

THE LATEST ARTINSKIAN/KUNGURIAN (EARLY PERMIAN) FLORA FROM TREGIOVO-LE FRAINE IN THE VAL DI NON (TRENTINO, NORTHERN ITALY) Additional and revised edition 2013

by MICHAEL WACHTLER



THE LATEST ARTINSKIAN/KUNGURIAN (EARLY PERMIAN) FLORA FROM TREGIOVO-LE FRAINE IN THE VAL DI NON (TRENTINO, NORTHERN ITALY) Additional and revised edition 2013

by Michael Wachtler P. P. Rainerstrasse 11, 39038 Innichen, Italy; E-mail: michael@wachtler.com

Abstract

The description of the latest Artinskian/Kungurian Permian flora from Tregiovo-Le Fraine (Val di Non, Trentino, Northern Italy), initiated in 2012, will be extended. Mainly, we have to do this with a conifer-dominated flora accompanied by other variegated plants, some also with autochthonous traits. The conifer Ortiseia daberi n. sp., due to different seed-scales and leaves, now displaces Ortiseia leonardii, a principally Upper Permian character conifer. Other widespread conifers are Cassinisia ambrosii, Trentia treneri, Albertia scopolii and Walchia viallii nov. comb. Some were also found in connection with leaves and fructifications, which enhances the potential for identification. The ovuliferous organ *Peltaspermum meyeri* n. sp., belonging to the group of Peltaspermales, found in straight connection with Lepidopteris foliage indeed is the dominating seed fern. However, Autunia conferta is also present. Scolecopteris sp. and Ozolia franei amplifies the number of species but are too poorly preserved to define further evaluations. The ferns are represented mainly by Sphenopteris suessi, described just in 1869 by H. B. GEINITZ from the mainly coeval and contiguous Collio Formation. The Ginkgophyta Baiera pohli n. sp., based on a very rudimentary leaf-organisation, differs essentially from the well-known Upper Permian Sphenobaiera digitata. The position of the further classified Taeniopteris valentinii remains ambiguous. Therefore, based on newly discovered material, a new genera Wachtleropteris valentinii nov. gen. will be introduced. The presence of the cycadophyta Bjuvia tridentina and Nilssonia perneri will be supported by further findings. The sphenophyta Neocalamites tregiovensis and some isolated Sphenophyllum sp. support the theory of a mostly savannah-like biocoenosis, with springtime inundations and a long-lasting dry season with never drying out lakes or rivers, an ideal habitat for a lot of reptiles, manifested by the numerous *Dromopus didactylus* track-ways.

Online: December 2013.

Key words: Permian floras, Cycadophyta, Coniferales, Northern Italy

Riassunto

Una prima descrizione della flora Permiana (Artinskiano-Kunguriano) di Tregiovo - Le Fraine (Val di Non, Trentino), iniziata nel 2012, viene tuttora approfondita. Si tratta di una vegetazione dominata dalle conifere ma arricchita da altre famiglie di piante, talvolta con affinità autoctone. La conifera Ortiseia daberi n. sp. sostituisce per i suoi coni e macrosporofilli ben diverse Ortiseia leonardi, conosciuta come conifera simbolo del Permiano Superiori delle Alpi. Altre conifere diffuse in questo sistema ecologico sono Cassinisia ambrosii, Trentia treneri, Albertia scopolii e Walchia viallii nov. comb. Alcuni strobili furono trovati in stretta connessione col ramoscello cosa che ne agevolava il suo riconoscimento. Gli sporofilli ovuliferi di Peltaspermum meyeri n. sp., da includere nel gruppo delle Peltaspermales, trovati insieme alle foglie di Lepidopteris

formano la felce a semi dominante in questi strati. Ma è presente anche Autunia conferta, un 'ulteriore Peltaspermaceae. Scolecopteris sp. e l'Ozolia franei allargano il numero delle piante, ma sono purtroppo rare e mal conservate per trarre ulteriori conclusioni. Le felci vengono dominate da Sphenopteris suessi, descritta già nell'anno 1869 dal ricercatore tedesco H.B. GEINITZ dai quasi coevali strati di Collio. La ginkgophyta Baiera pohli n. sp. si caratterizza per la sua semplice struttura fogliare e si distingue quindi considerevolmente dalla popolare e ben nota Sphenobaiera digitata del Permiano Superiore. Difficile rimane la situazione del genere Taeniopteris valentinii. Perciò sulla base di materiale del tutto nuovo, fu introdotto un nuovo genere: Wachtleropteris valentinii nov. gen. La presenza delle cicadee è dimostrata dalla Bjuvia tridentina e dalla Nilssonia perneri e viene consolidata da ulteriori ritrovamenti.

Le sphenophyta *Neocalamites tregiovensis* come anche qualche isolato ramoscello di *Sphenophyllum* sp., supportano ulteriormente la teoria di un paesaggio simile alle savane odierne, con inondazioni brevi ma intensi e periodi di siccità molto lunghi, seppure qualche laghetto o corrente d'acqua esiste tutto l'anno, un habitat per la sopravvivenza di rettili, come testimoniano le innumerevoli impronte lasciate inserite come *Dromopus didactylus*.

Zusammenfassung

Die erste Beschreibung der permischen Flora (Artinskium/Kungurium) von Tregiovo-Le Fraine (Val di Non, Trentino, Südalpen) begonnen im Jahr 2012 wird erweitert. Sie zeigt sich vor allem als eine von Koniferen dominierte Pflanzengesellschaft mit einigen anderen Pflanzenfamilien, die auch manchmal autochthone Züge tragen können. Die Konifere Ortiseia daberi n. sp. ersetzt nun wegen ihrer unterschiedlichen Samenanlagen Ortiseia leonardii, einen vor allem aus dem Oberperm der Dolomiten bekannten Charakter-Nadelbaum. Andere weit verbreitete Koniferen in diesen Schichten stellen Cassinisia ambrosii, Trentia treneri, Albertia scopolii und Walchia viallii nov. comb. dar. Einige Zapfen wurden zudem schon in Verbindung mit ihren Zweigen gefunden was ihre Erkennung erleichtert. Samenanlagen des Typs Peltaspermum meyeri n. sp. - zur Gruppe der Peltaspermales zählend wurden zusammen mit Lepidopteris Blättern gefunden und bilden somit den alles dominierenden Samenfarn. Aber auch Autunia conferta, eine weitere Peltaspermaceae ist präsent. Scolecopteris sp. and Ozolia franei erweitern die Anzahl der Pflanzenfamilien, sind aber zu selten, um weitere Einordnungsschlüsse ziehen zu können. Die Farne werden dominiert von Sphenopteris suessi, der schon im Jahr 1869 vom deutschen Forscher H. B. GEINITZ von der nahe gelegenen Collio Formation erstbeschrieben wurde. Das Ginkgogewächs Baiera pohli n. sp. zeichnet sich durch eine sehr einfache Blattstruktur aus und unterscheidet sich deshalb beträchtlich von der weit verbreiteten Sphenobaiera digitata aus dem Oberperm. Schwierig einzuordnen ist Taeniopteris valentinii. Deshalb wurde - aufgebaut auf neu entdecktes Material die neue Gattung Wachtleropteris valentinii nov. gen. eingeführt. Die Anwesenheit von Cycadeengewächsen wird durch Bjuvia tridentina und Nilssonia perneri belegt und durch weitere neue Funde bestätigt. Der Schachtelhalm Neocalamites tregiovensis sowie isoliert gefundene Sphenophyllum sp. unterstützen die Theorie einer von Savannen geprägten Landschaft, mit kurzzeitigen Überflutungen und lang andauernden Trockenzeiten, trotzdem aber mit niemals austrocknenden Seen und Bächen, ein überlebenswichtiges Habitat für viele Reptilien, wie die zahlreichen hinterlassenen Fußabdrücke von Dromopus didactylus zeigen.

Introduction

The first investigations about Permian Fossil Plants in the Southern Alps were made by Eduard SUESS, a famous Austrian geologist - he added the names of the supercontinent "*Gondwana*" and the "*Tethys Ocean*" - who, after indications of the skilful local naturalist Giuseppe RAGAZZONI, made a first stratigraphic succession around the village of Collio in the Eastern Lombardy (Über das Rothliegende im Val Trompia, 1869). Before publishing, he submitted the vegetal remains to the well-known German paleobotanist Hanns Bruno GEINITZ, who illustrated and described them (Über fossile Pflanzenreste aus der Dyas von Val Trompia, 1869), introducing some new species-names like Sphenopteris suessi, or comparing other plants with the German Rotliegend, like Walchia piniformis (CASSINIS & SANTI, 2001). Other plant fossil research was conducted some years later in 1873 by the German geologist C. W. GÜMBEL, which described from the Upper Permian Grödner Sandstein around Neumarkt in the Etschtal conifers, like Voltzia hungarica, Baiera digitata, ferns and horsetails.

Investigations about the macro-flora from Tregiovo meanwhile began in 1882, with M. VACEK, who correlated the Val di Non sites with the well-known German localities. He was able to elaborate a distinction between the age-different Lower Permian Rotliegend flora with *Walchia piniformis* and *W. filiciformis* and the typical Upper Permian Zechstein plant association with *Ullmannia frumentaria*. After VACEK (1882 and 1894), probably due to the scarce interest for fossil plants, due to the poorly preserved material, the interest declined or began moving towards the relatively abundant tetrapod footprints (AVANZINI ET AL., 2007).

In the late twentieth century, several palaeobotanists began to analyse the plant associations of the Val di Non, especially Tregiovo and Collio near the city of Brescia (REMY & REMY, 1978; KOZUR, 1980; VISSCHER ET AL., 2001; CASSINIS ET AL., 2002). In several cases, these investigations led to the assumption that typical Early Permian flora (Walchia, Lebachia, Autunia conferta) were described as pertaining to the same stratigraphic levels as characteristic plants from the Late Permian (Ullmannia frumentaria, Ortiseia, Pseudovoltzia liebeana, Taeniopteris eckardtii or Peltaspermum martinsii) (VISSCHER ET AL., 1999). Controversies arose, therefore, around whether the Tregiovo- and Collio-Formation was younger and should be placed in the Middle or even the Late Permian, or whether specimens were recovered from different geological different sites, or if a misinterpretation of the some-



Fig. 1: Map showing the Le Fraine-Tregiovo fossil plant site along the Revò-Laurein road in the Val di Non.

times poorly preserved plants did not allow an exact classification.

