. The ICS International Chronostratigraphic Chart. Episodes 36, 199–204. http://www.stratigraphy.org/ICSchart/ChronostratChart2017-02.jpg 28.08.2017

Conti, M.A., Mariotti, N., Manni, R., Nicosia, U., 1999. Tetrapod footprints in the Southern Alps: an overview. In: Cassinis, G., Cortesogno, L., Gaggero, Massari, F., Neri, C., Nicosia, U., Pittau, P., (Eds.), Stratigraphy and Facies of the Permian Deposits between Eastern Lombardy and the Western Dolomites. Field trip guidebook (Appendix), 23–25 September 1999. Earth Sciences Department, Pavia University, pp. 137–138.

Conti, M.A., Mariotti, N., Nicosia, U., Pittau, P., 1997. Succession of selected bioevents in the continental Permian of the Southern Alps (Italy): improvements in intrabasinal and interregional correlations. In: Dickins, J.M. Yang, Z.Y., Yin, H.F., Lucas, S.G., Acharyya, S.J., (Eds.), Late Palaeozoic and Early Mesozoic Circum–Pacific Events and their Global Correlation. Cambridge University Press, Cambridge, pp. 51–65.

Dal Corso, J., Preto, N., Kustatscher, E., Mietto, P., Roghi, G., Jenkyns, H.C., 2011. Carbon-isotope variability of Triassic amber, as compared with wood and leaves (Southern Alps, Italy). Palaeogeography, Palaeoclimatology, Palaeoecology 302, 187–193.

Dal Corso, J., Schmidt, A.R., Seyfullah, L.J., Preto, N., Ragazzi, E., Jenkyns, H.C., Delclòs, X., Nèraudeau, D., Roghi, G., 2017. Evaluating the use of amber in palaeoatmospheric reconstructions: The carbon-isotope variability of modern and Cretaceous conifer resins. Geochimica et Cosmochimica Acta 199, 351–369.

Della Porta, G., 2015. Carbonate buildups in lacustrine, hydrothermal and fluviatile settings: comparing depositional geometry, fabric types and geochemical signature. In: Bosence, D.WJ., Gibbons, K.A., Le Heron, D.P., Morgan, W.A., Pritchard, T., Vining, B. (Eds.) Microbial Carbonates in Space and Time: Implications for Global Exploration and Production. Geological Society, London, Special Publications, 418, 17–68.

Demicco, R.V., Hardie, L.A., 1994. Sedimentary structures and early diagenetic features of shallow marine carbonate deposits. SEPM Atlas series, 1, Tulsa, Oklahoma, USA, 265 pp.

de Wit, M.J., Gosh, J.G., de Villiers, S., Rakotosolofo, N., Alexander, J., Tripathi, A., Looy, C., 2002., Multiple organic carbon isotope reveals across the Permo–Triassic boundary of terrestrial Gondwana sequences: clues to extinction patterns and delayed ecosystem recovery. The Journal of Geology 110, 227–240.

DiMichele, W.A., 2014. Wetland-Dryland vegetational dynamics in the Pennsylvanian Ice Age Tropics. International Journal of Plant Sciences 175(2), 123–164.

DiMichele, W.A., S.H., Mamay, D.S., Chaney, R.W., Hook, 2001. An Early Permian flora with Late Permian and Mesozoic affinities from north- central Texas. Journal of Paleontology 75, 449–460.

DiMichele, W.A., Hook, R.W., Nelson, W.J., Chaney, D.S., 2004. An unusual Middle Permian flora from the Blaine Formation (Pease River group, Leonardian–Guadalupian series) of King County, west Texas. Journal of Paleontology 78, 765–782.

DiMichele, W.A., Tabor, N.J., Chaney, D.S., Nelson, W.J., 2006. From wetlands to wet spots: environmental tracking and fate of Carboniferous elements in Early Permian tropical floras. In: Grab, S.F., DiMichele, W.A., (Eds.), Wetlands Through Time. Geological Society of America Special Paper 399, pp. 223–248.

DiMichele, W.A., Kerp, H., Tabor, N.J., Looy, C.V., 2008. The so-called "Paleophytic-Mesophytic" transition in equatorial Pangea – Multiple biomes and vegetational tracking of climate change through geological time. Paleogeography, Palaeoclimatology, Palaeoecology 268, 152–163.

DiMichele, W.A., Montañez, I.P., Poulsen, C.J., Tabor, N.J., 2009. Climate and vegetational regime shifts in the late Paleozoic ice age earth. Geobiology 7(2), 200–226.

DiMichele, W.A., Cecil, C.B., Chaney, D.S., Elrick, S.D., Lucas, S.G., Lupia, R., Nelson, W.J., Tabor, N.J., 2011. Pennsylvanian–Permian vegetational changes in tropical Euramerica, in Harper, J.A., (Eds.) Geology of the Pennsylvanian–Permian in the Dunkard basin: Guidebook, 76th Annual Conference of Pennsylvanian Geologists, Washington, PA, p. 60–102.

Falcon-Lang, H.J., Kurzawe, F., Lucas, S., 2014. Coniferopsid tree-trunks preserved in sabkha facies in the Permian (Sakmarian) Community Pit Formation in south-central New Mexico, U.S.A. Systematics and palaeoecology. Review of Palaeobotany and Palunology 200, 138–160.

Falcon-Lang, H.J., Nelson, J., Heckel, P., DiMichele, W.A., Elrick, S., 2017. New insignts on the stepwise collapse of the Carboniferous Coal Forests: Evidence from cyclothems and coniferopsid tree-strumps near the Demoinesian-Missourian boundary in Peoria

County, Illinois, USA. Palaeogeography, Palaeoclimatology, Palaeoecology 490, 375–392.

Faure, K., Wit, W.J., Willis, J.P., 1995. Late Permian cola hiatus linked to ^{13}C-depleted CO_2 flux into the atmosphere during the final consolidation of Pangea. Geology 23(6), 507–510.

Forte, G., Kustatscher, E., Van Konijnenburg – van Cittert, J.H.A., Looy, C.V., Kerp, H., 2017. Conifer diversity in the Kungurian of Europe – Evidence from dwarf-shoot morphology. Review of Palaeobotany and Palynology. 10.1016/j.revpalbo.2017.01.004

Forte, G., Kustatscher, E., Van Konijnenburg – van Cittert, J.H.A., Kerp, H., submitted. Diversity in *Sphenopteris* fronds from the Kungurian of Tregiovo (Trento, NE-Italy). Review of Palaeobotany and Palynology.

Frakes, L.A., Francis, J.E., Syktus, J.I., 1992. Climate modes of the Phanerozoic. New York: Cambridge University Press, 274 pp.

Fritz, A., Krainer, K., 2006. Eine Rotliegendflora aus dem Seesedimenten des Bozner Vulkanitkomplexes bei Sinnich (Südtirol). GeoAlp 3, 33–45.

Glikson, M., Taylor, G.H., 1986. Cyanobacterial mats; major contributions to the organic matter in Toolebuc Formation oil shales. In: Contributions to the Geology and Hydrocarbon Potential of the Eromanga Basin (Eds.) D.I. Gravestock, P.S. Moore and G.M. Pitt, Geological Society of Australia Special Publication 12, 273–286.

Hayes, J.M., Strauss, H., Kaufman, A.J., 1999. The abundance of ^{13}C in marine organic matter and isotopic fractionation in the global biogeochemical cycle of carbon during the past 800 Ma. Chemical Geology 161, 103–125.

Hernandez-Castillo, G.R., Rothwell, G.W., Stockey, R.A., Mapes, G., 2003. Growth architecture in *Thucydia mahoningensis*, a model for primitive walchian conifer plants. International Journal of Plant Sciences 164, 443–452.

Horton, D.E., Poulsen, C.J., Montañez, I.P., DiMichele, W.A., 2012. Eccentricity-paced late Paleozoic climate change. Palaeogeography, Palaeoclimatology, Palaeoecology 331–332, 150–161.

Isbell, J.L., Miller, M.F., Wolfe, K.L., Lenaker, P.A., 2003. Timing of the late Palaeozoic glaciation in Gondwana: was glaciation responsible of the development of northern hemisphere cyclothems? In: Chan, M.A., Archer, A.W. (Eds.), Extreme Depositional Environments: Mega End Members in Geologic Time. Geol. Soc. Of Am. Spec. Pap., vol. 370, pp. 5–24.

Jones, A. T., Fielding, C. R., 2004. Sedimentological record of the late Paleozoic glaciation in Queensland, Australia. Geology, 32, 153–156.

Kerp, H., 1996. Post-Variscan late Palaeozoic Northern Hemisphere gymnosperms: the onset to the Mesozoic. Review of Palaeobotany and Palynology 90, 263–285.

Kidder, D.L., Worsley, T.R., 2004. Causes and consequences of extreme Permo–Triassic warming to globally equable climate and relation to the Permo–Triassic extinction and recovery. Palaeogeography, Palaeoclimatology, Palaeoecology 203, 207–237.

Klaus, W., 1963. Sporen aus dem südalpinen Perm (Vergleichsstudie für die Gliederung nordalpiner Salzserien). Jahrb. Geol. Bundesanst. (Austria), 106, 229–363.

Klaus, W., Mostler, 1983. Alpine Middle and Upper Triassic Pb-Zn deposits. In International Conference on Mississippi Valley-type lead-zinc Deposits – Proc. Vol., G. Kisvarsanyi, S.K. Grant, W.P. Pratt, J.W. Koenig (Eds.), p. 113–128. Rolla, Missouri: Iniv. Missouri Rolla Press.

Knoll, A.H., 1984. Patterns of extinction in the fossil record of vascular plants, In M. H. Nitecki (Eds.), Extinctions. University of Chicago Press, Chicago, 21–68 pp.

Kump, L.R., Brantley, S.L., Arthur, M.A., 2000. Chemical weathering, atmospheric CO_2 and climate. Annual Review of Earth and Planetary Sciences 28, 611–667.

Kustatscher, E., Bauer, K., Butzmann, R., Fischer, T.C., Meller, B., Van Konijnenburg-van Cittert, J.H.A., Kerp, H., 2014. Sphenophytes, pteridosperms and possible cycads from Wuchiapingian (Lopingian, Permian) of Bletterbach (Dolomites, Northern Italy). Review of Palaeobotany and Palynology 208, 65–82.

Kustatscher, E., Van Konijnenburg-van Cittert, J.H.A., Bauer, K., Butzmann, R., Meller, B., Fischer, T.C., 2012 2012. A new flora from the Upper Permian of Bletterbach (Dolomites, N-Italy). Review of Palaeobotany and Palynology 183, 1–13.

Labandeira, C.C., Kustatscher, E., Wappler, T., 2016. Floral assemblages and patterns of Insect herbivory during the Permian to Triassic of Northeastern Italy. PLoS ONE DOI:10.1371/journal.pone.0165205

Liu, C., Jarochowska, E., Du, Y., Vachard, D., Munnecke, A., 2017a. Stratigraphic and δ13C records of Permo–Carboniferous platform carbonates, South China: Responses to late Paleozoic icehouse climate and icehouse–greenhouse transition. Palaeogeography, Palaeoclimatology, Palaeoecology 474, 113–129.

Looy, C.V., 2007. Extending the range of derived Late Paleozoic conifers: *Lebowskia* gen. nov. (Majonicaceae). Internationa Journal of Plant Sciences 168, 957–972.

Looy, C.V., Hotton, C.L., 2014. Spatiotemporal relationships among Late Pennsylvanian plant assemblages: Palynological evidence from the Markley Formation, West Texas, U.S.A. Review of Palaeobotany and Palynology 211, 10–17.

Looy, C.V., Stevenson, R.A., 2014. Earliest occurrence of autorotating seeds in conifers: the Permian (Kungurian–Roadian) *Manifera talaris* gen. *et* sp. nov. International Journal of Plant Sciences 175(7), 841–854.

Looy, C.V., Kerp, H., Duijnstee, I.A.P., DiMichele, W.A., 2014. The late Paleozoic ecological-evolutionary laboratory, a land-plant fossil record perspective. The Sedimentary Record 12(4), 4–10.

Mädler, K., 1992. Die Rotliegend–Zechstinflora von Lieth bei Elmshorn, Schkeswig-Holstein. Geologisches Jahrbuch, A 133, 3–31.

Marchetti, L., Forte, G., Bernardi, M., Wappler, T., Harkopf-Fröder, C., Krainer, K., Kustatscher, E., 2015. Reconstruction of a Late Cisuralian (Early Permian) floodplain lake environment: Palaeontology and sedimentology of the Tregiovo Basin (Trentino-Alto Adige, Northern Italy). Palaeogeography, Palaeoclimatology, Palaeoecology 440, 180–200.

Marocchi, M., Morelli, C., Mari, V., Klötzli, U., Bargossi, G.M., 2008. Evolution of large silicic magma systems: new U-Pb zircon data on the NW Permian Athesian Volcanic Group (Southern Alps, Italy). Journal of Geology 116, 480–498.

Michel, L.A., Tabor, N.J., Montañez, I.P., Schmitz, M.D., Davydov, V.I., 2015. Chronostratigraphy and paleoclimatology of the Lodève Basin, France: evidence for a pan-tropical aridification event across the Carboniferous–Permian boundary. Palaeogeography, Palaeoclimatology, Palaeoecology 430, 118–131.

Montañez, I.P., Poulsen, C.J., 2013. The Late Paleozoic ice age: an evolving paradigm. Annu. Rev. Earth Planet. Sci. 41, 629–656.

Montañez, I.P., Tabor, N.J., Niemeier, D., DiMichele, W.A., Frank, T.D., Fielding, C.R., Isbell, J.L., Birgenheier, L.T., Rygel, M., 2007. CO_2-forced climate and vegetation instability during Late Paleozoic glaciation. Science 315, 87–91.