Geology

The primary purpose of this work is to correlate the different Early Permian plant associations in the Val di Non and afterwards also in the Collio Formation. First, a region between Revò and Laurein, below a large bridge crossing the "Le Fraine" streamlet, was analysed intensively. The small hamlet of Tregiovo, situated above, disposes its wastewater into the Rio Pescara, so that, unfortunately, the otherwise lovely fossil site is surrounded by a putrid stench.

Early Permian age datings

The fossil plant layer bearing horizons of Tregiovo is sandwiched between the rhyolitic volcanoclastic breccias of the Gries Formation and the pyroclastic flow deposits of the Ora Formation. The age of the Tregiovo Basin consisting of lacustrine deposits with alternating marls, limestones and shales was bracketed between radioisotope ages of the underlying and overlying volcanics with U-Pb-Zircon data respectively related to an age of 276.5 (+-1.2) and 274.1 (+-1.6) Ma., reclassifying them between the latest Artinskian (?) and Kungurian pro parte (CASSINIS & RONCHI, 2001; MAROCCHI ET AL., 2008). Correlating it with the German nomenclature forms, we can insert it in the Upper Rotliegend. Also, in that time, Tregiovo lay slightly closer to the Paleo-equator, therefore also including slightly diverse flora-elements. In this area, we have to add the last intercontinental habitat, and beginning from the Upper Permian, the landscape was more and more inundated from the Tethys-Sea for about 200 million years.

Volcanic outputs

Episodic breaks in the volcanic output may have lasted few million years. The stasis is recorded by the formation of the 200 m wide basin with fluvial and lacustrine sediments containing the remains of plants, pollens, and tetrapod footprints (MAROCCHI ET AL., 2008). Unfortunately, the plant material is so compressed and compacted that it impedes cuticular analysis, but the relative abundance of the material allows the development of statistical patterns.

Mining activities

Mineralisations, mainly of galena, sphalerite, copper and iron, are concentrated on the plant-richest zones; digging works in the past were also concentrated on these metals. Interesting and unusual is the frequency of the so-called Mogui Marbles, sometimes called "Palle del Fèro" (Féro's balls). Up to now, this newly discovered site is one of the few places in the world where concretions occur in the same habit and aspect as in the south-western US Navajo sandstone within the Early Jurassic Grand Staircase Escalante National Monument. But whereas the Mogui balls are iron oxide concretions, this "Palle del Fèro" based on X-Ray diffractometric analysis, is of explicit carbonatic nature, with over 90% calcite created probably by a sulphate reduction in organic C-rich sediments.

Palaeoecology and Palaeoclimatology

Xeromorphic habitat

The plants exhibit a xerophytic appearance expressed by the leathery needles of conifers, especially the conifer *Cassinisia* or ferns such as *Peltaspermum meyeri* or *Sphenopteris suessi* holding extremely small leaflets, even though water-loving spheno-



Fig. 2: Early Permian plate reconstruction with approximately the position of Tregiovo. Note the position of equator and tropics. (Modified from ZIEGLER & STAMPFLI, 2001).

Fig. 3: Deposition time of the Tregiovo plant beds: 276.5 (+-1.2) to 274.1 (+- 1.6) ma.

phyta (*Neocalamites tregiovensis*) or largeleafed cycadophyta are present in a variegated number of orders and species.

Reptile tracks

Well-preserved reptile footprints attest to an environment that was not hostile. In particular, *Dromopus* dominates the layers and often accompanies the flora elements. As stated by other authors, *Dromopus didactylus* have a great vertical distribution in the Permian and cannot therefore be regarded as good biostratigraphical markers (GAND & DURAND, 2006; CONTI ET AL., 1999; CASSINIS & PEROTTI, 2007).

Frequent forest fires

The commonness of burned wood or charcoal pieces indicates that forest fires destroy the vegetation (UHL & KERP, 2003). They could be caused by activities of the nearby volcanoes or more reasonably originated by natural circumstances like thunderbolts. Frequently, mud-cracks and concretions are indicators of meandering river systems channelling through a climate that was arid to semi-arid for most of the year. Torrential rivers after the monsoons brought enough precipitation from the hinterland to allow the survival of this variegated vegetation. A consistent part of the plants seems to be blown from wind and storms on the fine sandy areas along the riverbanks where they were buried by the fine-grained sludge.

Springtime assemblage

Because a substantial part of the fertile organs consist of male cones, accompanied by young female fructifications, it can be suggested that short and intensive rainfall periods followed months of drought where most of the lakes and lagoons dried out and conservation was therefore no longer possible.



Ancient galleries on Tregiovo evidencing mining activities. Galena-silver inclusions near fossilised plants are frequently found.



Mud cracks of dried-up watering places from Tregiovo (TRE 79) and below recent desiccation cracks.

The importance of the Tregiovo world

A new Early Permian flora composition

We have to add to the well-known Rotliegend-Flora of Germany another species-rich European Permian plant-deposit. Voltzialean *Cassinisia ambrosii, Agathis*-like *Trentia treneri, Albertia scopolii, Ortiseia daberi* have only little counterpart with German *Walchia, Otovicia, Wachtlerina* and *Ernestiodendron* or Upper Permian *Ullmannia* and *Pseudovoltzia.* Much more obvious and a highlight for further researches will be the richness of cycads like *Bjuvia trentina* and *Nilssonia perneri.* The propagation of the cycadophyta just in Permian constitutes another surprise. The ginkgophyta are present with a very rudimentary form, *Baiera pohli*. Paradoxically, the group of pterophyta is present only by a few and skeletonised species. Apart from some true ferns like *Sphenopteris suessi* and seed ferns inserted in the Peltaspermales, represented by *Peltaspermum meyeri* and *Autunia conferta*, the Filicales seem to be only poorly evolved. Mainly, no parental affinities could be established for the endemic *Wachtleropteris valentinii* with its strange bushy structure and bifurcating leaves.

A mainly "modern" plant association

The domination of conifers, the high percentage of cycadophyta, the presence of ginkgophyta, horsetails and ferns testify that Permian Tregiovo has more of a relationship with recent flora than the Carboniferous period.



Tracks of *Dromopus didactylus* often occur (TRE 85). Sometimes they are accompanied by plants such as the conifer Trentia treneri (TRE 61). This suggests that the plants were buried near lakes, swamps or marshes.



Charcoalified wood remains from Permian forest fires are common.

No arguments for a Permo-Triassic catastrophic-scenery

We can detect that the often indicated "mother of all catastrophes" on the Permo-Triassic boundary did not take place in the vegetation and probably not even in the fauna. It is obvious that, beginning with the Carboniferous-Permian border, a complete transformation in the flora system occurred leading in a relatively short time to almost all of today's flora components (conifers, sphenophyta, ginkgophyta, ferns, probably also some proto-angiosperms). It is obvious that in Permian we have an unprecedented decline of the richness of species, with a lot of dried up plants, but nevertheless there are still water-loving plants like horsetails and cycads enriching the same habitat. Interesting for further studies will be that the cycadophyta (*Bjuvia* and *Nilssonia*), the ginkgophyta (*Baiera*) and the sphenophyta (*Neocalamites* and *Equisetites*) crossed over, mainly unmodified from Permian to the Triassic, whereas in the pterophyta we have an exhausting change in variety beginning from the Triassic.

A savannah vegetation

The xerophytic character of many plants suggests a savannah-like climate with intense floods in springtime and long-lasting dry seasons for mainly all the year. We have a similar habitat today in some regions of the southern part of Africa such as the Okavango Delta or the Serengeti.



The subtle black layers of Tregiovo are easily to split. Unfortunately, no statistics about more or less plant bearing horizons could be established.

Components of the Tregiovo flora:

Lycophyta

Till now not recorded

Sphenophyta

Neocalamites tregiovensis Sphenophyllum sp.

Coniferophyta

Ortiseia daberi Cassinisia ambrosii Trentia treneri Albertia scopolii Alpia viallii

Pteridospermatophyta

Lepidopteris meyeri Autunia conferta

Cycadophyta

Bjuvia tridentina Nilssonia perneri Taeniopteris sp. Wachtleropteris valentinii

Pteridophyta

Sphenopteris suessi Scolecopteris sp.

Ginkgophyta *Baiera pohli*

Undefined orders

Ozolia frainei nov.

Repository

Most specimens were recovered by Fèro Valentini, and other parts also by Michael Wachtler. The macrofossil plant collection, including all holotypes and paratypes, is stored at the Tridentine Museum of Natural Sciences (Trento, Italy). Their numbers are prefixed by "TRE" for Tregiovo. The remainder of the collection is at the DoloMythos Museum at Innichen (Italy) or in Fèro Valentini's private collection.



Reconstruction of the Early Permian (Artinskian-Kungurian) Tregiovo-Flora: (From the left to the right):



X

perneri

Wachtleropteris valentinii

Nilssonia



Bjuvia tridentina

Lepidopteris

meyeri



pohli

Baiera Sphen





The origin of the concretions (Palle del Fèro)



Fig. 1 + 2. New Zealand's Rotorua Volcanic Plateau (Fig. 1) with its lively fields of geothermal activity hot springs (Fig. 2) and boiling mud pools is a good example of the conditions that prevailed in the Permian Tregiovo landscape.

The formation of the "Palle del Fèro" (Fèro's balls) concretions can be traced to an early diagenetic origin. This is supported by the accompanying plants deposited at the same time (Fig. 8).

The greatest affinity they have is with the Jurassic Moqui Marbles from the Navajo Sandstone in Utah. Both exhibit a wide variety of sizes from a few centimetres up to 40 to 50 cm; particularly when the concretions are fused together, they form geometric spheres, discs and nearby mythological figures (Fig. 9). The surface could be rough or grooved with ridges around their circumferences, in which case the Mogui Marbles in the Hopi Native American traditions were regarded as male-balls; or unmoved with a glossy surface as female. At present, no similar local myths have been discovered in the Val di Non region. Whereas the Moqui balls are iron oxide concretions and were created by the precipitation of iron which was dissolved in groundwater, the "Palle del Fèro" are of explicit carbonatic nature, with over 90% calcite. An X-Ray diffractometric analysis of the crystalline microstructure proved that the concretions (specimen 1) are composed of 93.3% calcite, 2.2% fluorite, 1.8% silica, 1.3% albite and 1.4% sanidine; the normal layers, containing all of the fossils, are 45.6%

silica, 18.1% fluorite, 15.5% albite, 13.1% calcite and 7.7% sanidine.

The most carbonate concretions grow - and this could be valid for the Tregiovo-concretions - from the alkalinity generated by sulphate reduction in organic C-rich sediments.

The frequent shrinkage cracks in the centre of the spheres (Fig. 5) were immediately filled by calcite or fluorite (MOSTLER, 1966). Their formation process and hardening was just finished with the deposition inside the other fine-grained aerobically digested sludge. Some concretions were carried in the marshes in a semi-hardened condition for a short way. Typical grooving-rings are the result of that shifting (Fig. 8).

Fig. 3 + 4. Analysis made by the R. & S./C.Q LABORATORI R.& S. Tassullo Materiali S.p.a. Specimen 1, concretion is of carbonatic affinity, specimen 2, part of the normal layers of the Tregiovo-Formation includes all the plant fossils is composed of 50 % silicia-material. Fig. 5. When they moved in their ancient area, grooving-rings were formed.

Fig. 6. They became flattened from their own weight in semi-solid state. Shrinkage cracks occurred in the interior, which were filled with calcite or fluorite.

Fig. 7. The lower horizons of Tregiovio hold mainly shrivelled balls. Only in the middle layers will they be found perfectly rounded.

Fig. 8. Other sediments and also plants (*Ortiseia daberi*) were deposited together with the concretions.

Fig. 9. Sometimes several aggregates form strange figures.

Spectrophotometric analysis of
the concentration of elements
in the concretions (speci-
men 1) and the normal layers
(specimen 2).

	CaO	SiO ₂	Al ₂ O ₃	Fe ₂ O ₃	MgO	K₂O	Na ₂ O	PAF	totale
Specimen 1	44,9	12,84	2,95	0,73	0,45	1,30	0,27	36,31	99,75
Specimen 2	11,4	73,10	5,42	2,23	0,71	2,20	0,78	4,03	99,86



Division: Coniferophyta Order: Coniferales (TAYLOR, 1981) Family: Walchiaceae (GÖPPERT, 1865) Genus: *Ortiseia* (FLORIN, 1964)

Ortiseia daberi sp. nov. (WACHTLER, 2013)

Ortiseia leonardii, FLORIN, Pl. 1-3 *Ortiseia leonardii* (Florin), CLEMENT-WESTHOF Pl. I-XXXIII *Ortiseia leonardii* (Florin), WACHTLER, p. 13

Holotype

TRE 182

Paratype

TRE 394

Material

TRE 285, 288, 197 + 210 (Cones), 259 + 360 (Seed-Scales), 226, 149, 235 (Male cones)

Type horizon and age

Early Permian (Artinskian-Kungurian) Tregiovo-Formation

Etymology

Named after the German paleobotanist Rudolf Daber, former director of the Museum für Naturkunde Berlin (Natural history Museum).

Diagnosis

Shoots pinnately branched, bearing hardly overlapping leaves. Foliage fleshy, with an acute to obtuse apex, leaf base slightly contracted. Ovuliferous dwarf shoots with a fair amount of sterile scales and one single fertile scale originating centrally, projected beyond the sterile scales.

Description

Branches: Widely spaced out to the sides. The spirally arranged leaves do not or only slightly overlap. Holotype TRE 182 evidences the arrangement of the leaves and the structure of the branchlet well.

Leaves: Ovate to lanceolate with nearly invisible grooves across the entire foliage and some median emargination. Apex acute to obtuse, sometimes slightly rounded. Leave-base slightly contracted. Single *Ortiseia*-leaves are normally from 1 to 2 cm (TRE 51, 146, 288) long and at the base up to 1 cm wide.

Polliniferous cones: Slender with an axis bearing numerous spirally arranged and overlapping microsporophylls. Young cones characterised by microsporophylls with longer narrowing appendixes (TRE 226). Adult cones (TRE 235, 111) at least 10 cm long and 3.5 cm wide.

Ovuliferous cones: Usually round bodied, at least 11 cm long, and 5 cm wide on the



Ortiseia daberi. a) Branchlet (TRE 182), b) Single shoot (TRE 285 c) Single leaf adaxial side (TRE 128) d) Single leaf abaxial side (TRE 146)



1) TRE 182. Ortiseia daberi sp. n. Designed Holotype. Part of a branchlet.

- 2) TRE 285. Ortiseia daberi sp. n. Single shoot.
- 3) TRE 116. Ortiseia daberi sp. n. Single terminal shoot.
- 4) TRE 128. Ortiseia daberi sp. n. Single leave lower side.
- 5) TRE 146. Ortiseia daberi sp. n. Single leave. Leaf evidencing abscission details.
- 6) TRE 270. Ortiseia daberi sp. n. Single leave upper side.

broadest side. Cone axis holding spirally arranged bracts, bearing on their inner side the ovuliferous seed-scale. They are composed of a certain number of sterile leaves and one single fertile that can be considered due to the multiple segments working as an aggregation. Accompanying leaves minute, elongated, usually pointed to oblate, fertile scale massive, coalesced four-lobed, and holding approximately in the middle the 10 mm rounded ovule/seed. Attachment groove of the fertile scale clearly visible on the centre of the seed.

Discussion

Although the genus *Ortiseia (leonardii)* was established by FLORIN in 1964, based on its leave habitus, it has since emerged that the characteristic features distinguishing them from *Walchia, Voltzia, Majonica, Dolomitia* or other Permian conifers depend from the construction plan of the seed-scales. From the Upper Permian *Ortiseia* species (*O.leonardii, jonkeri, vissheri), Ortiseia daberi* differs because of the different visual nature of its dwarf-shoots, looking fingershaped and seeming in that way to play an intermediate role between *Walchia* and *Ortiseia.*



Ortiseia daberi. Single fertile bract-seed-scale a) Bract (TRE 197), b) sterile leaves + fertile scale, TRE 259 c) seed-ovule (TRE 360) d) Composition of the seed scale



- 7) TRE 226. Ortiseia daberi. Young male cone.
- 8) TRE 111. Ortiseia daberi. Adult male cone.
- 9) TRE 235. *Ortiseia daberi*. Adult male cone, ready to release the pollen.
- 10) TRE 235. Ortiseia daberi. Detail of the microsporophylls.



11) TRE 197. Ortiseia daberi sp. n. Adult female cone.
 12) TRE 197. Ortiseia daberi sp. n. Detail of the megasporophylls.
 13) TRE 229. Ortiseia daberi sp. n. Adult female cone, interior aspect.
 14) TRE 259. Ortiseia daberi sp. n. Ovuliferous seed scale, with the more-lobed incisions.
 15) TRE 141. Ortiseia daberi sp. n. Ovuliferous seed scale with attached ovule.
 16) TRE 384. Ortiseia daberi sp. n. Ovuliferous dwarf-shoot abaxial view.
 17) TRE 360. Ortiseia daberi sp. n. Single seed. Note the attachment groove with the fertile scale.
 18) TRE 340. Ortiseia daberi sp. n. Coalesced four-fingered bract.

Division: Coniferophyta Order: Coniferales (TAYLOR, 1981) Family: Voltziaceae (GÖPPERT, 1865) Genus: *Pseudovoltzia* (FLORIN, 1927)

Cassinisia ambrosii sp. nov. (WACHTLER, 2012)

1996 *Cassinisia orobica*, KERP ET.AL. p. 67 - 68 2012 *Cassinisia ambrosii*, WACHTLER, p. 13

Holotype

TRE 100

Paratype

TRE 109

Material

TRE 98, 105, 140, 158, 171

Type horizon and age

Early Permian (Artinskian-Kungurian) Tregiovo-Formation

Etymology

Named after Francesco Ambrosi (Borgo Valsugana, 1821 – Trento, 1897), herdsman, autodidact, who increased botanic and

palaeontologic knowledge about his territory. Curator of the city museum of Trento, he left an ample naturalistic collection to the Natural History Museum. In addition, he was a condemned patriot under the Austrian empire.

Diagnosis

Conifer with protruding widely spread shoots. Foliage leathery and square-rounded at the apex, with one pronounced mid-vein crossing the whole leaf.

Description

Branches: Pendulous and irregularly diverging. Holotype TRE 100, but also TRE 109 and TRE 99, are good examples to demonstrate the organisation of the lateral twigs.

Leaves: Equally wide for the whole length, distinctively only converging where they end in a square-rounded apex (TRE 98). Leaves from 0.7-1 cm long, and 0.2-0.3 cm wide (TRE 98, TRE 109). One distinguishing prominent rib grows through almost the entire leaf. The needles are only slightly decurrent and do not usually overlap each other; they sprout laterally to curve easily upwards, only sometimes are slightly incurved (TRE 109), from the whole base of the branchlet.



Cassinisia ambrosii a) Leaves, b) Detail of a shoot with female cone (TRE 109), c) Twig (TRE 100) d) Twig with a young male cone (TRE 176) e) Microsporophyll.



1) TRE 100. Cassinisia ambrosii. Designed holotype. Mostly complete twig.

- 2) TRE 109. Cassinisia ambrosii. Paratype. Branch fragment.
- 3) TRE 171. Cassinisia ambrosii. Leathery branch fragment.
- 4) TRE 58. Cassinisia ambrosii. Detail of the arrangement of leaves. Branch fragment.
- 5) TRE 105. Cassinisia ambrosii. Extremely xerophytic arrangement of leaves.