Morelli, C., Bargossi, G.M., Mair, V., Marocchi, M., Moretti, A., 2007. The Lower Permian volcanics along the Etsch Valley from Meran to Auer (Bozen). Mitteilungen. Österreichische Geologische Gesellschaft 153, 129–152.

Neri, C., Avanzini, M., Bampi, T., Bargossi, G.M., Mair, V., Morelli, C., Pittau, P., Ronchi, A., Sapelza, A., 1999. The Tregiovo area and related volcanics in the Tregiovo section. In: Cassins, G., Cortesogno, L., Gaggero, L., Massari, F., Neri, C., Nicosia, U., Pittau, P., (Eds.), Stratigraphy and Facies of the Permian Deposits Between Eastern Lombardy and the Western Dolomites Field Trip Guide (Appendix), 23–25 Sept 1999. Pavia University, Earth Sciences Department, pp. 81–89.

O'Leary, M.H., 1988. Carbon isotopes in photosynthesis. Bioscience 38, 328–336.

Olszewiski, M.E., Patzkowsky, M.E., 2003. From cyclothems to sequences: record of eustacy and climate on an icehouse eperic platform (Pennsylvanian – Permian, North American Midcontinent). J. Sediment. Res. 73, 15–30.

Peters–Kottig, W., Strauss, H., Kerp, H., 2006. The land plant δ^{13}C record and plant evolution in the Late Palaeozoic. Palaeogeography, Palaeclimatology, Palaeoecology 240, 237–252.

Peyser, C.E., Poulsen, C.J., 2008. Controls on Permo–Carboniferous precipitation over tropical Pangea: a GCM sensitivity study. Palaeogeogr. Palaeoclimatol. Palaeoecol. 268, 181–192.

Pfefferkorn, H.W., Mustafa, H., Hass, H., 1975. Quantitative Charakterisierung oberkarboner Abdruckfloren. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 150, 253–269.

Rankey, E.C., 1997. Relations between relative changes in sea level and climate shifts: Pennsylvanian – Permian mixed carbonate–siliciclastic strata, western United States. Geol. Soc. Amer. Bull. 109, 1089–1100.

Remy, W., Remy, R., 1978. Die Flora des Perm im Trompia-Tal und die Grenze Saxon/Thuring in den Alpen. Argumenta Palaeobotanica 5, 57–90.

Rocher, M., Schneider, J.W., 2006. Permo-Carboniferous climate: Early Pennsylvanian to Late Permian climate development of central Europe in a regional and global context. Geological Society of London, Special Publications 265, 95–136.

Rowe, N.P., 2000. The insides and outsides of plants: the long and chequered evolution of secondary growth. In: Spatz, H.-C., Speck, T. (Eds.), Plant biomechanics 2000.

Proceedings of the 3rd plant biomechanics conference, Freiburg–Badenwiler. Theime, Stuttgart, New York, pp. 129–140.

Rygel, M.C., Fielding, C.R., Franl, T.D., Birgenheier, L.P., 2008. The magnitude of Late Paleozoic glacioeustatic fluctuations: a synthesis. Journal of Sedimentary Research 78, 500–511.

Schneider, J.W., Körner, F., Roscher, M., Kroner, U., 2006. Permian climate development in the northern peri-Tethys area – The Lodève basin, French Massif Central, compared in a European global context. Palaeogeography, Palaeoclimatology, Palaeoecology 240, 161–183.

Scotese, C.R., 2014. Atlas of Permo-Carboniferous Paleogeographic Maps (Mollweide Projection), Maps 53–64, Volumes 4, The Late Paleozoic, PALEOMAP Atlas for ArcGIS, PALEOMAP Project, Evanston, IL.

Strauss, H., Peter-Kottig, W., 2003. The Paleozoic to Mesozoic carbon cycle revisited: The carbon isotopic composition of terrestrial organic matter. Geochemistry, Geophysics, Geosystems 10, 1525–2027.

Tabor, N.J., Montañez, I.P., 2004. Morphology and distribution of fossil soils in the Permo–Pennsylvanian Wichita and Bowie Group, north-central Texas, USA: implications for western equatorial Pangean palaeoclimate during icehouse-greenhouse transition. Sedimentology 51, 851–884.

Tabor, N.J., Poulsen, C.J., 2008. Palaeoclimate across the Late Pennsylvanian–Early Permian tropical palaeolatitudes: A review of climate indicators, their distribution, and relation to palaeophysiographic climate factors. Palaeogeography, Palaeoclimatology, Palaeoecology 268, 293–310.

Taylor, T.N., Taylor, E.L., Krings, M., 2009. Paleobotany: the Biology and Evolution of Fossil Plants. Academic. Press 1252 pp.

Tyson, R.V., 1995. Sedimentary Organic Matter – Organic facies and palynofacies. Chapman & Hall, London p. 615.

Uhl, D, Kerp, H, 2002a. Die Makroflora des ostthüringischen und sächsischen Zechsteins: Stand der Forschung und Ausblick. Veroeff Mus Naturkunde Gera 29, 44–63.

Uhl, D., Kerp, H., 2005. Variability of stomatal density and index in the Upper Permian conifer *Quadrocladus* Mädler – a taphonomical case study. Palaeogeography, Palaeoclimatology, Palaeoecology 218, 205–215.

Uhl, D., Lausberg, S., 2008. Land plant diversity in selected latest Pennsylvanian? – Permian deposits form the Saar-Nahe Basin (SW–Germany) and the German Zechstein Basin. Studia Geologica Polonica, Krakòw, 129, 81–106.

Veizer, J., Ala, D., Azmy, K, Bruckschen, P., Buhl, D., Bruhn, F., Carden, G.A.F., Diener, A., Ebneth, S., Godderis, Y., Jasper, T., Korte, C., Pawellek, F., Podlaha, O.G., Strauss, H., 1999. $^{87}Sr/^{86}Sr$, $\delta^{13}C$ and $\delta^{18}O$ evolution of Phanerozoic seawater. Chemical Geology, 161, 59–88.

Visscher, H., Kerp, H., Clement-Westerhof, J.A, Looy, C.V., 2001. Permian floras of the Southern Alps. Natura Bresciana, Museo Civico di Scienze Naturali, Brescia, Monografia 25 pp. 117–123.

Wang, K., Geldsetzer, H.H.J., Krouse, H.R., 1994. Permian-Triassic extinction: organic $\delta^{13}C$ evidence from British Columbia, Canada. Geology 22, 580–584.

Wing, S.L., DiMichele, W.A, 1995. Conflict between local and global changes in plant diversity through geological time. Palaios 10, 551–564.

Yans, J., Gerards, T., Gerrienne, P., Spagna, P., Dejax, J., Schnyder, J., Storme, J., Keppens, E., 2010. Carbon-isotope analysis of fossil wood and dispersed organic matter from the terrestrial Wealden facies of Hautrage (Mons Basin, Belgium). Palaeogeography, Palaeoclimatology, Palaeoecology 291, 85–105.

Zhang, H., Shen, G., He, Z., 1999. A carbon isotopic stratigraphic pattern of the late Palaeozoic coals in the North China Platform and its palaeoclimatic implications. Acta Geologica Sinica, 72(1), 111–119.

Ziegler, A.M., Hulver M.L., Rowley, D.B., 1997. Permian world topography and climate. In: Martini, I.P. (Ed.), Late Glacial and Post-Glacial Environmental Changes – Quaternary, Carboniferous–Permian and Proterozoic. Oxford University Press, Oxford, pp. 111–146.

CHAPTER 4

The Tregiovo conifers – a morphological and geochemical study

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Abstract

The fossil locality "Le Fraine" near Tregiovo village (Trento Province, N-Italy) yielded one of the few well-documented Kungurian floras of the eastern palaeoequatorial Pangea. Two rich plant assemblages (respectively A and B), both dominated by conifers but with different floral compositions are known. A $\delta^{13}C$ curve from bulk organic carbon shows a negative shift along the section with the most negative values of the curve corresponding to the upper floral assemblage (assemblage B). This work focuses on the most representative plant group of Tregiovo, the conifers. We performed a taxonomical and morphological study on the conifer foliate shoots, with the aim to increase the knowledge on the distribution and diversification of this important group of plants in the Kungurian of eastern palaeoequatorial Pangea. Four taxa of conifers, namely *Feysia* sp., *Quadrocladus* sp., *Hermitia* sp. and *H. geinitzii* were determined on the basis of branch morphology and leaf morphometry. Moreover, a taxon-specific study on the carbon stable isotopic composition of Tregiovo conifer coalified tissues showed that there are no significant differences between different taxa of conifers from the same plant assemblage, but conifers of the same taxon have lighter isotopic composition in the upper floral assemblage. This confirmed the negative shift recorded by the carbon of bulk organic matter and allowed to exclude the possibility that it resulted from a change in floral cpmposition along the section. The δ^{13}C curve of Tregiovo correlates with coeval continental records in other Permian sites (e.g., China, South Africa), which suggests that it may have recorded a global change of the carbon atmospheric composition.

Keywords: Permian, Cisuralian, Kungurian, plant fossils, $\delta^{13}C_{org}$

1. Introduction

1.1. Permian climate and environmental changes

The Late Pennsylvanian to early Permian (323–272 million years ago) was characterized by major palaeogeographic and climate changes. The last phases of the assembly of the supercontinent Pangea lead to the formation of a long and wide mountain chain, the Central Pangean Mountains (CPM), which extended from WSW to ENE across Pangea (Ziegler, 1997). The Late Palaeozoic Ice Age (LPIA), which lasted from ~ 335 to 256 Ma, resulted in the most severe glaciation in the Phanoerozoic (e.g., Isbell, et al., 2003; Jones and Fielding, 2004; Montañez et al., 2007; Tabor et al., 2008). The waxing and waning of the multiple ice sheets located in the southern emisphere produced sea level oscillations, which reorganized land and sea areas (e.g., Heckel, 1977, 1986, 1990; Veevers and Powell, 1987; Rankey, 1997; Olszewski and Patzkowsky, 2003; Rygel et al., 2008; Heckel 2008). The step-wise transition from an icehouse to a greenhouse world, which took place during late Carboniferous–Cisuralian times, is reflected in the equatorial Euramerican realm by climate oscillations characterized by wetter and dryer periods (e.g., Montañez et al., 2007; DiMichele et al., 2008, 2009; Tabor and Montañez, 2004; Roscher and Schneider, 2006; Schneider et al., 2006; Peyser and Poulsen, 2008; Tabor and Poulsen, 2008; Horton et al., 2012; Montañez and Poulsen, 2013; Michel et al., 2015), likely in synchrony with glacial-interglacial cycles, and possibly driven by Milanckovich forcing (van den Belt et al., 2015).

The collision between the continents of Gondwana and Laurasia, which led to the formation of the CPM (Central Pangean Mountains) and the supercontinent Pangea, contributed to the fragmentation and the reduction of the lowland floras, dominated by spore producing plants like arborescent lycophytes, sphenophytes and tree-ferns and seed plants such as seed ferns and cordaitaleans (e.g., DiMichele et al., 2001, 2006, 2008, 2009, 2011; Rees et al., 2002), which characterized the palaeoequatorial regions during most of Carboniferous time (DiMichele and Phillips, 1994, 1996). As a result of the aridification, the wetland area shrank and more drought-tolerant communities that formerly occupied extrabasinal, well-drained environments, started gradually to be more widespread, migrating into the lowland environments (e.g., DiMichele and Aronson, 1992; DiMichele et al., 2000; Looy et al., 2014).

Among the seasonally dry floras that spread during the Permian floristic transition, conifers played an important role, becoming dominant elements of the Euramerican landscapes (e.g., Rothwell et al., 1997; Rees, 2002; DiMichele et al., 2008). The replacement of the wetland floras with these communities dominated by seed plants that were less water dependent was a stepwise process, which pregressed from the western to the eastern parts of palaeoequatorial Pangea (e.g., Knoll, 1984; DiMichele, 2014; DiMichele et al., 2001, 2008). Both the deglaciation and change in global vegetation cover strongly influenced the atmospheric CO_2 concentration and the isotopic composition of carbon in the atmosphere (e.g., Arens, et al., 2000; Beerling et al., 2002; Berner, 2003; Peters-Kottig et al., 2006; Montañez et al., 2007; Tabor and Poulsen, 2008; Montañez et al., 2016).

During the Cisuralian the $\delta^{13}C$ of atmospheric carbon started to increase, as recorded by marine carbonates (e.g., Hayes et al., 1999; Veizer et al., 1999; Liu et al., 2017a) and terrestrial organic matter (e.g., Faure et al., 1995; Zhang et al., 1999; Peters-Kottig et al., 2006). Later, from the Guadalupian (272–259 Ma) onwards, the values started to decrease (e.g., Peters-Kottig et al., 2006). This shift could have been caused by several processes, such as minor burial of the organic matter in terrestrial sediments (Berner et al., 2003), increasing weathering (Peters-Kottig et al., 2006), climatic and tectonic changes related to the last phases of the consolidation of Pangea (e.g., Faure et al., 1995; Kerp, 1996; Kidder and Worsley, 2004), and/or the release of the ^{13}C-depleted methane from clathrate deposits (de Wit et al., 2002).