Male cones: TRE 158 represents a young polliniferous cone connected with *Cassinisia* leaves (TRE 158); TRE 149 and 140 also have the same resemblance. They are mostly elongated and bulbous, from 2-5 cm long 1.5-2.5 cm wide. The peltate microsporophylls end in a modestly long appendix. Whether the pollen sacs are arranged on the lower surface of the microsporophyll and recurved there to the cone axis (*Willsiostrobus*-type), as is typical for the Triassic Voltziales, could not be established.

Female cones: At Tregiovo, a fair amount of bilaterally symmetrical ovuliferous seed scales of Proto-Voltzialean character resembling most Upper Permian Dolomitia were found. They were provided with some sterile leaves and a one-levelled but three-fingered fertile scale, described as Dolomitia. The three lobes are rounded with the median slightly bigger and the other two laterally mirrored disposed. Some assumptions state that they belong to Cassinisia ambrosii and therefore this conifer has to be put in the range of Proto-Voltziales. TRE 355 is an example of the organisation of a female cone; slab TRE 176 shows fossilised Cassinisia twigs with a young female cone.

Discussion

Usually Cassinisia ambrosii could not be confused with the other conifers from the Tregiovo-Formation. Trentia treneri foliage, measuring 10-12 cm, is much bigger; Ortiseia daberi leaves are lanceolate and Walchia vialli holds needle-like falcate needles. Similar in appearance, the foliage-type Cassinisia orobica (KERP ET AL., 1996) from the nearby Orobian Alps could be considered. Due to their poorly preserved fragmented parts and the impossibility of stating whether some of the leaf-fragments belong to more conifer species, further analysis or comparisons could not be made. But it seems that Cassinisia orobica holds much more xeromorphic leaves than C. ambrosii.

However, all classification remains superficial if we are not able to connect this leaftype with their fertile components. A small bulbous male cone in connection with *Cassinisia ambrosii* leaves was obtained; but frequent in the Tregiovo-Formation are seed-scales with Proto-Voltzialean affinities, which could be correlated with *Cassinisia*. From the Upper Permian Southern Alps, conifers with Voltzialean affinities were described (CLEMENT-WESTERHOF, 1984) like *Dolomitia cittertiae, Pseudovoltzia liebeana* (frequent also in the German Zechstein) and *Pseudovoltzia sjerpii*, recovered mainly from the Bletterbach Gröden-Formation and the Vicentinian Alps (Scocchi, Ulbe, Casarotti). All of these conifers have therefore to be inserted into the group of Proto-Voltzialean conifers of the northern hemisphere due to their arrangement of more or less adnate scale-bracts.

Division: Coniferophyta

Order: Coniferales (TAYLOR, 1981) Family: Voltziaceae (GÖPPERT, 1865) Genus: *Dolomitia* (CLEMENT-WESTERHOF, 1986

Dolomitia nonensis sp. nov. (WACHTLER, 2013)

1986 *Dolomitia cittertiae*, CLEMENT-WESTERHOF p. 393 pl. 7 2012 *Cassinisia ambrosii,* WACHTLER, p. 18 - 19

Holotype

TRE 335

Paratype

TRE 88 (abaxial)

Material

TRE 83, 387, 348

Etymology

Named after the Val di Non in Trentino (Southern Alps), where the plant was found for the first time.

Type horizon and age

Early Permian (Artinskian-Kungurian) Tregiovo-Formation

Diagnosis

Ovuliferous seed-scale provided with a fair amount of protection leaves and one flat three-lobed apically rounded fertile scale.

Description

The isolated ovuliferous conifer scales reached a length from up to 15 to 20 mm and a width from 14 to 18 mm and are



- 6) TRE 121. Cassinisia ambrosii. Probably adult male cone.
- 7) TRE 149. Cassinisia ambrosii. Typical ellipsoid male cone.
- 8) TRE 140 Cassinisia ambrosii. Male cone.
- 9) TRE 158. Cassinisia ambrosii. Male cone with attached leaves.

bilaterally symmetrical with a slightly bigger middle lobe. The coalesced lobes are oval and characterised by an obtuse apex. Holotype TRE 335, for example, is 15 mm wide and 10 mm long, while TRE 83 is 17 mm wide, 20 mm long, and with an axis of 9 mm. The axis is sometimes very long in proportion to the rest of the dwarf-shoot (TRE 387 axis length 12 mm). The accompanying sterile leaves are minute, with a pointed apex, reaching a number from 10 to 15.

Discussion

The leaf morphology could be part of the determination of fossil plants, but not the only factor. Especially in the Permian-Triassic conifers, the arrangement of the fertile scalebracts with the collocation of the ovules/seeds and their habitus plays a fundamental rule. By describing the Fossil Flora from Lower Permian Tregiovo Formation (WACHTLER, 2012), I noticed a fair amount of scales, which hold Voltzialean affinities. But to be inserted in the regular *Voltzia*-tribe, a one level seed-scale

is indispensable. Neither Voltzia nor Pseudo*voltzia* could be taken as an analogy. But one group of ovuliferous scales bears strinking resemblances: Dolomitia, described by J. CLEM-ENT-WESTERHOF in 1986 for Upper Permian Alpine ovuliferous organs. Dolomitia cittertiae is characterised by a compound of one threefingered fertile scales, with a certain number of the sterile leaves sprouting from the basal part. It seems that the fertile scale from Dolomitia nonensis is more compact. Therefore, with the newly described Seymourina niederhauseni (PERNER & WACHTLER, 2013), we have another example that the Voltziales have their origin in the Earliest Permian, and a direct evolving scenery from the Walchiaceae to the Voltziaceae becomes practically impossible. Leaves and branchlets corresponding with most of this concept in the latest Artinskian/Kungurian Permian flora from Tregiovo-Le Fraine are those of Cassinisia ambrosii, but until no branches are found in connection with Proto-Voltzialean cones or seed scales, both names have to remain.



Reconstruction of an ovuliferous scale of *Dolomitia nonensis*. a) adaxial view showing the attachment point of the three ovules (After holotype TRE 335). b) abaxial view with a higher amount of sterile leaves (after TRE 88). pl = protection leaves, fs = fertile scale, oa = ovule attachment.



10) TRE 176. Cassinisia ambrosii. Young female cone.



11) TRE 355. *Dolomitia nonensis* sp. n. Cone belonging probably to the described seed scales. Cone size 3 cm.
12) TRE 335. *Dolomitia nonensis* sp. n. Designed holotype. Seed-scale adaxial view with the place of the ovule attachment. 15 mm x 10 mm.

13) TRE 88. *Dolomitia nonensis* sp. n. Paratype. Seed scale abaxial view evidencing well the sterile scales. 13 mm x 11 mm.

14) TRE 83. Dolomitia nonensis sp. n. Seed scale, abaxial view. 17 mm wide, 20 mm long, length peduncle 9 mm.
15 TRE 387. *Dolomitia nonensis* sp. n. Seed scale with a 12 mm long peduncle. 15 mm wide 20 mm long.
16) TRE 348. *Dolomitia nonensis* sp. n. Seed scale. 15 mm wide 20 mm long, peduncle 12 mm.

Division: Coniferophyta Order: Coniferales (TAYLOR, 1981) Family: Walchiaceae Genus: *Walchia* (SCHLOTHEIM ex STERN-BERG 1825)

Walchia viallii (WACHTLER, 2012) nov. comb. 2013

2012 Alpia viallii, , WACHTLER, p. 23

Holotype

TRE 50

Paratype

TRE 53

Material

TRE 20, 33, 54, 96, 102.

Etymology

This was named in honour of Vittorio Vialli (Cles 1914–Bologna 1983), an Italian geologist and palaeontologist, who was deported under the Nazi regime to a concentration camp. There, he took innumerable pictures undercover, which appeared in a famous book ("Ho scelto la prigionia" – I chose the prison) following the war.

Diagnosis

Conifer with slender, symmetrical bipinnate branches, densely covered with short, falcate only sometimes overlapping needles. Female cones extraordinary long sitting on the terminal parts of the branchlets.

Description

Branches: *Walchia viallii* bear protruding, slender symmetrical twigs. Heterophyllous foliage is common; in that case, the leaves could also reach several centimetres. Paratype TRE 53 represents a mostly entire juvenile branchlet, while holotype TRE 50 corresponds to a 60 cm long adult twig with long protruding leaves, especially on the main axis.

Leaves: Adult needles are lanceolate, at most 2–3 mm wide at the base, but up to 5 cm long on the main trunk (TRE 20). They are incurved and decurrent and overlap occasionally tightly. Juvenile foliage is up to 1 cm long, awl-shaped and sharply pointed at the apex. Heterophyllous foliage occurs sometimes on the same twigs (TRE 54, TRE 3).

Male cones: Usually till 5-7 cm long, 1.5 cm wide, ovoid to elongated, with protruding bracts. TRE 119, 210 are good examples of male cones. TRE 411 is in straight connection with *Walchia viallii* branchlets.

Female cones: TRE 408 represents a young female cone. It is typically Walchiacean, extraordinarily long (16 cm x 2 cm wide), and is in connection with *Walchia viallii* leaves. No consideration can be made about the number of ovules. TRE 96 represents an adult, mainly decomposed female cone.

Discussion

When I described this conifer in 2012, based on the incurved subtle needles, my problem was in which genera or which evolving lineage to put them into. There were at least two conifer tribes which fit reasonably in this concept: The genus Walchia, especially W. piniformis, which is a character conifer of European Lower Permian (WACHTLER, 2012). Some older authors have described Walchia piniformis (VACEK, 1882, 1884; REMY & REMY, 1978; KOZUR, 1980; VISSCHER ET AL., 1999) as being found in the Tregiovo-Formation. Also, the Early Triassic conifer Alpia holds the same branching system and incurved subtle needles (WACHTLER, 2010). A correct insertion would not be a problem if the seed scales of the female cones were recovered, and known or well preserved cones are in direct connection with the branchlets. After intensive researches and identifying some female cones attached to the twigs, I can now establish with caution that this conifer belongs to the genus of Walchiaceae. The arrangement of the sterile leaves with the seed-scales prove this. TRE 408 represents a typical Walchian cone, characterised as others from the German Rotliegend by its extraordinary length and high number of fertile scales. Until the exact organisation of the fertile and sterile scales and the ovules is reported, a further classification and insertion is not possible. Thus, at present I am convinced enough to insert this conifer-branchlets in the Walchiaceae as Walchia viallii, hoping that eventually it will be possible to obtain more information. The elongated female cone has some affinities with the newly described Seymourina from the Earliest Permian, but does not correspond to the wing-seeded cones from the



- 1) TRE 50. Walchia viallii. Designed holotype. Entire adult twig.
- 2) TRE 50. Walchia viallii. Holotype. Detail showing the long needles.
- 3) TRE 20. Walchia viallii. Branch fragment.
- 4) TRE 53. Walchia viallii. Paratype. Entire juvenile twig.
- 5) TRE 266. Walchia viallii. Detail of a young frond.



- 6) TRE 96. Walchia viallii. Adult female cone.
- 7) TRE 408. Walchia viallii. Young female cone in connection with a branchlet.
- 8) TRE 408 Walchia viallii. Detail of the female cone. Basal part.
- 9) TRE 143 Walchia viallii. Young male cone.

Majonica-family. Also, Ortiseia bears much more bulbous female cones, as well as characteristic leathery leaves. In addition, Voltzialean Cassinisia leaves are equally wide for the whole length, square-rounded and dotated with a midrib have enough distinction potential to not being confused. Walchia viallii occurs at Tregiovo in mainly equal numbers as Ortiseia daberi and Cassinisia ambrosii.



10) TRE 411. *Walchia viallii*. Male cone in connection with branchlet.11) TRE 210. *Walchia viallii*. Young male cone.



Walchia viallii. a) Branchlet with cones, b) Detail of a juvenile branchlet TRE 53.

Division: Coniferophyta Order: Coniferales (TAYLOR, 1981) Family: Voltziaceae

Trentia (WACHTLER, 2012)

2012 Trentia treneri, WACHTLER, p. 19

Etymology

Named after the region of Trentino, where this conifer was discovered for the first time.

Diagnosis

Conifer with consistent and fleshy, lanceolate foliage. Leaves parallel veined, sessile, leaving rounded abscission pits on the leaves. Apex obtuse.

Trentia treneri (WACHTLER, 2012)

2012 Trentia treneri, Wachtler, p. 15, 16

Holotype

TRE 61

Paratype

TRE 14, TRE 21

Material

TRE 7, 49, 55, 61, 62, 63

Etymology

Honouring Giovanni Battista Trener (1877– 1954), one of the leading geologists and naturalists of Trentino and the first director of the Natural History Museum of Trento. He was also a determined local patriot, fighting with his famous brother-in-law Cesare Battisti in the First World War.

Diagnosis

Trentia treneri has extraordinary fleshy and leathery leaves, with the widest part near or before the middle, tapering gradually to a rounded or bluntly pointed tip. Multiple parallel veins sprout from the base cross each leaf. The abscission point from the branches is large and concave.

Description

Branches: Probably wide-sprouting conifer resembling the extant *Agathis*. Leaves spirally arranged on slender branchlets (TRE 21).

Leaves: The foliage of *Trentia treneri* is very distinctive: adult leaves are 10 (TRE 61) to 12 cm long (TRE 55), and on the widest side from 2 to 3 cm broad. They bear no axis or petioles but are directly and for the whole length attached to the foliage shoot. The leaves are ovate-lanceolate, reaching their maximum width just before the middle. The apex is rounded. Sometimes they can be extremely fleshy and leathery (TRE 55, TRE 62), suggesting a habitat with longer dry seasons. Parallel, never forking mid-veins (TRE 61 = 15 veins) cross the whole leaf.

Male cones: One completely preserved cone (TRE 49) suggests that it belongs to *Trentia treneri*. It is 10 cm long and 2.5 cm wide. Two attached leaves on the base 5 cm in length are a further element, as well as a 7 cm long naked stem. They are from the *Willsiostrobus*-type, the morphogenus for Triassic Voltziales, another demonstration of araucarian affinity, to which today's Podocarpaceae, *Wollemia* and *Agathis* belong.

Female cones: Up to 10 cm long and 2.5 cm wide. TRE 21 represents a young female cone. Its bushy, not ligneous character fits well with the concept of juvenile Voltzialean cones, especially from the Triassic period.



Trentia treneri. a) Single leaf, b) Shoot.



- 1) TRE 61B. Trentia treneri. Designed hlotype. Isolated leaf.
- 2) TRE 61A. Trentia treneri. Holotype. Counterpart evidencing the fine parallel veins.
- 3) TRE 61A. Trentia treneri. Holotype. Leaf basis showing the abscise-form from the main stem.
- 4) TRE 55. Trentia treneri. Isolated fleshy leaf.
- 5) TRE 14. Trentia treneri. Paratype. Two leaves.
- 6) TRE 21. Trentia treneri. Paratype. A slender stem with one attached leaf and a female cone.

Discussion

This conifer-species has striking resemblances with some of the contemporary Kauri pines or Agathis trees, predominately occurring in the tropical rainforests of the southern hemisphere (Australia, New Zealand). Not only do its fleshy tongue-shaped veined leaves have an external similarity with Trentia, but also the male cones differs only a little from Agathis. Also, today's Agathis australis male cones commonly hold two leaves on the petiole, close to the sprouting pollen cone, even though the normal size is about 7 cm in length. Only the elongated female cones - roughly spherical in mostly Agathis-plants incorporate more features of Palaeozoic-Mesozoic conifers.

From the outer aspect, Carboniferous-Lower Permian Cordaitales, thought to be an ancestor of the conifers or having at least parental affinities with them – with their strap-shaped leaves and veins running also parallel with the long axis of the leaf – have some affinities with *Trentia*. Apart from decreasing or extinction in the earliest Permian times, its leaves reach up to 1 m in length. Also, their fertile organs are completely different from *Trentia*.

Ortiseia leaves are not as long and their branchlets are covered with needles.

More similarities exist between Middle Triassic (Ladinian) *Pelourdea vogesiaca* (WACHTLER, VAN KONIJNENBURGH & VAN CITTERT, 2000; KUSTATSCHER ET AL., 2004), and were largely recovered in the Olenekian German Buntsandstein. Also, their leaves are from 8 to 15 cm long and 1.5 to 2.2 cm wide and hold an obtuse apex. Therefore, it could be assumed that *Trentia treneri* figures as a progenitor for this group of Triassic conifers.



7) TRE 49A *Trentia treneri*. Suggested male cone.8) TRE 49B *Trentia treneri*. Counterpart of the male cone.9) TRE 21. *Trentia treneri*. Details of the young female cone.

Division: Coniferophyta Order: Coniferales (TAYLOR, 1981) Family: Albertiaceae Genus: *Albertia* (SCHIMPER & MOUGEOT, 1844)

Albertia scopolii (WACHTLER, 2012)

Albertia; SCHIMPER & MOUGEOT, Pl. XVI, Fig. A1 *Albertia*; RENAULT, Pl. 7, Fig. 14 2011 Albertia alpina, WACHTLER, pag. 127, Fig. 1 - 15 *Albertia scopolii*, WACHTLER, p. 21

Holotype

TRE 9

Paratype

TRE 4

Material

TRE 32, 126, 159

Etymology

Named after Giovanni Antonio Scopoli (Cavalese 1723—Pavia 1788). He spent the majority of his time studying botany and put together extensive plant collections. Scopoli was also the author of several publications about flora and fossils but became involved in several rivalries between other scientists and died embittered and misunderstood.

Diagnosis

Conifer with sharply pointed foliage standing straight outwards or only slightly curved. Leaves decurrent, only sometimes overlapping the next ones.

Description

Leaves: In extreme cases, up to 5 cm long (TRE 4), but usually up to 3 cm long and 2 to 3 mm wide on the base (TRE 9, TRE 32). Sword-shaped, ending with a long, stiff point. A midrib is observably only sometimes, and then mostly on the decurrent basis. Usually, they do not overlap each other.

Male cones: Of the *Darneya* type. They are consistently (TRE 57) 11 cm long, 4 cm wide and bulky. From a massive cone axis diverge the fertile foliage, which is up 1.5 cm long. They end lanceolate and sharply pointed. The subtle pollen clusters are densely aggregated around the sporophylls.

Female cones: Of the *Pusterostrobus* type. Young seed cones are ovoid to sub-globose, up to 4 cm long (TRE 4) and 3.5 cm wide. Scale-bracts are entire.

Discussion

Albertia scopolii foliage could sometimes be confused with Ortiseia leaves, which are, however, much more rounded on the apex and wider on the base. A. scopolii, with its sword-shaped needles, has a striking resemblance to Early Triassic Albertia alpina from the Dolomites, Also, their strange massive pollen-cones, resembling Anisian Darneya schaurothi (WACHTLER, 2011), thought to belong to Albertia alpina foliage, is a further indication that the Albertiaceae are of Permian origin. Darneya dentata from the Anisian Grés à Voltzies of Vosges male cones are smaller (only up to 7 cm long, 2 cm wide). Only French Early Triassic Darneya peltata (up to 10 cm long) and especially D. mougeottii

> *Albertia scopolii.* a) branch, b) male cone (TRE 9); c) Microsporophylls





1) TRE 4. Albertia scopolii. Branch with an attached young female cone.

- 2) TRE 4. Albertia scopolii. Detail of the female cone.
- 3) TRE 9. Albertia scopolii. Designed holotype. Part of a twig.
- 4) TRE 159. Albertia scopolii. Twig.
- 5) TRE 57. Albertia scopolii. Mature male cone.