1.2. Paleozoic conifers

The earliest evidence for conifers are small shoot fragments in Middle Pennsylvanian sediments from the Illinois Basin and Yorkshire (e.g., Plotnik et al., 2009; Falcon-Lang et al., 2009; Galtier et al., 1992). These plants were likely growing on well-drained substrates along the wetland vegetation in areas adjacent to basins (Gothan and Gimm, 1930; Barthel, 1976). From the Late Pennsylvanian, floras rich in the so-called walchian conifers (walchian Voltziales, *sensu* Rothwell et al., 2005) became more common in the Euramerican floral realm (e.g., Clement-Westerhof, 1984, Mapes and Rothwell, 1991; Rothwell et al., 1997). Based on the size of the penultimate branches, the Pennsylvanian walchians are reconstructed as relatively small trees (Hernandez-Castillo et al., 2003). They are characterized by a plagiotropic branching pattern, linear needle-like to narrow triangular leaves and stomata aligned in bands or rows (e.g., Hernandez-Castillo et al., 2001a, 2003, 2009a, 2009b, 2009c; Rothwell et al., 2005). In western Euramerica (Texas, New Mexico) even more drought-tolerant floras characterized by more derived voltzian conifers (voltzian Voltziales), occur in the equatorial lowlands from the Kungurian onwards. Voltzian conifers have ovate to linear leaves, irregularly patterned, orthotropic branch system and seed cones or fertile zones that are distinctively different from those of walchian conifers (Rothwell et al., 2005). The voltzians are the only lineage of coniferophytes that survive the end-Permian mass extinction (252 Ma; e.g., Poort et al., 1996).

The Permian thus represents an important time for the evolution of conifers. Up to now, the evidence for the walchian-voltzian transition during the Cisuralian mostly comes from western Pangea (e.g., DiMichele et al., 2001, 2004; Looy, 2007; Looy and Duinstee, 2013; Hernandez-Castillo et al., 2014; Looy et al., 2014; Falcon-Lang et al., 2015), whereas Permian conifer occurrences in eastern Pangea are few, especially from the Artinskian–Kungurian (e.g., Remy and Remy 1978. Visscher et al., 2001; Barthel et al., 2010)

The discovery of two new Kungurian plant assemblages from the “Le Fraine” section in NE-Italy (Tregiovo, Trento province, Trentino-Alto Adige region), provides new insights on Kungurian conifer communities in this floral realm (Marchetti et al., 2015; Forte et al., 2017). The Tregiovo flora stands out because it contains vegetative and reproductive material of both walchian and voltzian conifers (Forte et al., 2017). The assemblage includes numerous isolated leaves, foliated (pen) ultimate shoots, but also dispersed ovuliferous dwarf-shoots and cones. A study of dwarf shoots indicated the presence of at least five different conifer species (Forte et al., 2017). The dwarf shoots 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 walchian conifers (e.g., Rothwell et al., 2005), to stalked forms with fused sterile scales and sporophylls, comparable with early to late

Permian voltzian taxa (e.g., Clement-Westerhof, 1987; Schweitzer, 1996; Looy 2007; Looy and Stevenson, 2014).

It is more complicated to establish the botanical affinity of the isolated leaves and shoots. These vegetative plant parts are not found in connection with the reproductive material, and the absence of cuticles rules out the association of such organs based on epidermal features (e.g., Clement-Westerhof, 1987).

The first aim of this work is to increase the knowledge of Permian conifers, since this group had a major role in Permian ecosystems. This has been done by 1) providing a taxonomical-morphological study of the Tregiovo conifers on the basis of the foliate shoots and 2) comparing the Tregiovo taxa with other Permian conifers. Moreover, we also made a taxon-specific geochemical study of the conifer coalified tissues, in order to obtain an isotopic characterization of the conifer taxa, and to investigate the significance of the shift recorded by stable carbon isotopes of bulk organic matter at Tregiovo (Forte et al., sumbitted). In particular, we aim to determine if the difference in bulk isotopic composition between the two plant horizons is due to different taxonomic composition, or is a reflection of different external environmental factors imprinted on all elements of each flora.

2. Material and methods

2.1. Geological setting and material

The material studied here comes from the Tregiovo Basin in the Italian Southern Alps. The Tregiovo Basin is located in a ca. 2 km wide tectonic depression bounded by the Giudicarie Line to the west and by the Foiana Line to the east (Cassinis and Neri, 1990), within the Athesian Volcanic Complex (Fig. 1). The sedimentary fill of the basin has a variable thickness of 0–200 m, which, according to Neri et al. (1999), suggests that volcanism and tectonism were not completely absent during its time of deposition. The Tregiovo Formation is Kungurian in age. This can be determined because the formation is intercalated between the volcanic Gargazzone and Ora formations, which are dated, based on radiometric U/Pb zircon geochronology, respectively at 276.5 ± 1.1 Ma and 274.1 ± 1.6 Ma (Avanzini et al., 2007; Marocchi et al., 2008).

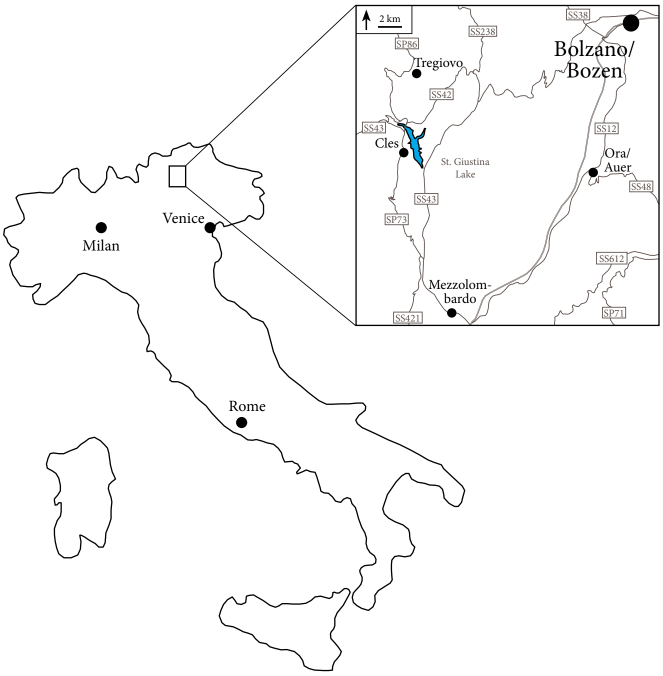

Fig. 1. Location of Tregiovo village.

The old type section, which crops out near the small village of Tregiovo between Trento and Bolzano provinces in the Trentino-Alto Adige region, was studied by geologists in the 19th century (Vacek, 1882, 1894; Vacek and Hammer, 1911), and later investigated for its fossil content, including plant macroremains, palynomorphs, both vertebrate and invertebrate fossil tracks and conchostracans (Mostler 1966; Remy and Remy, 1978; Cassinis and Doubinger, 1991, 1992; Cassinis and Neri, 1992; Barth and Mohr, 1994; Conti et al., 1997, 1999; Neri et al., 1999; Visscher et al., 2001; Marchetti et al., 2015; Forte et al., 2017). After road work in the 1990s, the section was covered by nets and blocked off by walls, and is no longer accessible (Marchetti et al., 2015). A new section was discovered along the Tregiovo – Lauregno provincial road, also near the village of Tregiovo. This is called "Le Fraine" section, and it is ca. 130 m thick (Fig. 2; Marchetti et al., 2015). The lower and central parts of the section consist of very dark thinly laminated clays and mudstones, and are interpreted as organic-rich (more than 1% of Total Organic Carbon) playa-lake deposits (Forte et al., submitted). At some levels, the sediments are pyritised, which indicates anoxic to sub-oxic conditions at the bottom of the lake or within the first few cm of sediment. The upper part of the section consists of laminated silt- and claystones that are more cemented by carbonates than the lower part, but carbonates never exceed 10% (Forte et al., in press).

Two plant fossil horizons correspond to finely laminated clay and mudstones respectively at 45 and 105 m from the base of the "Le Fraine" section (Marchetti et al., 2015). The plant assemblages are preserved as impressions/compressions without cuticles and include sphenophytes (*Annularia*), ferns and/or seed ferns (cf. *Lodevia*, *Peltaspermum*-like discs, *Sphenopteris*), putavite ginkgophytes (cf. *Sphenobaiera*), taeniopterids (*Taeniopteris*) and two incertae sedis taxa, here informally indicated as Morphotypes 1 and 2. Both the lower and upper plant assemblages (A and B in Fig., 2) are dominated by vegetative (shoots and leaves) and reproductive material (cones and isolated dwarf-shoots) of conifers (Forte et al., 2017). The vegetative conifer remains from the lower assemblage (assemblage A) include 120 isolated shoots, of which 4 preserve two or three orders of branching. Fewer conifer fossils were recovered from the upper assemblage (assemblage B), namely 63 isolated shoots and 4 branches. The vegetative conifer material from assemblage A was identified as *Hermitia geinitzii*, *Hermitia* sp., *Feysia* sp. and *Quadrocladus* sp. by Forte et al. (2017).

Fossil plants from “Le Fraine” were collected by a local collector, Mr. Ferruccio Valentini (Tuenno in Trento Province, Italy). Part of this collection is temporarily stored at the Museo delle Scienze of Trento (MUSE) and labelled with the prefix MUSE PAG followed by a progressive number, whereas part (Collezione Valentini) is still temporarily stored at the collector.

Twelve additional plant specimens were collected during the seventies from the old Tregiovo type section by different collectors. They were studied by Remy and Remy (1978) and reviewed by Visscher et al. (2001). This material is stored in the palaeobotanical collections of the Museo Civico di Scienze Naturali of Brescia (Brescia Province, Lombardy Region, N-Italy); the specimens are labelled with the prefix “PA” followed by progressive but not consecutive numbers (00058–91).

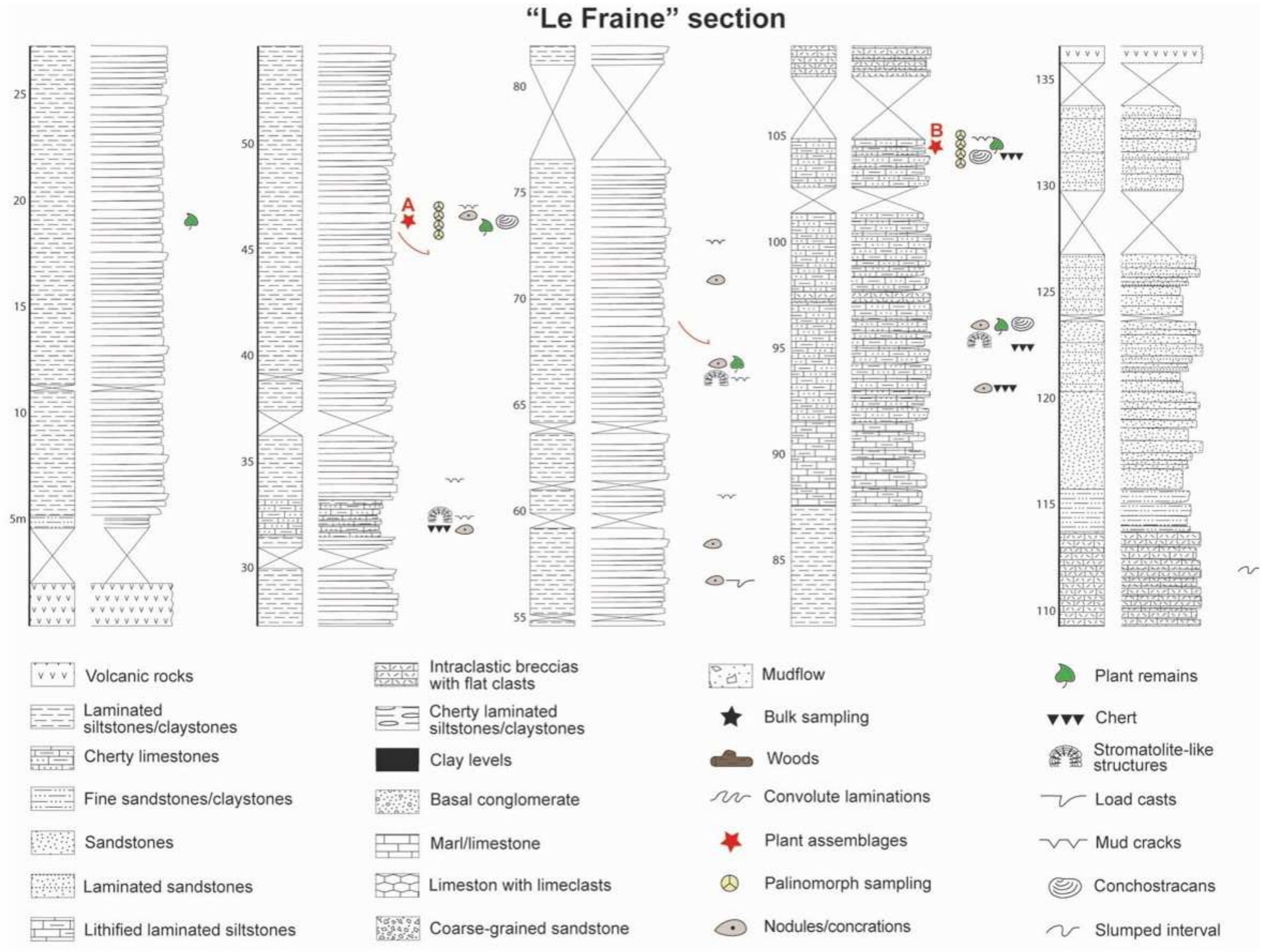

Fig. 2. Detailed log of the "Le Fraine" section (modified from Marchetti et al., 2015)

2.2. Morphometric analysis of conifer shoots

Conifer shoots of the “Le Fraine” section were photographed using a Canon EOS 550D camera. The best preserved shoots of the collection were analyzed using the free software ImageJ64® (National Institutes of Health, Bethesda, MD). We measured: 1) the distance between the apex and the base of the leaves (L); 2) the width of the leaves in face view (W); and 3) the angle between the main axis and the leaves at the point of inflexion (A) (Fig. 3).

To identify the different types of leaves, we referred to de Laubenfels (1953), which provides a classification of conifer leaves morphologies, distinguishing among: Type I, leaves that are distinctly tetragonal in cross-section with a falcate profile; Type II, linear or lanceolate bilaterally flattened leaves with a straight profile; Type III, scale leaves that are wider than thick; and Type IV, that groups broad, ovate, flat, multi-veined leaves. Several other leaf characters were recorded including 1) the shape of the leaf apex (acute or obtuse), the attachment to the axis (decurrent or rhomboid), leaf arrangement (helically arranged or opposite), and whether the leaves are imbricated or not. Only a few specimens show the branching architecture. In most of the cases, specimens are single branches, which may suggest that a transport contributed to their fragmentation or that branches were abscised by the plant. Nonetheless, leaf margins are almost not damaged, thus we can presume that the material was not subjected to a long transport.

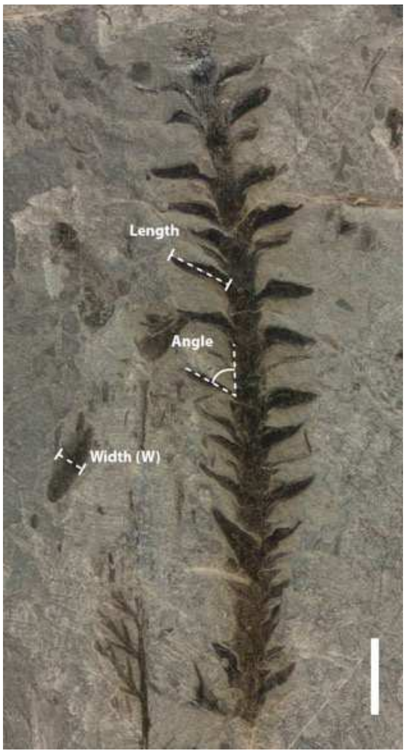

Fig. 3. Lenght, width and angle measured on a specimen of *Feysia* sp.

2.3. Geochemical analyses

Carbon stable isotopic analyses were performed on the coalified tissues of 50 specimens of Tregiovo conifers, sphenopterids, and fragments of coal, exclusively from the material from "Le Fraine" section.

Coalified tissues were sampled from at least two or three parts of the same specimen, such as from the leaves and from the stem, in order to capture the isotopic variability within a specimen. For each sample of coal and coalified tissues, ca. 35 µg of material were weighted in silver cups and then etched two times with 20 µl of HCL 10% on a heating plate at 70°C, in order to remove carbonate minerals. When dried, silver cups were wrapped and analyzed at the Geochemical Laboratory of the Department of Geoscience of the University of Padova, with a Thermo Flash 2000 Elemental Analyzer connected to a Thermo Delta V Advantage Isotope Ratio Mass Spectrometer. The results were normalized with two international standards: CH-6 (–10.449‰ VPDB) and CH-7 (–32.151‰ VPDB). A further quality assurance standard (ZER, C3 plant sucrose) was run along with the samples and yielded an internal reproducibility of 0.16‰ (standard deviation based on >20 repetitions).

3. Systematic palaeontology

3.1. Genus *Hermitia* Kerp et Clement-Westerhof 1986

Two different morphotypes attributable to the genus *Hermitia* Kerp et Clement-Westerhof 1986 have been recovered from the "Le Fraine" section. Nonetheless, only one could be determined to species level. The other has been determined at a genus level because of the limited preservation of the plant remains.

Plate. I. Specimens of conifers from the “Le Fraine” section of Tregiovo: 1–2. *Hermitia* sp.; 3. *Hermitia geinitzii*; 4. a specimen of *Hermitia* sp. withan almost 90° leaf angle. Scale bar is 1 cm.

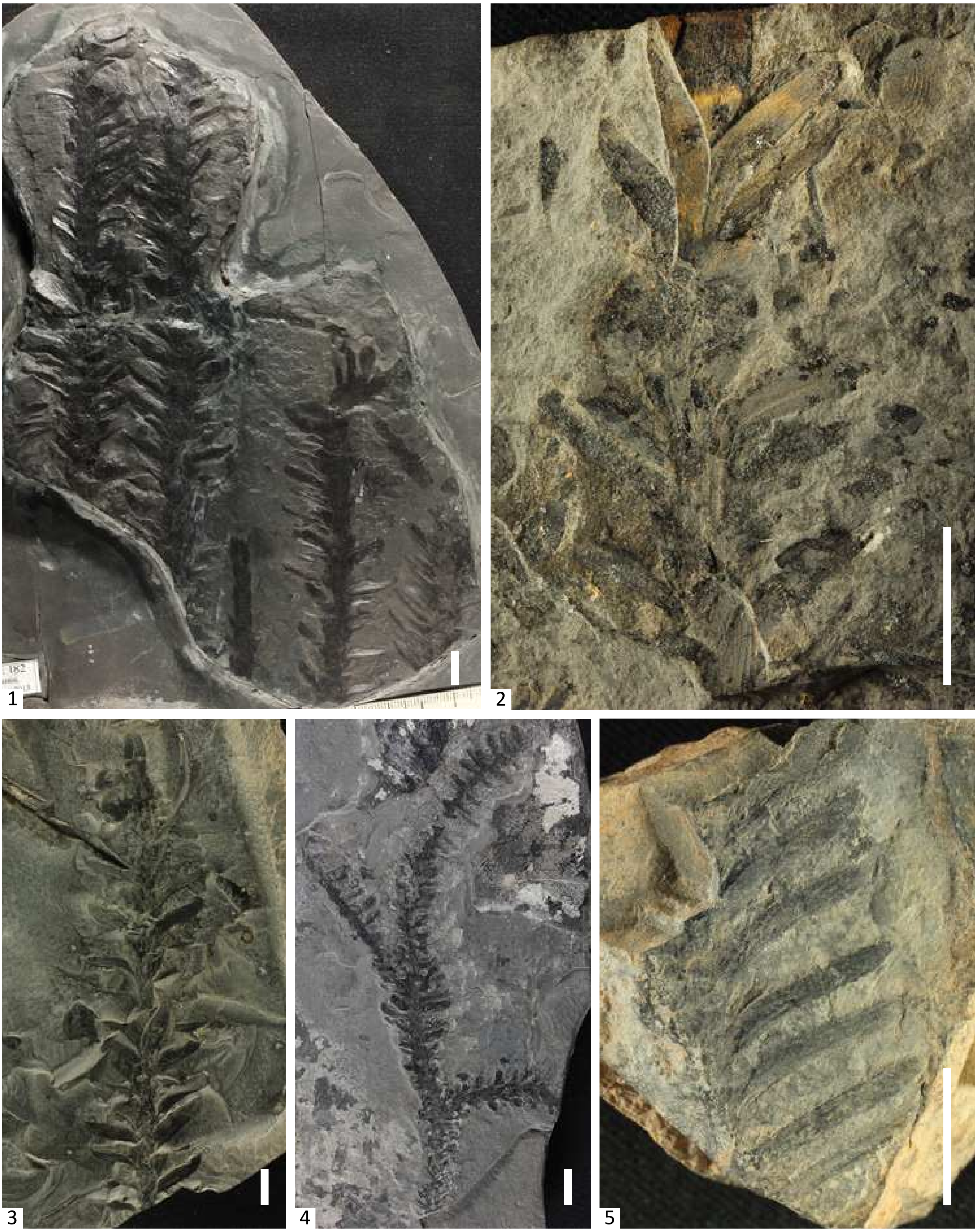

Plate II. Conifers of Tregiovo: 1. *Feysia* sp.; 2. Specimen of *Feysia* sp. with visible parallel rows on the leaves; 3. *Feysia* sp. from the old section of Tregiovo, specimen from the old section of Tregiovo; 4. *Quadrocladus* sp. from “Le Fraine” section; 5. *Quadrocladus* sp. from the old section of Tregiovo. Scale bar is 1 cm.

3.1.2. *Hermitia geinitzii* (Florin) Kerp et Clement-Westerhof 1986

Description: Hermitia geinitzii is represented by 13 isolated shoots, and one 7.8 cm long penultimate plagiotropic branch. Ultimate branches are irregularly alternating at angles 40–70 degrees (e.g. P1600851). The foliated ultimate shoots are up to 40 mm in length and depart at angles of roughly 45–70°. Ultimate leaves are helically arranged, round to oval in face view, have a round to obtuse apex, and are up to 1.5–2.5 mm long and 1.5–3 mm wide (Pl. I, Fig. 3; Table 1b). The leaves have a thick basal cushion, which tapers to a short free curved tip that extends less than or equal to the length of the cushion. The leaves of the ultimate shoots are bifacial, triangular but slightly concave in profile view, ovate in face view with a round apex, 2–3 mm long and 1 mm wide at the base. Remy and Remy (1978) analyzed the same material, and described the ultimate leaves as being triangular in shape and 4 mm long and 3 mm wide, 2 mm thick at the base in profile view, round to oval with a round apex in face view.

Discussion: Dispersed foliate shoots of *H. geinitzii* only occur in the assemblage A of the “Le Fraine” section. The species is easily recongnizable due to the typical small, rounded, often wider than long oval shape of the leaves.

Hermitia geinitzii was originally described by Florin (1939) as *Walchia* (?*Lebachia*) *geinitzii* based on a penultimate branch system. Visscher et al. (1986) emended the genera *Walchia* and *Hermitia* and moved several species to the genus *Hermitia*, among which was *Walchia geinitzii* (Visscher et al., 1986). Several authors mentioned this species as *Hermitia*/*Walchia geinitzii* from the lower Permian Collio Formation of the Collio Basin in the Southern Alps (upper Val Trompia, northern Italy; Cassinis et al., 1966; Remy & Remy, 1978; Visscher et al., 2001).

3.1.3. *Hermitia* sp.

Description: The specimens assigned to *Hermitia* sp. are represented by 130 isolated foliated shoots and one plagiotropic penultimate branch system, which cannot be assigned to any species because of their poor preservation. The branch system is 23 cm long with alternatively inserted ultimate shoots up to 12 cm long that arise at an angle of 70° from the axis (Pl. I, Fig. 2). Penultimate leaves are triangular in profile view, 1 mm wide at the base, with keel; the face view is unknown. Leaves of ultimate shoots are linear, s-shaped and spirally arranged, 1.7–8.5 mm long and 1.3–1.6 mm wide (Table 1b).

Discussion: The specimens of *Hermitia* sp. occur in both assemblages of “Le Fraine”. The material is pretty fragmented and the specimens are represented often by short shoot fragments. Two forms have been recognized among the Tregiovo specimens. The first form is represented by shoot fragments with very adpressed triangular, needle-like leaves, that arise from the axes with an angle that never exceeds 30°, and mostly resemble *Walchia piniformis* Sternberg 1825 emended Clement-Westerhof 1984 (Pl. I, Fig. 1). The second form is characterized by fragments of shoots, the leaves of which are s-shaped in lateral view, and arise from the axes with an angle of ca. 90° (Pl. I, Fig. 4). For the overall morphology this second form resembles *Ernestiodendron filiciforme* (Sternberg) Florin 1934 emended Clement-Westerhof 1984. Nonetheless, *E. filiciforme* is characterized by longer than wider very falcate leaves. This might suggest that *Hermitia* sp. group of Tregiovo might lump together two different taxa. Unfortunately, because of the high fragmentation and poor preservation of the material, we cannot exclude that the two forms of *Hermitia* belong to different stages of development of the same species or are the result of heterophylly. Thus, we here assign these two forms to the genus *Hermitia,* erected by Kerp et Clement-Westerhof (1986) to accommodate several species that were previously assigned to the genus *Walchia* but that have no epidermal features preserved and therefore can only be diagnosed in terms of leaf morphology (Visscher et al., 1986).

3.2. Genus *Feysia* Broutin et Kerp 1994

3.2.1. Feysia sp.

At Tregiovo, *Feysia* sp. is represented by 42 isolated foliate shoots, some of which have the branch tip preserved (e.g. MUSE PAG 7096, 7364; Table 1a), and a partial plagiotropic branch system. The leaves are helically arranged, non- or hardly-decurrent, 11 mm long and 4 mm wide on average. They are lanceolate in face view, slightly restricted at the base and with an obtuse to rounded apex (Pl. II, Fig., 1–3, MUSE PAG 7096). Leaves in profile view are linear or s-shaped, with tips curved toward the axis; they arise from the axis at a variable angle (from 25 to 85°). In some of the best preserved specimens (e.g. PA–00071; PA–00062) parallel rows can be discerned on the leaf surfaces (Pl. II, Fig. 2,). They could be attributed to veins or rows of stomata. Within the de Laubenfels (1953) classification, *Feysia* from Tregiovo can be attributed to Type IV, which includes broad, ovate, flat, multi-veined leaves. Parallel rows that have been observed in *Feysia* from Tregiovo, however, do not occur in any Type IV leaves of de Laubenfels (1953; figs. 58–62).

Discussion: Conifer foliate shoots attributable to *Feysia* sp. occur in both assemblages of "Le Fraine" (A and B), and constitute the most abundant conifer taxon representing the 54% of all conifer specimens. The genus *Feysia* was erected by Broutin and Kerp (1994) for broad leaved conifers taxa with "a distichous branching pattern and broad, bifacial, non- or hardly decurrent leaves". Two species, *F. minutifolia* and *F. puntii*, were described based on lower Permian material respectively from northern Africa (Tiddas Basin, Morocco) and Germany (Saar Nahe Basin, southern Germany; Broutin and Kerp, 1994). *Feysia* leaves are spirally arranged, triangular, oblong to obovate in face view, constricted at the base, with leaf apices that sometimes slightly curve towards the axis (Broutin and Kerp, 1994). The leaves of the two taxa differ in size, diameter and type of leaves of the axis of ultimate order, with *F. puntii* being more robust than *F. minutifolia* (Broutin and Kerp, 1994). Because of the fragmentation and preservation of the Tregiovo material, we refrain from any attribution at species level. The broad-leaved morphology and size of the *Feysia* specimens of Tregiovo overall resembles the two late Permian genera *Ulmannia* Göppert 1850 and *Ortiseia* Florin 1964, respectively from the Zechstein of western and central Europe (Schweitzer 1962, 1986), and from the Gröden/Val Gardena Sandstone of the Southern Alps (Florin, 1964). This is of particular interest since broad-leaved conifers were previously considered derived forms restricted to the late Permian, when they formed a very common element of the floras (e.g., Broutin and Kerp, 1994). However, discoveries of the last tens of years have shown that these conifers were already common during the early Permian, from the western to the eastern part of Pangea.