(up to 11 cm) reach about the same size as *Darneya* cones of the Permian of Tregiovo (GRAUVOGEL-STAMM, SCHAARSCHMIDT & MAUBEUGE, 1979). *Albertia* was recognised in the nineteenth century (SCHIMPER & MOUGEOT, 1844) and has been regarded as an Early-Middle Triassic conifer, although there are doubts about its insertion and growing stages. The foliage habitus resembles in many respects today's *Araucaria bidwillii*

but the cone structure, and in particular the male, is completely different. Male cones of this appearance are not recorded in any other living conifers, so it is assumed that they became extinct in the Late Triassic.

Also, the usually small-sized female cones, known as *Pusterostrobus* (WACHTLER, 2011), stand with their spherical, slightly elongated shape, and not lobed aspect, isolated in the group of Permian-Triassic conifers.



Till now undefined conifer cones

1) TRE 316. Ortiseiastrobus sp. Young female cone with clearly visible bracts.

- 2) TRE 379. Undefined cone, probably Ortiseia.
- 3) TRE 209. Ortiseiastrobus sp. Adult female cone.
- 4) TRE 165. Undefined female cone.
- 5 + 6) TRE 341, TRE 118. Undefined cones.

Division: Sphenophyta Order: Equisetales (DUMORTIER, 1829) Family: Equisetaceae (MICHAUX, ex DC 1804) Genus: *Neocalamites* (HALLE, 1908)

Neocalamites tregiovensis (WACHTLER, 2012)

2012 Neocalamites tregiovensis, WACHTLER, p. 29

Holotype

TRE 76

Paratype

TRE 77

Material

TRE 6, 16, 78, 82, 166, 299

Type localities

Tregiovo - Le Fraine

Type horizon and age

Early Permian (Artinskian-Kungurian) Tregiovo-Formation

Etymology

Named after Tregiovo in the Italian province Trentino.

Diagnosis

Sphenophyta, with massive stems characterised by broad longitudinal ribs passing without alternation through the nodes. The nodal diaphragms resemble rounded discs. From the main stems diverges a secondary axis with whorls of needle-like leaves. Linear leaves conjoin close to the base to form a narrow collar at nodes.

Description

Stem: Tangential striae relatively widely separated. In paratype TRE 77, we have a distance of 1.5 mm each from the other; so that only 20 ridges cover the 3 cm wide part of the stem. The same habitus exhibits all other material (TRE 111, TRE 6, and TRE 16). The ribs pass without evident interruption through the node (TRE 77). TRE 111, as well as TRE 160, correspond to apical parts and ends like many Paleozoic-Mesozoic Equisetiales, broadly rounded. TRE 299 evidences the branching system of the mas-

sive lateral stems. The diaphragms (TRE 16, TRE 78) are consistent, from 3 to 5 cm wide with protoxylem canals on the outer margin. **Leaves:** The secondary shoots consist of several whorls at a distance of approximately 2 cm with 2 to 10 (holotype TRE 76) acicular leaves sprouting out. They arch steeply upward from their position without overlapping the whorls above. Leaves are fused into nodal sheaths and coalesce to form a short basal collar. The leaves, usually 3 cm long, evidence a thick texture, and are narrow, wedge-shaped and straight, with nearly the same width from the base to the apex.

Discussion

Isolated remains of horsetails build some of the common elements of the Early Permian (Artinskian-Kungurian) flora of Tregiovo.



8) TRE 299. Neocalamites tregiovensis with massive lateral branches. The tangential striae in the lateral whorls are also relatively wide spaced.



1) TRE 76. Neocalamites tregiovensis. Designed holotype. Part of the secondary whorls and the axis with the leaves.

- 2) TRE 77. Neocalamites tregiovensis. Paratype. Portion of stem with one internodium.
- 3) TRE 111. *Neocalamites tregiovensis*. Paratype. Apical part of a main stem.
- 4) TRE 160. Neocalamites tregiovensis. Big stem (24 cm long).
- 5 7) TRE 115, TRE 16, TRE 78. Neocalamites tregiovensis. Isolated diaphragms.

They demonstrate that the climate was wet enough or that there were enough rivers or lakes to allow colonisation with sphenophyta.

Neocalamites tregiovensis cannot be included in the genus Equisetites because the microphylls do not form sheaths. Triassic Equisetites (E. mougeotii, E. arenaceus) (KUSTATSCHER ET AL., 2007; WACHTLER, 2011), as well as Upper Permian Neocalamites mansfeldicus from German Kupferschiefer (BRANDT, 1997), hold the linear ribs much more closely than N. tregiovensis. Only some newly discovered Upper Permian Alpine Neocalamites (WACHTLER, in press) hold the ribs broadly, in the same manner as N. tregiovensis.

Carboniferous-Early Permian *Calamites*, with its leaves of the last order, known as

Asterophyllites or Annularia, exhibit the same broad striae, but their secondary whorls have another leaf structure.

An insertion in the group of *Asterophyllites* was even taken into consideration for their needle-like structure of last order born in whorls, but their reduced number of sometimes only two leaves has to be regarded as different.



Neocalamites tregiovensis a) Suggested whole plant with lateral shots b) whole plant naked, c) Diaphragm, d) Apical part with lateral whorls (TRE 299).

Division: Sphenophyta Order: Equisetales (DUMORTIER, 1829) Family: Sphenophyllales (MICHAUX, ex DC 1804) Genus: Sphenophyllum (BRONGNIART, 1828)

Sphenophyllum sp. (BRONGNI-ART, 1828)

Material

TRE 136 sterile pinnula

Type localities

Tregiovo - Le Fraine

Type horizon and age

Early Permian (Artinskian-Kungurian) Tregiovo-Formation

Discussion

That in the Tregiovo-Flora were present also other Sphenophyta will be documented by wedge-formed, apically rounded leaves sprouting out from a relatively massive central axis and inserted actually as *Sphenophyllum* sp. They are arranged bilaterally and symmetrically. Whether they can be inserted into one of the *Sphenophyllum* species from the German Rotliegend like *S. oblongifolium* or *S. verticillatum* (BARTHEL, 2009) can only be determined when more material is recovered.

In summary, the importance of these horsetails lies in the contestation of the common belief that the arid Permian age holds as well as a lot of xerophytic humidity-loving plant representatives. Moist areas or spaces with enough groundwater where their rhizomes reach down to the water-saturated soil were apparently frequent. There, they may have formed more or less extensive monocultures.



TRE 200. *Sphenophyllum* sp. Theseu nusual secondary whorls suggest, that in the Tregiovo-Flora different horsetails-species were present.

Division: Ginkgophyta Order: Ginkgoales (ENGLER, 1897) Family: Ginkgoceae (ENGLER, 1897) Genus: Baiera (BRAUN, 1843)

Baiera pohli sp. nov. (WACHT-LER), 2013

1876 Baiera digitata (BRONGNIART) HEER P. 7, pl. 21, fig. 1 1936 Sphenobaiera digitata FLORIN, p. 108 2012 Sphenobaiera digitata, WACHTLER, p. 18 - 19

Holotype

TRE 45

Paratype

TRE 86

Material

TRE 5, 239, 233, 242, 297

Etymology

Named after the German collector Burkhard Pohl, who helped to develop paleontology worldwide.

Type horizon and age

Early Permian (Artinskian-Kungurian) Tregiovo-Formation

Diagnosis

Leaves irregularly lobed with a collar at the base. Foliage-width constant, apex obtuse. Ovules formed at the end of a stalk.

Description

Leaves: Baiera pohli foliage can reach a considerable length: TRE 297 is more than 20 cm long, but with a width of only 0.5 cm. It forks irregularly and more closely resembles a dried shrub than a leafy plant. That the Early Permian ginkgophytes have mainly all of the characteristics of the extant, apart from the strange foliage aspect, can be seen in specimen TRE 86, an adult leave (about 15 cm long) with 4 cm long basal spur shoots. The leaves are obtuse, deeply dissected into linear segments with innumerable fine veins. Fragmentary ginkgo-leaves are difficult to establish, so that only whorls are suggestive of regard them as Baiera. **Ovules:** TRE 45 shows several fossilised

seeds, evidencing that the fructification



Baiera pohli. a) Leaf (TRE 297), b) Leaf with basal spur shoot (TRE 86) c) Young leaf with attached seeds (TRE 45).


1) TRE 45. Baiera pohl sp. n. Designed holotype. Leaf with two seeds on the upper right side and one on the left side.

- 2) TRE 5. Baiera pohli sp. n. Leaf.
- 3) TRE 239. Baiera pohli sp. n. Detail of repeatedly dichotomizing veins
- 4) TRE 87. Baiera pohli sp. n. Young male cone or basal spur shoot.
- 5) TRE 86. Baiera pohli sp. n. Mature leaf with a basal spur shoot.



Baiera pohli. TRE 401. Suggested male cone

modified marginally from the Palaeozoic to the present. The leaves – in this case juvenile – are up to 7 cm long, minute (1.5 mm wide), and forking twice. Also, TRE 233 holds characteristic two ovules. The ovules are borne at the apex of one leaf, (about 5 mm) having mainly the same width as the sterile ones. It is presumed that the extant short shoots are nothing other than modified leaves. Between the sterile leaves, a slightly curved stalk-leave sprout out is directly attached, and on the top are one to two ovules.

Pollen cone: TRE 87 is the only male cone found. The catkin-like pollen cone consists of a main axis showing divided microsporophylls. From this aspect, it must be an immature cone.

Discussion

In 1843 Friedrich Wilhelm BRAUN described with the name *Baiera* ginkgo-like fossil

leaves from the Rhaetio-Liassic of Bayreuth. However Rudolf FLORIN (1936) presented a new genus *Sphenobaiera* for Russian Triassic ginkgophyta, only based on the lack of or a not distinct petiole. Establishing a new genus with only these criteria can be regarded as doubtful and retaining the old term *Baiera* is therefore more reasonable (BAUER ET AL., 2013).

Today's ginkgo leaves are fan-shaped with veins radiating out into the leaf blade, sometimes bifurcating, but never anastomosing to form a network. Two veins enter the leaf blade at the base and fork repeatedly in two. The leaves can sprout out on long and also on short, stubby spur shoots, where they are clustered at the tips.