Vegetative morphology	***Feysia* sp. (this paper)**	***Ortiseia leonardii***	***Feysia minutifolia***	***Feysia puntii***	***Quadrocladus* sp. (this paper)**	***Lebowskia grandifolia***	***Quadrocladus solmsii***	***Quadrocladus orobiformis***
Ultimate branching arrangement	plagiotropic	plagiotropic	plagiotropic	plagiotropic	irregular	–	–	–
Mode attachment	decurrent	Non-decurrent	Non-slightly decurrent	Non-slightly decurrent	Non-decurrent	decurrent	decurrent	Non-decurrent
Angle insertion ultimate shoot	25–85	20–45	45–90	50–90	28–110	30	45	90
Ultimate leaf (face view)	Ovate, lanceolate	Triangular, oblong, ovate	Triangular, oblong, obovate	Oblong-obovate	linear	Linear, narrow oblanceolate	linear	linear
Ultimate leaf (profile view)	Linear to s-shaped	Slightly lanceolate	Linear to s-shaped	Linear to s-shaped	Linear to s-shaped	–	–	–
Ultimate leaf apex	Obtuse, rounded	Acute, obtuse	Obtuse	Obtuse, rounded	Obtuse, rounded	Obtuse	Obtuse	Obtuse
Leaf margin	smooth	smooth	smooth	smooth	Smooth?	smooth	smooth	smooth
Ultimate leaf in cross-section	–	rhomboid	–	–	–	Thin, flattened	rounded	Diamond
Ultimate leaf length (mm)	Mean 11	11 (35 penult.?)	3.5	Max. 7	4–28	19–110	10–20	20–35
Ultimate leaf width (mm)	Mean 4	4 (6–35 penult.?)	1.3	Max. 3	–	2–6	2–3	2–3
Leaf dimorphism on the same braches	–	no	no	no	yes	yes	May occur?	May occur?
Epidermal features								
Adaxial stomata	–	Rows, double rows	–	–	–	Scattered	scattered (or in short unclear rows)	scattered (sometimes app. in rows)
Abaxial stomata	–	Rows	–	–	–	Scattered	scattered (or in short unclear rows)	scattered (some apparent in rows)
Structure stomata complex	–	Dicyclic to inc. tricyclic	–	–	–	Monocyclic	mono- to inc. dicyclic	mono- to inc. dicyclic
Number subsidiary cells	–	5–5 (4–8)	–	–	–	5–6 (3–8)	4–5 (3–7)	4–5 (3–6)

Table 1a. Comparison between vegetative morphology of *Feysia* sp., *Quadrocladus* sp., *Hermitia* sp. and *Hermitia geinitzii* from Tregiovo and other Permian conifer taxa. It continues in table 1b

Vegetative morphology	**Majonica alpina**	***Dolomitia cittertiae***	***Voltzia hexagona***	***Ullmannia frumentaria***	***Ullmannia bronni***	***Pseudovoltzia liebeana***	***Ernestiodendron filiciforme***	***Hermitia* sp. (this paper)**	***Hermitia geinitzii***	***Hermitia geinitzii* (this paper)**
Ultimate branching arrangement	–	–	Irregular	irregular	irregular	–	plagiotropic	Plagiotropic	plagiotropic	Plagiotropic
Mode attachment	decurrent	decurrent	Decurrent	decurrent	Slightly decurrent	decurrent	Non-decurrent	Decurrent, non-decurrent	Non decurrent	Non decurrent
Angle insertion ultimate shoot	–	–	50–55	45–60	–	45	70–110	23–90	40–60	40–70
Ultimate leaf (face view)	Ovate, lanceolate	Ovate, oblong, lanceolate	Linear, triangular	Triangular, lanceolate	Ovate, lanceolate	Narrow triangular, lanceolate	Narrow triangular to linear	–	ovate	Ovate, round
Ultimate leaf (profile view)	?	?	Slightly concave	Falcate to slightly s-shaped	–			linear	Triangular	Linear
Ultimate leaf apex	Obtuse	Obtuse	Acute	Acute, obtuse	–	Acute	Acute?	Acute?	Rounded	Obtuse, rounded
Leaf margin	Smooth		Smooth	Smooth, serrated	Smooth (?)	Smooth (serrated)	–	–	Shooth	Smooth
Ultimate leaf in cross-section	–		Diamond	Diamond	–	–	–	–	Diamond	–
Ultimate leaf length (mm)	Max- 35	Max. 20	60–150	12–35	5–15	11–51	10–23	1.7–8.5	2–3	1.5–2.5
Ultimate leaf width (mm)	Max. 6	Max. 4	5–6	2–5	1.5–7	2–5	1.5–3.5	1.3–1.6	1	1.5–3
Leaf dimorphism on the same braches	May occur?	?	yes	–	–	Yes	no	No	No	no
Epidermal features										
Adaxial stomata	Interrupted rows	Interrupted rows	Rows	Rows (interrupted rows)	Rows, scattered	Rows (interrupted rows)	Parallel rows	–	–	–
Abaxial stomata		Scattered	Rows	Rows (interrupted rows)	Rows, scattered	Rows (interrupted rows)	Parallel rows	–	–	–
Structure stomata complex	Monocyclic	Monocyclic	–	Monocyclic	Monocyclic	Monocyclic	Monocyclic, incomplete dicyclic	–	–	–
Number subsidiary cells	7–8(5–10)	7–8(5–10)	–	5–7 (4–10)	6–12	6–7 (4–11)	4–8	–	–	–

Table 1b. See caption Table 1a.

3.3. Genus *Quadrocladus* Mädler 1957

3.3.1. Quadrocladus sp.

Description: Quadrocladus sp. is represented by 84 isolated shoots, and 2 specimens preserving two or three orders of (irregular) branching (e.g. MUSE PAG 7273, Pl. II, Fig. 4). Leaves are non-decurrent, helically arranged, likely linear in front view and linear to slightly s-shaped in profile view, with a smooth margin and rounded or obtuse apex. They arise from the axis at a variable angle, which ranges from 28 to 110°, and heterophylly occurs. On specimen (PA-00090) parallel rows are visible on the leaves (Pl. II, Fig. 5), whereas on some other specimens it is possible to see some small wrinkles on the leaves, suggesting that the leaves were succulent. Referring to de Laubenfels (1953) classification, *Quadrocladus* sp. can be considered within Type II, which groups linear or lanceolate bilaterally flattened leaves with a straight profile.

Discussion: *Quadrocladus* sp. occurs both in the lower and the upper assemblages. Eightysix shoots belong to this type, which represents 17 % of all Tregiovo conifers.

Leaves with preserved epidermal features of *Quadrocladus* Mädler 1957 are well known from the Lopingian of Europe and Russia (e.g., Mädler, 1957; Schweitzer, 1962; Meyen, 1997; Uhl and Kerp, 2005b; Kustetscher et al., 2012). Moreover, the reproductive organ *Sashinia* Meyen, 1978 from Angara has been associated with the vegetative parts of the genus *Quadrocladus* (e.g., Meyen 1987, 1997; Clement-Westerhof, 1988). Two typical Lopingian species of Central Europe are *Quadrocladus solmsii* (Gothan et Nagalhard 1921) Schweitzer 1962 and *Q. orobiformis* (Schlotheim 1820) Schweitzer 1962. In the Tregiovo specimens, although the range of leaf-length is considerable (Tab. 1a; 4–27 mm), it falls within the range of *Q. orobiformis*. Nonetheless, since we are missing more distinctive characters, including the epidermal composition, we do not consider the length of leaves sufficient for a specific attribution.

In the general morphology, Tregiovo *Quadrocladus* leaves from Tregiovo also might resemble *Lebowskia grandifolia* Looy 2007. This species is only known so far from the Cisuralian of north-central Texas (Lower Pease River flora; Looy, 2007). *Lebowskia* is characterized by vegetative shoots with helically arranged linear to narrow oblanceolate leaves with obtuse apex that arise from the axis at an angle of 30°. Despite this general similarity of the leaves*,* the leaves of *Lebowskia* may reach a length of 110 mm (Looy, 2007), which is much longer than those of any European

Quadrocladus species. For all these reasons, we refrain from attributing the Tregiovo material to any species.

	N	Assemblage A		N	Assemblage B	
		Average	St. dev.		Average	St. dev.
***Feysia* sp.**	9	–22.31	1.19	16	–24.01	0.56
***Quadrocladus* sp.**	11	–21.62	1.05	14	–24.56	1.21
***Hermita* sp.**	4	–19.93	0.87	6	–23.58	0.10
Hermitia geinitzii	6	–20.93	1.03	–	–	–
Bulk	4	–21.30	1.41	4	–24.13	0.95

Table 2. Averages and standard deviations of the δ^{13}C of the bulk organic matter and conifer taxa respectively from the assemblages A and B of "Le Fraine" section. N indicates the number of samples.

4. Geochemistry of the Tregiovo conifers

Coalified tissues were collected from samples of each conifer genus from Tregiovo, which include are *Feysia* sp., *Quadrocladus* sp., *Hermitia* sp. and *Hermitia geinitzii*. For the first three taxa, samples have been collected from specimens that occur in both assemblages A and B, whereas for *Hermitia geinitzii*, occurs only occurs in assemblage A. The δ^{13}C values obtained for each taxon show a wide scatter in both assemblages, with standard deviations of 1.41‰ in assemblage A and 0.95‰ in assemblage B (Table 2). This spread is more pronounced in *Feysia* sp. from assemblage A and *Quadrocladus* sp. from assemblage B, which have standard deviations well above 1‰ (Table 2), whereas *Hermitia* sp. in assemblage B has the lowest standard deviation 0.09‰ (Table 2).

There are no clear isotopic differences between the taxa. Instead, a clear overlapping is visible in each of the assemblages (Fig. 4). A significant difference instead occurs between the same taxon from different assemblages (Fig. 4), with conifers from assemblage B being more negative than conifers from assemblage A. The isotopic composition of coalified tissues compare differently with the bulk in the two assemblages. The conifers from assemblage A have an average δ^{13}C of –22.31‰, very close to the average of the bulk that is –22.30‰ (Table 2; Fig. 4). Conversely, in assemblage B, the δ^{13}C values of the conifers are more negative, on average, than the average δ^{13}C of the bulk organic carbon (Fig. 4).

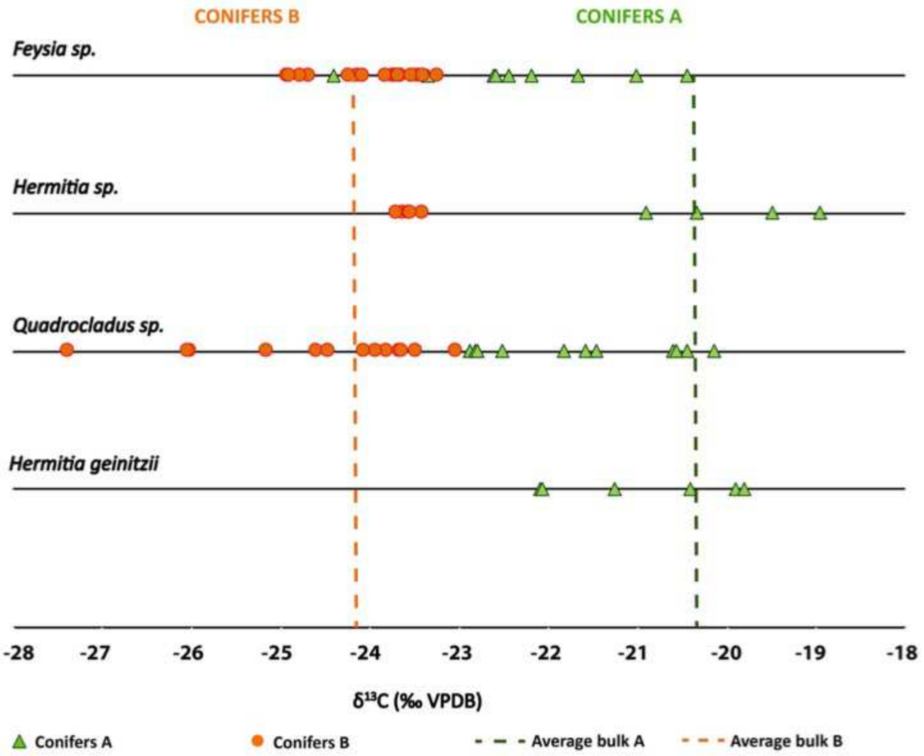

Fig. 4. Carbon stable isotopic composition of conifers from assemblages A and B. On each line the values of each single taxon are given, whereas the dashed vertical lines represent the average $\delta^{13}C$ of the bulk organic matter. Orange: upper assemblage (B); green: lower assemblage (A).

5. General discussion and conclusions

Conifers are the most abundant group in both the assemblages of the "Le Fraine" section and show a certain diversity of species, both considering vegetative shoots and dwarf-shoots (Forte et al. 2017). The discovery indeed of five different morphologies of conifer dwarf-shoots supports the presence of at least five different conifer taxa. In this work we studied the leaf morphology of the sterile material, in order to see whether same or a greater diversity would be found in the foliage shoots than is found among the dwarf-shoots. Moreover, a taxon-specific geochemical analysis on the coalified tissues of conifers was carried out. This had the aim to: 1) determine if an isotopic characterization of different taxa of conifers was possible, and 2) use the isotopic values of conifers as a comparison tool to check the $\delta^{13}C$ isotopic shift recorded by Forte et al. (in press) from the bulk material collected along the two sections ("Le Fraine" and Tregiovo village section) of Tregiovo (Fig. 5; Forte et al., in press).

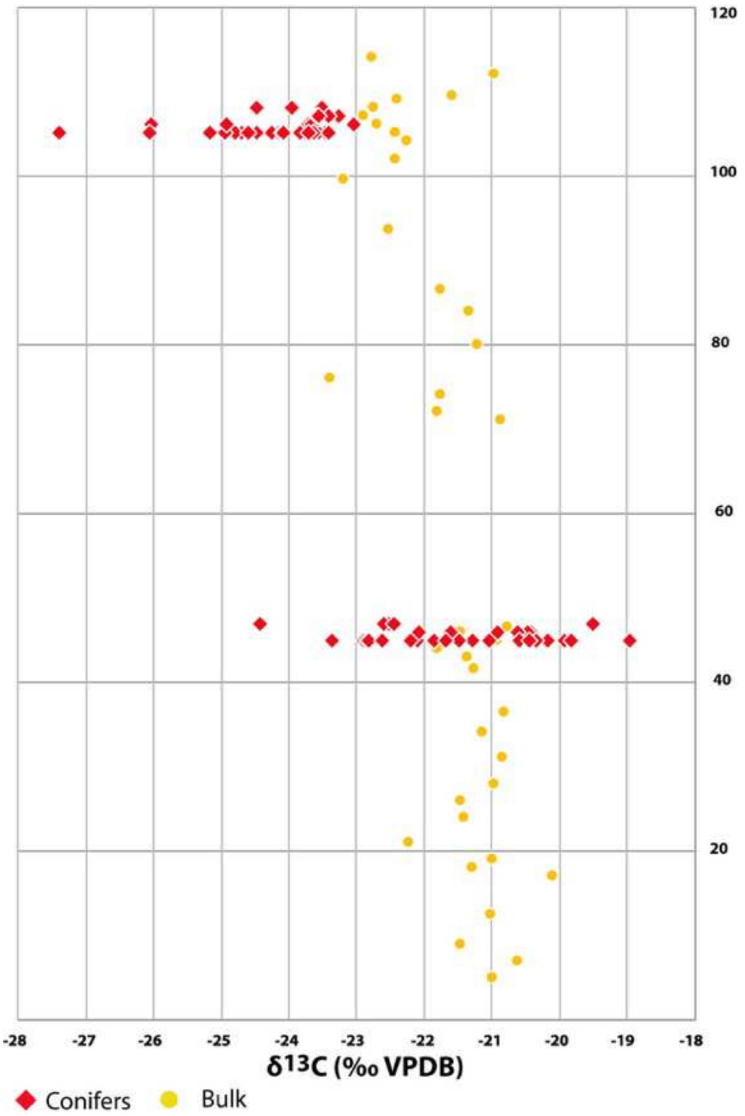

Fig. 5. “Le Fraine” δ^{13}C curve with the isotopic values from conifers A and B.

The taxonomical study on the foliate shoots was made difficult by the imperfect preservation. Fossils are compression/impressions and the tissues, when present, are strongly coalified, thus no cuticles could be separated. The conifer remains are often fragmented and almost complete branching systems are rare. The taxonomical study of foliate plant material was thus possible on the basis of morphology and morphometric analysis of leaves and terminal branches. Despite these limitations, four different taxa have been identified based on the foliate shoots, three of them, *Feysia* sp., *Quadrocladus* sp. and *Hermitia* sp. at genus level, and *Hermitia geinitzii* at the species level. The morphology of leaves conifrms the co-occurrence, in the Tregiovo flora, of walchian and voltzian conifers (Forte et al. 2017). Moreover, two different forms were distinguished within *Hermitia* sp. that might correnspond to two different species. We suspect that the Tregiovo conifer diversity is greater than found in the present study, but the degree of preservation of the material does not allow a finer taxonomical classification.

The carbon stable isotopic taxon-specific analyses on the Tregiovo coalified tissues proved very revealing. The isotopic values of the different taxa are dispersed, but overlap within the same association. This suggests that the analyzed taxa were not discriminating differently for carbon isotopes at Tregiovo (Fig. 4). This observation compares well with the notion that C3 plants within the same type of ecosystem discriminate uniformly (e.g., Kaplan and Colin Prentice, 2002). This wide range of isotopic composition within each of the taxa might be due to the fact that we collected tissues from several leaves at different distances from the apex of the axis and also from the axis itself. Thus the wide range could represent the isotopic diversity of all the specimens analysed for a certain taxon. Moreover, at the assemblage level, the range of the isotopic values of the taxa that occur in both assemblages (e.i. *Feysia* sp., *Hermitia* sp. and *Quadrocladus* sp.) are all more negative in assemblage B (Fig. 4).

Since the δ^{13}C values of bulk organic carbon recorded from the two sections of Tregiovo are within the range of the C3 plants, and given the fully continental depositional environment, the isotopic values of the bulk should be strongly influenced by the terrestrial plant isotopic composition. It was thus expected that the negative shift (more than 1‰) from the base of the “Le Fraine” section toward the upper part should be recorded also by plant tissues.

However, such a remarkable isotopic shift could have been caused by several factors. Two main hypotheses can be postulated. The first one is that the negative shift, recorded by the Tregiovo sediments, could represent a change in the isotopic composition of the atmospheric CO_2, which in turn influenced the δ^{13}C of the terrestrial organic matter. The other hypothesis is that the negative shift of Tregiovo recorded the change in the floral composition through time, i.e. the increase of seed ferns and sphenopterids and parallel decrease of conifers in assemblage B (see the discussion in Forte et al., in press). In this second hypothesis, variation in the abundance of plant groups with different carbon fractionation could have influenced the δ^{13}C of the bulk organic carbon. The first hypothesis, i.e. a global decrease of atmospheric δ^{13}C, would be supported by the findings of a negative shift in the terrestrial and marine organic carbon isotopic composition from other Kungurian localites (e.g., Faure et al., 1995; Zhang et al., 1999; Peters-Kottig et al., 2006; Liu et al., 2017a, 2017b). Nonetheless, it would be risky to make a clear correlation between the Tregiovo $\delta^{13}C_{bulk}$ curve and the ones in literature (Faure et al., 1995; Zhang et al., 1999; Peters-Kottig et al., 2006; Liu et al., 2017a, 2017b), because the latter cover a longer interval of time and, in the

Kungurian, are represented by smaller number of samples than Tregiovo (lower sampling resolution).

Here we have shown that the isotopic compositions of three different conifer taxa are more negative in the upper assemblage B than in assemblage A. This means that the negative shift could not be linked to a change of floral composition between the two assemblages. We thus infer that the negative shift in the $\delta^{13}C$ must be related to either a change in the isotopic composition of atmospheric carbon, or to some external environmental factors that influenced the isotopic discrimination of all conifer species at Tregiovo, and was thus reflected in the isotopic composition of bulk organic carbon (Fig. 5). Recently, Liu and colleagues provided the stratigraphical and $\delta^{13}C$ records of South China Permo-Carboniferous platform carbonates, where they found a negative $\delta^{13}C$ excursion in the Kungurian (Liu et al., 2017a) with the same amplitude recorded by the Tregiovo sediments (ca. 4–5‰). In their hypothesis, a climatic event took place in the tropical/subequatorial belt that gave rise to major changes in the global carbon cycle which resulted in the descending trend of $\delta^{13}C$. In the light of these results, we are led to think that the $\delta^{13}C$ negative shift at Tregiovo recorded a global perturbation of the carbon cycle in the Kungurian.

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References

Arens, N.C., Jahren, A.H., Amundson, R., 2000. Can C3 plants faithfully record the carbon isotopic composition of atmospheric carbon dioxide? Paleobiology 26(1), 137–164.

Avanzini, M., Bargossi, G., Borsato, A., Castiglioni, G.B., Cucato, M., Morelli, C., Prosser, G., Sapelza, A., 2007. Note illustrative della Carta Geologica d'Italia alla scala 1:50.000, Foglio 026 Appiano. Servizio Geologico d’Italia APAT, Dipartimento Difesa del Suolo, Roma (184 pp.)

Barth, S., Mohr, B.A.R., 1994. Palynostratigraphically determined age of the Tregiovo sedimentary complex in relation to radiometric emplacement ages of the Athesian Volcanic Complex (Permian, Southern Alps, N Italy). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 192(2), 273–292.

Barthel, M., 1976. Die Rotliegendflora Schsens. Abh. Staatl. Mus. Min. Geol. Dresden 24, 1–190.

Barthel, M., Eichler, B., Reichel, W., 2010. The Lower Permian (Rotliegend) flora of the Weissig Basin. Geologica Saxonica 56(2), 159–192.

Beerling, D.J., Lake, J.A., Berner, L.J., Taylor, D.W., Royer, D.L., 2002. Carbon isotope evidence implying high O2/CO2 ratios in the Permo-Carboniferous atmosphere. 66(21), 3757–3767.

Berner, R.A., Beerling, D.J., Dudley, R., Robinson, J.M., Wildman, R.A., 2003. Phanerozoic atmospheric oxygen. Annual Review of Earth and Planetary Geosciences 31, 105–134.

Bocherens, H., Friis, E.M., Mariotti, A., Pedersen, K.R., 1993. Carbon isotopic abundances in Mesozoic and Cenozoic fossil plants: palaeoecological implications. Lethaia 26, 347–358.

Broutin, J., Kerp, H., 1994. Aspects of Permian Palaeobotany and Palynology. XIV. A new form-genus of broad-leaved Late Carboniferous and Early Permian Northern Hemisphere conifers. Review of Palaeobotany and Palynology 83, 241–251.

Cassinis, G., Doubinger, J., 1991. On the geological time of the typical Collio and Tregiovo continental beds in the southalpine Permian (Italy), and some additional observations. Atti Ticinesi di Scienze della Terra 34, 1–20.

Cassinis, G., Doubinger, J., 1992. Artinskian to Ufimian palynomorphs assemblages from the Central Southern Alps, Italy and their regional stratigraphic implications. In: Nairn, A.E.M., Koroteev, V. (Eds.), Contributions to Eurasian Geology, Papers Presented at the International Congress Permian System of the World, Part I. University of South Carolina, Columbia, pp. 9–18.

Cassinis, G., Neri, C., 1990. Collio and Tregiovo Permian continental basins (Southern Alps, Italy): a general comparison. Atti Ticinesi di Scienze della Terra 33, 11–15.

Cassinis, G., Neri, C., 1992. Sedimentary and palaeotectonic evolution of some Permian continental basins in central Southern Alps, Italy. Cuad. Geol. Iber. 16, 145–176.

Cassinis, G., 1966. La Formazione di Collio nell'area-tipo dell'alta Val Trompia (Permiano inferiore bresciano). Rivista Italiana di Paleontologia e Stratigrafia 72, 567–590.

Clement-Westerhof, J.A., 1984. Aspects of Permian palaeobotany and palynology. IV. The conifer *Ortiseia* Florin from the Val Gardena Formation of the Dolomites and the Vicentinian Alps (Italy) with special reference to a revised concept of the Walchiaceae (Göppert) Schimper. Review of Palaeobotany and Palynology 41, 51–166.

Clement-Westerhof, J.A., 1987. Aspects of Permian Palaeobotany and Palynology, VII. The Majonicaceae, a new family of Late Permian Conifers. Review of Palaeobotany and Palynology 52, 375–402.

Clement-Westerhof, J.A., 1988. Morphology and phylogeny of Palaeozoic conifers. In; Beck, C (Ed.), Origin and evolution of gymnosperms. Columbia University Press, New York, pp. 298–337.

Conti, M.A., Mariotti, N., Nicosia, U., Pittau, P., 1997. Succession of selected bioevents in the continental Permian of the Southern Alps (Italy): improvements in intrabasinal and interregional correlations. In: Dickins, J.M. Yang, Z.Y., Yin, H.F., Lucas, S.G., Acharyya, S.J., (Eds.), Late Palaeozoic and Early Mesozoic Circum–Pacific Events and their Global Correlation. Cambridge University Press, Cambridge, pp. 51–65.

Conti, M.A., Mariotti, N., Manni, R., Nicosia, U., 1999. Tetrapod footprints in the Southern Alps: an overview. In: Cassinis, G., Cortesogno, L., Gaggero, Massari, F., Neri, C., Nicosia, U., Pittau, P., (Eds.), Stratigraphy and Facies of the Permian Deposits between Eastern Lombardy and the Western Dolomites. Field trip guidebook (Appendix), 23–25 September 1999. Earth Sciences Department, Pavia University, pp. 137–138.

de Laubenfels, D.J., 1953. External morphology of coniferous leaves. Phytomorphology 3,1–19.

de Wit, M.J., Gosh, J.G., de Villiers, S., Rakotosolofo, N., Alexander, J., Tripathi, A., Looy, C., 2002., Multiple organic carbon isotope reveals across the Permo–Triassic boundary of terrestrial Gondwana sequences: clues to extinction patterns and delayed ecosystem recovery. The Journal of Geology 110, 227–240.

DiMichele, W.A., 2014. Wetland-Dryland vegetational dynamics in the Pennsylvanian Ice Age Tropics. International Journal of Plant Sciences 175(2), 123–164.

DiMichele, W.A, Aronson, R.B., 1992. The Pennsylvanian–Permian Vegetational Transition: A terrestrial Analogue to the Oneshore–Offshore Hypothesis. Evolution 46(3), 807–824.

DiMichele, W. A., and T. L. Phillips. 1994. Paleobotanical and paleoecological constraints on models of peat formation in the Late Carboniferous of Euramerica. Palaeogeography, Palaeoclimatology, Palaeoecology 106: 39–90.