The most known Paleozoic ginkgophyta (Spheno)Baiera digitata - recorded from the younger Gröden Formation of Bletterbach (FISCHER et al., 2010) - was a widespread flora element in the European Upper Permian. Particularly in the German Kupferschiefer (common near Mansfeld), as well as in Rotliegend, the plant was known from the beginning of the nineteenth century. The leaves reach a length of 15 cm, in that they are shorter than Baiera pohli; the dichotomous branching is also much more regular in Baiera digitata, and the lamina is wedgeshaped. Other basal Permian, and therefore interesting as an early ancestor of Ginkgophyta, are Ginkgophytopsis, Ginkgophyllum (BAUER ET AL. 2013), and also Psygmophyllum (Permo-Carboniferous from Eurasia). Trichopitys from the Lower Permian of France was thought to could be included in the list of potential Ginkgoalean precursors, but after the discovery of so many high evolved ginkgoales from Early Permian, this seems more and more improbable. Otherwise, Baiera perneri (WACHTLER, 2013) from the Earliest Permian holds much more regular leaves and could in the same way be regarded as most primitive ginkgo with affinities to some progymnosperm plant. Surprisingly, we can establish that *Baiera* pohli have - due to its inchoate and irregular branching-system and the shrub like appearance - all of the characteristics of an extremely rudimental ginkgophyta, but it holds all of the items of real ginkgos: The collar or the ovules are borne on the apex of modified leaves.



6) TRE 297 Baiera pohli sp. n. Big ginkgophyte "shrub".

7) TRE 242. *Baiera pohli sp. n.* Strangely branching ginkgophyta, characteristic for the Tregiovo-Formation.
8) TRE 233. *Baiera pohli sp. n.* Several ginkgo-leaves. The leave on the right upper side corresponds most the Permian leave-type known from other parts. In the center two ovules.
9) TRE 233. *Baiera pohli sp. n.* Detail of the young ovules.

Division: Pteridosperma Order: Peltaspermales (TAYLOR, 1981) Family: Peltaspermaceae (PILGER and MEL-CHIOR in MELCHIOR and WERDERMANN, 1954)

Genus: Lepidopteris (SCHIMPER, 1869)

Lepidopteris meyeri sp. nov. (WACHTLER, 2013)

1869 *Lepidopteris ottonis*, SCHIMPER, Traité I. p. 574 1906 *Callipteris martinsii*, ZEILLER, BLANZY ET CREUS-OT, p. 71

1959 - *Lepidopteris martinsii,* TOWNROW S.345 Text Fig. 1L, 2J, 3G-K, 4A,B 5J, 6D

1990 *Peltaspermum martinsii*, POORT AND KERP, Pl II, III, IV; V.

2012 - Peltaspermum martinsii WACHTLER p. 32

Holotype

TRE 351

Paratype

292 (megasporophyll) TRE 293 (megasporophyll adaxial side)

Material

TRE 71 (leaves), TRE 263 (frond bearing fertile peltate discs), TRE 247, 343 (peltate discs)

Type localities

Tregiovo - Le Fraine

Type horizon and age

Early Permian (Artinskian-Kungurian) Tregiovo-Formation

Etymology

Named after German Jürgen Meyer, Zwickau, a profound expert of the Carboniferous-Permian floras.

Diagnosis

Minute megasporophylls in the form of peltate discs dorsiventrally holding the ovules. Megasporophylls papillose, bordered with hairs, global aspect plump. Leaves leathery, midget, with intermediate pinnula.

Description

Leaves: At Tregiovo, sterile as well as fertile *Lepidopteris meyeri* material is common (TRE 10, 11, 17, 71, 72, 292, 293, 247, 343, 351). Their usually bipinnate fleshy fronds hold minute entire to crenulated small pinnules. The venation is mostly obscured by the thick cuticle, and the mid-vein is relatively weak. The foliage is up to 5 mm long and wide, covering as "Zwischenfiedern (intercalary pinnulas) the axis. A good example of a mainly complete branch is TRE 353. The pinnulas are extremely coriaceous, no distinct veins are visible, whereas TRE 71 evidence well the intermediate pinnulas, covering densely the axis with leaves. Sometimes some intermediate veins are recognisable. TRE 263 shows the disposal of the umbrella-like megasporophylls connected by a long petiole with the main axis.

Megasporophylls: The ovuliferous organs *Peltaspermum meyeri* - reaching from 5 to 8 mm in diameter - consist of more or less flattened, radially symmetrical umbrella-shaped peltate discs (TRE 18, 73). They are subdivided into several (from 8 to 10) segments, dorsiventrally holding the seeds. Holotype 292 shows aggregates around the inner circle on the backside 8 ribs with as many ovules. The discs are densely covered with visible hairs. TRE 293 and 247 show the front side. A 10 mm long, subtle peduncle connects the megasporophyll with the main axis.

Discussion

The worldwide ranging Peltaspermales, a group of seed-ferns known for its fronds and leaves, such as Autunia, Arnhardtia, Rhachiphyllum, Hurumia, Scytophyllum, Lepidopteris, Matatiella, Townrovia or Thinnfeldia, belong to the most suggestive Palaeozoic and Mesozoic flora elements, although they seem to be extinct in the Jurassic. Typically for all of these seed-fern species, their female reproductive organs are formed by umbrella-like peltate heads (therefore the name latin name Peltaspermum), whereas their pollen-organs are known as Antevsia. The order of Peltaspermales originates mainly on the Permian-Carboniferous boundary. In a relatively short time, they arose to a widespread group with about 30 genera and 135 species encountered around the world, with Permian Autunia con*ferta* as one of the most representative plants in the Northern hemisphere. The earliest true Peltaspermales came from the German basin. Hurumia (Odontopteris) lingulata also holds peltate ovuliferous organs arranged around the main rachis as Rachiphyllum or Peltaspermum dammannii (BARTHEL, 2009; PERNER &



1) TRE 351 Lepidopteris meyeri sp. n. Designed holotype. Frond with the minute leathery leaves.

- 2) TRE 271. Lepidopteris meyeri sp. n. Young leaflet.
- 3) TRE 71. Lepidopteris meyeri sp. n. Frond evidencing the "Zwischenfiedern" (Intercalary pinnulas).
- 4) TRE 263. Lepidopteris meyeri sp. n. Part of frond with several fertile peltate discs.

WACHTLER, 2013), but their foliage is too different from *Lepidopteris meyeri*. *Hurumia* and *Rachiphyllum* generate also flatten shields, and only *Peltaspermum dammannii* ovuliferous organs fulfil the typical aspect of the segmented megasporophylls.

The genus *Lepidopteris* was erected in 1869 for ferns with bipinnate or tripinnate fronds, thick pinnules with often-unclear evidenced veins, holding intercalary leaves. After that, attempts were made to change this name to *Peltaspermum (martinsii)* (POORT & KERP, 1990). Because the names of all peltate megasporophylls holding seed-ferns with a total different foliage like Triassic *Scytophyllum* had to be changed, I believe that the name *Lepidopteris* must be maintained, maybe leaving *Peltaspermum* as the name for peltate ovuliferous organs.

Abundant *Lepidopteris (Peltaspermum) martinsii* fronds and fragmented fertile peltate shields furnishing cuticle material crop out from the Upper-Permian Gröden-Formation in the Bletterbach-Butterloch (CLEMENT-WESTERHOF, 1984), and near Recoaro. Entire fronds of Lepidopteris martinsii measure in the best cases from 18 cm to 30 cm (POORT & KERP, 1990). Apart from the Alpine flora, Lepidopteris martinsii is also well represented in Germany and England, with representatives ranging to China. Lepidopteris meyeri has some affinity with Lepidopteris martinsii, but apart from its younger age, misses the papillose character of the megasporophylls, being also of much more furry and plump appearance. The megasporophylls of Lepidopteris meyeri (TRE 18, 292, 293, and 247 = 0.8 cm in size) reach only one-third of the size of Early Triassic Peltaspermum bornemannii (having a normal size of 2.5 cm (VAN KONIJNENBURGH-VAN CITTERT, WACHTLER & KUSTATSCHER, 2007), belonging to Scytophyllum bergerifoliage.



Lepidopteris meyeri a) Frond (TRE 351), b) Pinnula fragment (TRE 71), c) *Peltaspermum meyeri*. Entire female fructification (TRE 263), d) Megasporophyll front side (TRE 293), e) Megasporophyll back side (TRE 292).



5) TRE 292. *Peltaspermum meyeri.* Paratype. Characteristic female fructification with the peltate umbrella-like discs. Abaxial side. Note the minute hairs. Ovules lie dorsiventral.
6) TRE 293. *Peltaspermum meyeri.* Paratype. Megasporophyll. Adaxial side thought to belong to *Lepidopteris meyeri.*7) TRE 247. *Peltaspermum meyeri. P*eltate umbrella-like discs with the holding long peduncle. Adaxial side.
8) TRE 343. *Peltaspermum meyeri.* Abaxial side.

Division: Pteridosperma Order: Peltaspermales (TAYLOR, 1981) Family: Peltaspermaceae (PILGER and MEL-CHIOR in MELCHIOR and WERDERMANN, 1954)

Genus: Peltaspermum (HARRIS, 1937)

Autunia conferta (STERNBERG, 1893) KERP 1988)

1893 *Callipteris conferta*, (STERNBERG) BRONGNIART - POTONIÈ 111 Taf. I Fig. 1, 2 1988 *Autunia conferta* (STERNBERG 1826) KERP nov. comb. KERP & HAUBOLD, 143

1988 Autunia (al. Callipteris) conferta (STERNBERG 1826) KERP nov. comb. KERP, BARTHEL & RÖSSLER 61 pl. 4 fig. 4

Material

TRE 308 sterile pinnula, TRE 327 Megasporophyll

Type localities

Tregiovo - Le Fraine

Type horizon and age

Early Permian (Artinskian-Kungurian) Tregiovo-Formation

Discussion

One of the best-known genera of callipterids from Lower Permian is *Autunia (conferta)*. In the Tregiovo-Formation, some rare pinnula attached obliquely to the axis, tongue-shaped, with a size of about 10 mm and width of 5 mm will be found (TRE 308). The mid-vein is sunken, well-defined and therefore readily visible. It persists for about three quarters of the pinnule length. The branching of the veins is featherlike, whereas some veins are coming directly from the main axis.