DiMichele, W. A., and T. L. Phillips. 1996a. Climate change, plant extinctions and vegetational recovery during the Middle-Late Pennsylvanian transition: The case of tropical peat-forming environments in North America. In: M. B. Hart (ed.), Biotic Recovery from Mass Extinction Events, The Geological Society, London, UK. Special Publication 102, 201–221.

DiMichele, W.A., Chaney, D.N., Dixon, W.H., Nelson, W.J., Hook, R.W., 2000. An Early Permian Coastal Flora from the Central Basin Platform of Gaines County, West Texas. Palaios 15, 524–534.

DiMichele, W.A., Mamay, S.H., Chaney, D.S., Hook, R.W., Nelson, W.J., 2001. An early Permian flora with late Permian and Mesozoic affinities from North-Central Texas. Journal of Paleontology 75(2), 449–460.

DiMichele, W.A., Pfefferkorn, E.W., Gastaldo, R.A., 2001. Response of Late Carboniferous and Early Permian plant communities to Climate Change. Ann. Rev. Earth Planet. Sci. 29, 461–487.

DiMichele, W.A., Hook, R.W., Nelson, W.J., Chaney, D.S., 2004. An unusual Middle Permian flora from the Blaine Formation (Pease River Group, Leonardian–Guadalupian Series) of King County, west Texas. Journal of Paleontology 78, 765–782.

DiMichele, W.A., Tabor, N.J., Chaney, D.S., Nelson, W.J., 2006. From wetlands to wet spots: Environmental tracking and the fate of Carboniferous elements in Early Permian tropical floras. In: Greb, S.F., DiMichele, W.A. (Eds.), Wetlands through time. Geological Society of America Special Paper 399, pp. 223–248.

DiMichele, W.A., Kerp, H., Tabor, T.J., Looy, C.V., 2008. The so-called “Paleophytic-Mesophytic” transition in equatorial Pangea: multiple biomes and vegetational tracking of climate change through geological time. Palaeogeography, Palaeoclimatology, Palaeoecology 286, 152–163.

DiMichele, W.A., Montañez, I.P., Poulsen, C.J. and Tabor, N.J. 2009. Climate and vegetational regime shifts in the late Paleozoic ice age earth, Geobiology 7(2), 200–226.

DiMichele, W.A., Cecil, C.B., Chaney, D.S., Elrick, S.D., Lucas, S.G., Lupia, R., Nelson, W.J., Tabor, E.J., 2011. Pennsylvanian-Permian vegetational changes in tropical Euramerica. In Harper, J.A., (Eds), Geology of the Pennsylvanian–Permian in the Dunkard basin:

Guidebook, 76th Annual Field Conference of Pennsylvanian Geologists, Waschington, PA, 60–102.

Falcon-Lang, H.J., Nelson, W.J., Elrick, S., Looy, C.V., Ames, P.R., DiMichele, W.A., 2009. Incised channel fills containing conifers indicate that seasonally dry vegetation dominated Pennsylvanian tropical lowlands. Geology 37, 923–926.

Falcon-Lang, H.J., Lucas, S.G., Kerp, H., Krainer, K., Montañez, I.P., Vachard, D.V., Chaney, D.S., Elrick, S.D., Contreras, D.L., Kurzawe, F., DiMichele, W.A., Looy, C.V., 2015. Early Permian (Asselian) vegetation from a seasonally dry coast in western equatorial Pangea: Paleoecology and evolutionary significance. Palaeogeography, Palaeoclimatology, Palaeoecology 433, 158–173.

Faure, K., Wit, W.J., Willis, J.P., 1995. Late Permian cola hiatus linked to 13C-depleted CO2 flux into the atmosphere during the final consolidation of Pangea. Geology 23(6), 507–510.

Florin, R., 1938-1945, Die Koniferen des Oberkarbons und des unteren Perms I-VII: Palaeontographica B 85, p. 1–729.

Florin, R., 1964. Über Ortiseia leonardii n. gen. et sp. eine Konifere aus den Grödener Schichten in Alto Adige (Südtirol). Memorie Geopaleontologiche dell'Università di Ferrara 1(1), 3–11.

Forte, G., Kustatscher, E., Roghi, G., Preto, N., in press. The Kungurian (Cisuralian) palaeoenvironment and palaeoclimate of the Southern Alps – palaeobotanical, palynological and geochemical investigations of the Tregiovo Basin. Palaeogeography, Palaeoclimatology, Palaeoecology.

Forte, G., Kustatscher, E., Van Konijnenburg van Cittert, J.H.A., Looy, C.V., Kerp, H., 2017. Conifer diversity in the Kungurian of Europe – Evidence from dwarf-shoot morphology. Review of Palaeobotany and Palynology 244, 308–315; 10.1016/j.revpalbo.2017.01.004

Galtier, J., Scott, A.C., Powell, J.H., Glover, B.W., Waters, C.N., 1992. Anatomically preserved conifer-like stems from the Upper Carboniferous of England. Proceedings of the Royal Society of London Series B 247, 211–214.

Gothan, W., Gimm, O., 1930. Neuere Beobachtungen und Betrachtungen über die Flora des Rotliegende in Thüringen. Arb. aus d. Inst. Paläobot. Preuss. Geol. L. Amt. Berlin, 2, 39–74.

Hayes, J.M., Strauss, H., Kaufman, A.J., 1999. The abundance of 13C in marine organic matter and isotopic fractionation in the global biogeochemical cycle of carbon during the past 800 Ma. Chemical Geology 161, 103–125.

Heckel, P.H., 1977. Origin of phosphatic black shale facies in Pennsylvnian cyclothems of mid-continent North America. Am. Assoc. Pet. Geol. Bull. 61, 1045–1068.

Heckel, P.H., 1986. Sea-level curve for Pennsylvanian eustatic marine transgressive–regressive depositional cycles along mid-continent outcrop belt, North America. Geology 14, 330–334.

Heckel, P.H., 1990. Evidence for global (glacial–eustatic) control over Upper Carboniferous (Pennsylvanian) cyclothems in Midcontinent North America. Geol. Soc. Spec. Publ. 55, 35–47.

Heckel, P.H., 2008. Pennsylvanian cyclothems in Midcontinent North America as far-field effects of waxing and waning of Gondwana ice sheets. In: Fielding, C.R., Frank, T.D., and Isbell, J.L., eds., Resolving the Late Paleozoic Ice Age in Time and Space: Geological Society of America Speciap Papers 441, 275–289.

Hernandez-Castillo, G.R., Rothwell, G.W., Mapes, G., 2001a. Thucydiaceae fam. nov., with a review and reevaluation of Paleozoic walchian conifers. International Journal of Plant Sciences 162, 1155–1185.

Hernandez-Castillo, G.R., Rothwell, G.W., Stockey, R.A., Mapes, G., 2003. Growth architecture in *Thucydia mahoningensis*, a model for primitive walchian conifer plants. International Journal of Plant Sciences 164, 443–452.

Hernandez-Castillo, G.R., Stockey, R.A., Mapes, G., Rothwell, G.W., 2009a. A new voltzialean conifer *Emporia royalii*, sp. nov. (Emporiaceae) from the Hamilton Quarry, Kansas. International Journal of Plant Sciences 170(9), 1201–1227.

Hernandez-Castillo, G.R., Stockey, R.A., Rothwell, G.W., Mapes, G., 2009b. Reconstruction of the Pennsylvanian-age walchian conifer *Emporia cryptica* sp. Nov. (Emporiaceae: Voltziales). Review of Palaeobotany and Palynology 157, 218–327.

Hernandez-Castillo, G.R., Stockey, R.A., Rothwell, G.W., Mapes, G., 2009c. Reconstructing *Emporia lockardii* (Voltziales: Emporiaceae) and initial thoughts on Paleozoic conifer ecology. International Journal of Plant Sciences 170(3), 1056–1074.

Hernandez-Castillo, G.R., Silva-Pineda, S.A., Cevallos, S.R.S., Early Permian conifers from Central Mexico and Reevaluation of Paleozoic conifer morphotaxa. Buletín de la Sociedad Geológica Mexicana 66(1), 85–96.

Horton, D.E., Poulsen, C.J., Montañez, I.P., DiMichele, W.A., 2012. Eccentricity-paced late Paleozoic climate change. Palaeogeography, Palaeoclimatology, Palaeoecology 331–332, 150–161.

Isbell, J.L., Miller, M.F., Wolfe, K.L., Lenaker, P.A., 2003. Timing of the late Palaeozoic glaciation in Gondwana: was glaciation responsible for the development of northern hemisphere cyclothems? In: Chan, M.A., Archer, A.W. (Eds.), Extreme Depositional Environments: Mega End Members in Geologic Time. Geol. Soc. of Am. Spec. Pap., vol. 370, pp. 5–24.

Jones, A. T., Fielding, C. R., 2004. Sedimentological record of the late Paleozoic glaciation in Queensland, Australia. Geology 32, 153–156.

Kaplan, J.O., Colin Prentice, I., 2002. The stable carbon isotope composition of the terrestrial biosphere: Modeling at scales from the leaf of the globe. Global Biogeochemical Cycles 16(4), 1–11.

Kerp, H., 1996. Post-Variscan late Palaeozoic Northern Hemisphere gymnosperms: the onset to the Mesozoic. Review of Palaeobotany and Palynology 90, 263–285.

Kerp, H., Penati, F., Brambilla, G., Clement-Westerhof, J.A., van Bergen, P.F., 1996. Aspects of Permian palaeobotany and palynology. XVI. Three-dimensionally preserved stromatolite-incrusted conifers from the Permian of the western Orobic Alps (northern Italy) 91, 63–84.

Kidder, D.L., Worsley, T.R., 2004. Causes and consequences of extreme Permo–Triassic warming to globally equable climate and relation to the Permo–Triassic extinction and recovery. Palaeogeography, Palaeoclimatology, Palaeoecology 203, 207–237.

Knoll, A.H., 1984. Patterns of extinction in the fossil record of vascular plants, In: M. H. Nitecki (Eds.), Extinctions. University of Chicago Press, Chicago, 21–68 pp.

Kustatscher, E., van Konijnenburg, J.H.A., Bauer, K., Butzmann, R., Meller, B., Fischer, T.C., 2012. A new flora from the Upper Permian of Bletterbach (Dolomites, N-Italy). Review of Palaeobotany and Palynology 182, 1–13.

Liu, C., Jarochowska, E., Du, Y., Vachard, D., Munnecke, A., 2017a. Stratigraphic and δ13C records of Permo–Carboniferous platform carbonates, South China: Responses to late

Paleozoic icehouse climate and icehouse–greenhouse transition. Palaeogeography, Palaeoclimatology, Palaeoecology 474, 113–129.

Liu, C., Jarochowska, A., Du, Y., Munnecke, A., Dai, X., 2017b. Prevailing anoxia in the Kungurian (Permian) of South China: Possible response to divergent climate trends between the tropics and Gondwana. Gondwana Research 49, 81–93.

Looy, C.V., 2007. Extending range of derived Late Paleozoic conifers: *Lebowskia* gen. nov. (Majonicaceae). International Journal of Plant Sciences 168, 957–972.

Looy, C.V., Duijnstee, I.A.P., 2013. Characterizing morphologic variability in foliated Paleozoic conifer branches – a first step in testing its potential as proxy for taxonomic position. In: Lucas S.G., et al. (eds), The Carboniferous-Permian transition. New Mexico Museum of Natural History and Science Bulletin 60: 215–223.

Looy, C.V., Stevenson, R.A., 2014. Earliest occurrence of autorotating seeds in conifers: the Permian (Kungurian–Roadian) *Manifera talaris* gen. et sp. nov. International Journal of Plant Sciences 175, 841–854.

Looy, C.V., Kerp, H., Duijnstee, I.A.P., DiMichele, W.A., 2014. The late Paleozoic ecological-evolutionary laboratory, a land-plant fossil record perspective. The Sedimentary Record 12(4), 4–9.

Mädler, K., 1957. *Ullmannia*-Blätter und andere Koniferenreste aus dem Zechstein der Bohrung Friederich Heinrich 57. Geologisches Jahrbuch 73, 75–90.

Mapes, G. & Rothwell, G. W. 1991. Structure and relationship of primitive conifers. Neues Jahrb. Palaeontol. Abh. 183, 269–287.

Marchetti, L., Forte, G., Bernardi, M., Wappler, T., Hartkopf-Fröder, C., Krainer, K., Kustatscher, E., 2015. Reconstruction of a Late Cisuralian (Early Permian) floodplain lake environment: Palaeontology and sedimentology of the Tregiovo Basin (Trentino-Alto Adige, Northern Italy). Palaeogeography, Palaeoclimatology, Palaeoecology 440, 180–200.

Marocchi, M., Morelli, C., Mair, V., Klotzli, U., Bargossi, G.M., 2008. Evolution of large silicic magma systems: remarks new U-Pb zircon data on the NW Permian Athesian Volcanic Group (Southern Alps, Italy). Journal of Geology 116, 480–498.

Meyen, S.V., 1987b. Fundamentals of palaeobotany. Chapman and Hall, London.

Meyen, S.V., 1997. Permian conifers of Western Angaraland. Review of Palaeobotany and Palynology 96, 351–447.

Marocchi, M., Morelli, C., Mair, V., Klotzli, U., Bargossi, G.M., 2008. Evolution of large silicic magma systems: remarks new U-Pb zircon data on the NW Permian Athesian Volcanic Group (Southern Alps, Italy). Journal of Geology 116, 480–498.

Michel, L.A., Tabor, N.J., Montañez, I.P., Schmitz, M.D., Davydov, V.I., 2015. Chronostratigraphy and Paleoclimatology of the Lodève Basin, France: Evidence for a pan-tropical aridification event across the Carboniferous–Permian boundary. Palaeogeography, Palaeoclimatology, Palaeoecology 430, 118–131.

Montañez, I.P., Poulsen, C.J., 2013. The Late Paleozoic ice age: an evolving paradigm. Annual Review of Earth and Planetary Sciences 41, 629–656.

Montañez, I.P., Tabor, N.J., Niemeier, D., DiMichele, W.A., Frank, T.D., Fielding, C.R., Isbell, J.L., Birgenheier, Rygel, M.C., 2007. CO_2-forced climate and vegetation instability during Late Paleozoic deglaciation. Science 315, 87–91.

Montañez, I.P., McElwain, J.C., Poulsen, C.J., White, J.D., DiMichele, W.A., Wilson, J.P., Griggs, G., Hren, M.T., 2016. Climate $p\mathrm{CO}_2$ and terrestrial carbon cycle linkages during late Palaeozoic glacial-interglacial cycles. Nature Geosciences 9(11), 824–839.

Mostler, H., 1966. Sedimentäre Blei-Zink-Verezung in den mittelpermischen “Schichten von Tregiovo” (Nonsberg, Nord-Italien). Mineralium Deposita 2,89–103.

Neri, C., Avanzini, M., Bampi, T., Bargossi, G.M., Mair, V., Morelli, C., Pittau, P., Ronchi, A., Sapelza, A., 1999. The Tregiovo area and related volcanic in the Tregiovo section. 1.2. The Tregiovo section. In: The Continental Permian, International Congress, 15–25 Sept., 1999, Brescia, Italy – Stratigraphy and facies of the Permian deposits between Eastern Lombardy and the Western Dolomites, Field Trip Guidebook, 23–25 Sept. 1999, Earth Science Department, Pavia University, Pavia, pp. 81–82.

O’Leary, M.H., 1988. Carbon isotopes in photosynthesis. Bioscience 38, 328–336.

Olszewiski, M.E., Patzkowsky, M.E., 2003. From cyclothems to sequences: record of eustacy and climate on an icehouse eperic platform (Pennsylvanian – Permian, North American Midcontinent). J. Sediment. Res. 73, 15–30.

Peters–Kottig, W., Strauss, H., Kerp, H., 2006. The land plant δ13C record and plant evolution in the Late Palaeozoic. Palaeogeography, Palaeclimatology, Palaeoecology 240, 237–252.

Peyser, C.E., Poulsen, C.J., 2008. Controls on Permo–Carboniferous precipitation over tropical Pangea: a GCM sensitivity study. Palaeogeography, Palaeoclimatology, Palaeoecology 268, 181–192.

Plotnik, R.E., Kenig, F., Scott, A., Glasspool, I., Eble, C.F., Lang, W.J., 2009. Pennsylvanian paleokarst and cave fills from northern Illinois, USA: a window into Late Carboniferous environments and landscapes. Palaios, 24: 627–637.

Poort, R.J., 1996. The reproductive biology and extinction of the Walchiaceae (Late Palaeozoic conifers). LPP Contributions Series, Utrecht, 4, 159 p.

Rankey, E.C., 1997. Relations between relative changes in sea level and climate shifts: Pennsylvanian – Permian mixed carbonate–siliciclastic strata, western United States. Geol. Soc. Amer. Bull. 109, 1089–1100.

Rees, P.M., 2002. Land-plant diversity and the end Permian mass extinction. Geology 30(9), 827–830.

Rees, P.M., Zeigler, A.M., Gibbs, M.T., Kutzbach, J.E., Behling, P.J., Rowley, D.B., 2002. Permian phytogeographic patterns and climate: data model comparisons. J. Geol. 110, 1–31.

Remy, W., Remy, R., 1978. Die Flora des Perms im Trompia-Tal und die Grenze Saxon/Thuring in den Alpen. Argumenta Palaeobotanica 5, 57–90.

Roscher, M., Schneider, J.W., 2006. Permo–Carboniferous climate: Early Pennsylvanian to Late Permian climate development of central Europe in a regional and global context. In: Lucas, S.G., Cassinis, G., Schneider, J.W. (Eds.), Non-Marine Permian biostartigraphy and Biochronology. Geological Society of London, Special Publications 265, 95–136.

Rothwell, G.W., Mapes, G., Mapes, R.H., 1997. Late Paleozoic conifers of North America: structure, diversity, and occurrences. Review of Palaeobotany and Palynology 95, 95–113.

Rothwell, G.W., Mapes, G., Hernandez-Castillo, G.R., 2005. *Hanskerpia* gen. nov. and phylogenetic relationships among the most ancient conifers (Voltziales). Taxon 54, 733–750.

Rygel, M.C., Fielding, C.R., Franl, T.D., Birgenheier, L.P., 2008. The magnitude of Late Paleozoic glacioeustatic fluctuations: a synthesis. Journal of Sedimentary Research 78, 500–511.

Schneider, J.W., Körner, F., Roscher, M., Kroner, U., 2006. Permian climate development in the northern peri-Tethys area – The Lodève basin, French Massif Central, compared in a

European global context. Palaeogeography, Palaeoclimatology, Palaeoecology 240, 161–183.

Schweitzer, H.J., 1962 Die Makroflora des niederrheinischen Zechsteins. Fortschr Geol Rheinl Westfal 6,331–376.

Schweltzer, H.J., 1986. The land flora of the English and German Zechstein sequences. In: Harwood G.M. and Smith D.B. (eds), The English Zechstein and Related Topics Geol. Soc. Spec Publ. 22, 31–54.

Schweitzer, H.J., 1996. *Voltzia hexagona* (Bisschoff) Geinitz aus dem mittleren Perm Westdeutschlands. Palaeontographica 239(1–3), 1–22.

Tabor, N.J., Montañez, I.P., 2004. Morphology and distribution of fossil soil in the Permo–Pennsylvanian Wichita and Bowie Group, north-central Texas, USA: implications for western equatorial Pangean palaeoclimate during icehouse-greenhouse transition. Sedimentology 51, 851–884.

Tabor, N.J., Poulsen, C.J., 2008. Palaeoclimate across the Late Pennsylvanian-Early Permian tropical palaeolatitudes: A review of climate indicators, their distribution, and relation to palaeophysiographic climate factors. Palaeogeography, Palaeoclimatology, Palaeoecology 268, 293–310.

Tabor, N.J., Montañez, I.P., Scotese, C.R., Poulsen, C.J., Mack, G.H., 2008. Paleosol archives of environmental and climatic history in paleotropical western Pangea during the latest Pennsylvanian through Early Permian. In: Fielding C.R., Frank, T.D., Isbell, J.L., (Eds.) Resolving the Late Paleozoic Ice Age in Time and Space: Geological Society of America Special Paper vol. 441, 291–303.

Uhl, D., Kerp, H., 2005b. Variability of stomatal density and index in the upper Permian conifer *Quadrocladus* Mädler – a taphonomical case study. Palaeoecology, Palaeoclimatology, Palaeoecology 218, 205–215.

Vacek, M., 1882. Vorlage der geologischen Karte des Nonsberges. Verhandlungen der kaiserlich-königlich geologischen Reichsanstalt 3, 42–47.

Vacek, M., 1894. Ueber die geologischen Verhältnisse des Nonsberges. Verhandlungen der kaiserlich-königlich geologischen Reichsanstalt 16, 431–446.

Vacek, M., Hammer, W., 1911. Erläuterungen zur Geologischen Karte, der im Reichsrate vertretenen Königreiche und Länder der Österrungar. Monarchie. SW-Gruppe Nr. 79 Cles. Verhandlungen der aiserlich-königlich geologischen Reichsanstalt, Wien.

van den Belt, F.J.G., van Hoof, T.B., Pagnier, H.J.M., 2015. Revealing the hidden Milankovitch record from Pennsylvanian cyclothem successions and implications regardin late Paleozoic chronology and terrestrial-carbon (coal) storage. Geosphere 11(4), 1062–1076.

Veevers, J.J., Powell, C.McA., 1987. Late Paleozoic glacial episodes in Gondwanaland reflected in transgressive-regressive depositional sequences in Euramerica. Geol. Soc. Amer. Bull. 98, 475–487.

Veizer, J., Ala, D., Azmy, K, Bruckschen, P., Buhl, D., Bruhn, F., Carden, G.A.F., Diener, A., Ebneth, S., Godderis, Y., Jasper, T., Korte, C., Pawellek, F., Podlaha, O.G., Strauss, H., 1999. 87Sr/86Sr, δ13C and δ18O evolution of Phanerozoic seawater. Chemical Geology, 161, 59–88.

Visscher, H., Kerp, J.H.F., Clement-Westerhof, J.A., 1986. Aspects of Permian palaeobotany and palynology. VI. Towards a flexible system of naming Palaeozoic conifers. Acta Botanica Neerlandica 35(2), 87–99.

Visscher, H., Kerp, J.H.F., Clement-Westerhof, J.A., Looy, C.V., 2001. Permian floras of the southern Alps. Natura Bresciana 25, 117–123.

Yao, Z. Q., Liu, L.J., Mapes, G., Rothwell, G.W., 2000. Leaf morphology and cuticular features of *Sphenophyllum* in the *Gigantopteris* flora from South China. Review of Palaeobotany and Palynology 110, 67–92.

Zhang, H., Shen, G., He, Z., 1999. A carbon Isotopic Stratigraphic Pattern of the Late Palaeozoic Coals in the North China Platform and Its Palaeoclimatic Implications. Acta Geologica Sinica, 72(1), 111–119.

Ziegler, A.M., Hulver, M.L., Rowley, D.B., 1997. Permian world topography and climate. In: Martini, I.P. (Eds.), Late Glacial and Post-Glacial Environmental Changes — Quaternary, Carboniferous–Permian and Proterozoic. Oxford University Press, Oxford, pp. 111–146.

CONCLUSIONS

The study of the middle Kungurian Tregiovo Basin adds an important tile to the complex and incomplete mosaic of Permian paleoclimates, with its global-scale deglaciation and aridification and its palaeofloristic transition that mainly characterized the Pangean palaeoequatorial regions. The study on the two plant fossil assemblages of the Tregiovo "Le Fraine" evidenced a complex and diverse flora that populated the palaeoequatorial region of central Pangea during the middle Kungurian. Conifers and sphenopterids showed a remarkable diversity at Tregiovo and knowledge of these two groups is now increased. The study on conifer dwarf-shoots revealed a diversity of forms; three new morphotypes (A, B and C), previously unknown in the fossil record, have been described. Moreover, the finding of *Dolomitia* Clement-Westerhof in the Tregiovo sediments pushed its appearance, previously thought to be Lopingian, back to the middle Kungurian. The study on the Tregiovo sphenopterids documented pretty well preserved and almost complete fronds of five different species, some of which already were known from other localities (e.g., *Sphenopteris kukukiana*, *S. suessii*) but less completely preserved than in the Tregiovo specimens. Moreover a new species, *Sphenopteris valentinii* Forte et Kerp sp. nov., has also been identified and newly established. The sphenopterids of Tregiovo are characterized by a surprisingly coriaceous appearance suggesting adaptation to drier conditions. This also suggests that the sphenopterids of Tregiovo might belong rather to the seed ferns than to the ferns.

Additional elements in the two plant assemblages are sphenophytes (*Annularia*), ginkgophytes (*Sphenobaiera*), seed ferns (*Peltaspermum*) and taxa with uncertain affinity such as taeniopterids (*Taeniopteris*) and the two morphotyes 1 and 2.

Also the palynomorphs are diverse with a dominance of taeniate and non taenitae bisaccate forms, poliplicate and monosaccate, which reflect indeed the dominance of conifers and seed ferns showed by the macroflora.

The multidisciplinary study carried out on the two Tregiovo sections, respectively "Le Fraine" and Tregiovo village sections, allowed a palaeoenvironmental and palaeoclimatic reconstruction of the Tregiovo lacustrine environment, and also to frame it in a more global context. The sedimentological results confirmed the results of early works, which identified a playa-like environment, characterized by an alternation of more stable and unstable lacustrine conditions. Despite the change in the floral composition between the two assemblages, which sees the increase of the seed ferns and sphenopterids parallel with the decrease of conifers, the general composition of the flora indicates a constant xerophytic character, also confirmed by the palynoflora, where spore are extremely rare in both assemblages.

The geochemical study has been here performed for the first time on the organic carbon (TOC) of Tregiovo. The lacustrine sediments of the two sections are rich in organic matter, which mainly originates from terrestrial plants. The isotopic data on the bulk rock from the two sections fit well with the high resolution $\delta^{13}C$ curve for Kungurian terrestrial organic carbon. The isotopic composition of the Tregiovo organic matter changed through time, with a decrease of $\delta^{13}C$ along the sections. Moreover, further analyses made on the organic carbon of coalified tissues of plants demonstrated the same negative shift. The analysis on different taxa of the two assemblages showed, on average, more negative values in the upper assemblage (i.e., assemblage B). In particular, the results on conifer coalified tissues showed that each of the three taxa that occur in both assemblages has carbon isotopic compositions that become more negative in the upper floral assemblage. It is thus possible to exclude that the change in the floral composition, such as more sphenopterids and seed ferns and fewer conifers, may have influenced the $\delta^{13}C$ of the bulk, because it has been shown that the different groups of plants also show a change in their isotopic composition as well between the two assemblages. It is known that ecological factors, such as water-stress, may affect the isotopic composition of plants though a change in the size of stomatal aperture, that in turn influences the fractionation rate during photosynthesis. Nonetheless, it is also known that high concentrations of CO_2 in the atmosphere ($p$$CO_2$) have a positive effect on the fractionation rate as well, and that the isotopic composition of atmospheric CO_2 is the most important factor that influences the isotopic composition of plants. Considering that the negative trend at Tregiovo correlates well with different Kungurian sites, it is here concluded that the geochemical results from Tregiovo reflect a global perturbation of the carbon cycle, and thus of the isotopic composition of atmospheric CO_2. On the other hand, we cannot exclude the influence, in some undetermined proportion, of local ecological factors on the isotopic composition of the Tregiovo flora.