Probably some bigger peltate shields, up to 2 cm long and wide (TRE 327), belong to the species *Autunia conferta* and we have to accept that two different *Peltaspermum*species were present at Tregiovo. *Peltaspermum meyeri* holds minute leathery leaves with ovulate organs that do not reach 1 cm in size, and double-sized megasporophylls thought belong to *Autunia conferta*. The fertile shields are also dotated with a higher amount of ovules.



1) TRE 308. Small fragment of the Peltaspermaceae Autunia conferta.

2) TRE 403. Adaxial side.

2) TRE 327. Autunia conferta. Megasporophyll.

Division: Pteridophyta Genus: Neuropteridium (SCHIMPER, 1879)

Scolecopteris sp. (ZENKER, 1837)

Material

TRE 136 (sterile pinnula)

Type localities Tregiovo - Le Fraine

Type horizon and age

Early Permian (Artinskian-Kungurian) Tregiovo-Formation

Discussion

Isolated leaf remains of some neuropterid fern-families occur occasionally. Due to their fragmentary character, to date, no detailed species have been established. Pinnula TRE 136, 3 cm long, 1.2 cm wide, corresponds to an isolated leaf, and is attached to a 2 mm broad stipe. The pinnula arise perpendicularly, the venation is neuropterid with a more or less clear midrib that extends more than halfway along the pinnula. Secondary veins sometimes diverge and fork.

This leaf-type is common in the Permian and could pertain to several ferns or seed ferns. Beneath the real fern, *Scolecopteris*, it could belong to *Pecopteris*, *Alethopteris*, *Neurocallipteris* or *Callipteridium*. Some parental affinities are also possible with *Odontopteris*, especially *O. schlotheimii*, which generate neuropterid foliage. However, until the fertile organs are known, an exact determination is impossible. It could be more important therefore to establish that the Late Permian Alpine flora was not so species poor and scant as always thought.



TRE 136. Neuropteridium sp. Single pinnula.



Neuropteridium sp. Reconstruction of a single pinnula.

Division: Pteridophyta Family: Osmundaceae (BERCHTOLD & PRESL, 1820) Genus: Sphenopertis (STERNBERG, 1825)

Sphenopteris suessi (GEINITZ, 1869)

1869 Sphenopteris suessi, Sphenopteris tridactylites, Sphenopteris oxydata, GEINITZ, fig. 2-8, table V
1999 Sphenopteris suessi VISSHER ET. AL. fig. 6,Table
1, Sphenopteris kukukiana fig. 12, Table 1
2012 Spehnopteris dichotoma WACHTLER, p. 35

Material

TRE 301, 166 sterile fronds, TRE 201, 329, 328 fertile frond, TRE 130 sterile pinnula, TRE 37 fertile pinnula

Type localities

Tregiovo - Le Fraine

Type horizon and age

Early Permian (Artinskian-Kungurian) Tregiovo-Formation

Description

Sphenopteris constitutes one of the most dominant flora elements of the whole Permian, in that it can be regarded as morphogenus, especially when sometimes older authors inserted it in the seed ferns, as well as a normal fern, because the fertile parts were not known.

This happened in the same way for the Alpine Fossil Floras where Sphenopteris was one of the first known plant species. In 1869, Hanns Bruno GEINITZ described from the region not far from Tregiovo, the Early Permian Collio-Formation in the Lombardian Prealps, several flora elements; amongst them, a new Sphenopterisspecies was reported and these were illustrated in a publication about fossils from Val Trompia. Apart from some doubtful Sphenopteris tridactylites (BRONGNIART) and Sphenopteris oxydata (GOEPPERT) previously known from the European Rotliegend, all figures (from 3-7, Table V) mainly show a new species honouring with Sphenopteris suessi the famous geologist Eduard SUESS, who handed him these specimens. Subsequently, other authors (REMY & REMY, 1978; VISSHER

ET AL., 1999), by describing some plant fragments from Tregiovo, introduced other Sphenopteris-species, mostly taking names from German Upper Permian localities (Zechstein) like Sphenopteris kukukiana or S. patens. Usually, all of the material, as published by GEINITZ, was always fragmentarily preserved. From the Upper Permian German Zechstein, other Sphenopteris-species were introduced (SCHWEITZER, 1960) (S. dichotoma, S. geinitzii, S. bipinnata, S. gillitzeri), often only based on the existence of one specimen, disregarding the fact that we have to include it with a fern with extremely changing leaflets (HAUBOLD & SCHAUMBERG, 1985). Sphenopteris-species with similar fronds (S. mathetii) were described from the Lower Permian Rotliegend of Thüringen (BARTHEL, 2009).

Several findings from the Tregiovo-Formation in recent years have established that the fern *Sphenopteris* constitutes the most frequent fern there. Although the leaflets are extremely multifaceted it can be assumed that we should include it with only one fern-species, and it would be reasonable to preserve the species name *Sphenopteris*



Hanns Bruno GEINITZ, (1869). Über Fossile Pflanzenreste aus der Dyas von Val Trompia. The only table figuring plants from the Early Permian Collio Formation. 1. Schizopteris fasciculata, 2. Sphenopteris tridactylites, 3-7. Sphenopteris suessi, 8. Sphenopteris oxydata, 9. Noeggerathia expansa.



TRE 301. Sphenopteris suessi. Sterile frond.
 TRE 301. Sphenopteris suessi. Part of a branching system with sterile pinnulas.
 TRE 166. Sphenopteris suessi. Sterile frond.

4) TRE 329. Sphenopteris suessi. Fertile frond.



Sphenopteris suessi. a) Single sterile frond TRE 130, b) Fertile leaf (TRE 37) c) supposed reconstruction of the whole plant.

suessi (GEINITZ, 1869). The differences in the foliage are mainly based on whether we use sterile fronds (TRE 301, 166, 328) or the much more skeletonised fertile ones (TRE 37, 329, 328), also figured by GEINITZ (1869).

Bigger fronds usually ramify the sterile leaflets (TRE 130, 301) being up to 3.5 cm long and 1.3 cm wide, evidencing undefinable vein-structure. Fertile single leaflets (TRE 37, 329, 328) reach a length of 1.4 cm and a width of 0.5 cm and are much more skeletonised, with the sporangia on the lower side of the leaflets (TRE 37). Especially in TRE 37B, two of the lower leaflets on the right side are good evidence of the attachment of the sporangia.

It could be stated that the desiccated looking *Sphenopteris* constitutes the true characteristic fern from the Alpine Permian, being present also in the Upper Permian

(WACHTLER, in press). Often it constitutes the only one fern traced, a hard to believe phenomenon when we think about the extraordinary richness of ferns beginning from the Early Triassic (Anomopteris, Ladinopteris, Gordonopteris, Anotopteris, Wachtleria etc.) and also the Carboniferous. Why the ferns declined so much in the Permian after a peak in the Carboniferous and Triassic must be studied further, because other water-loving plants like cycads and horsetails were not affected in this decline. Another unresolved question is whether in contrast to the Peltaspermales, the Cycadales or Sphenophyta, a direct descendant from Sphenopteris to the Triassic floras is harder to trace. It may be that the fern Anotopteris has the same parental affinities. Also difficult is the insertion in the fern-family, but with caution it could be regarded as Osmundaceae.



5) TRE 130A. Sphenopteris suessi. Part of a sterile leaflet.
 6) TRE 201 Sphenopteris suessi. Fertile frond.
 7) TRE 37B. Sphenopteris suessi. Part of a fertile frond.
 8) TRE 37B. Sphenopteris suessi. Detail of the sporangia.
 9) TRE 201. Sphenopteris suessi. Detail of fertile frond Fig. 6.

Division: Cycadophyta Order: Cycadales (DUMORTIER, 1829) Genus: *Nilssonia* (BRONGNIART, 1828)

Nilssonia perneri, (WACHTLER, 2012)

2012 Nilssonia perneri, WACHTLER p. 43

Holotype

TRE 2

Material

TRE 3

Etymology

Honouring Thomas Perner a German collector, who specialised in fossil cycads.

Diagnosis

Cycadalean-like plant with fine-veined leaves arising at right angles from a broad rachis. They are often and irregularly lacerated, but a tendency to geometrical segmentation is cognisable. Trunk ovoid, formed by elongated leaves, rounded on the apex.

Description

Whole plant: Holotype TRE 2 evidences a typical cycadalean aspect. A single frond is attached to the trunk and constitutes one of the rare cases in which a whole plant could be studied. The entire length of the preserved part of the plant is 36 cm.

Trunk: The bulbous trunk reaches a length of 10 cm and a maximal width of 6 cm. It is covered or consists of densely arranged compact leaves. The foliage of the stem evidences no similarity with the main fronds outgrowing from the upper side of the bulb. The leaves are tightly packed and show neither a central rachis nor veins. They are up to 4 cm long, a maximum of 0.6 cm wide, and are rounded on the apex.

Fronds: *Nilssonia perneri* (holotype TRE 2) evidences one 26 cm long frond arising



Nilssonia perneri n. sp. a) Detail of a pinnula showing cycadalean venation. b) Whole frond (TRE 2), c) whole plant



- 1) TRE 2. Nilssonia perneri. Designed holotype. Plant with one entire frond attached on the bulb.
- 2) TRE 2. Nilssonia perneri. Holotype. Apical part of the frond with segmented leaves.
- 3) TRE 2. Nilssonia perneri. Holotype. Detail showing the veins of a single pinnula.
- 4) TRE 2. Nilssonia perneri. Holotype. Rounded leaves of the bulb.
- 5) TRE 2. Nilssonia perneri. Holotype. Bulb.

from the upper side of the trunk. The frond is irregularly lacerated, although manifesting a disposition to a 1 cm broad segmentation. The main rachis, nerved by several strong and clearly visible mid-veins and consistently measuring 1 cm, holds the sometimes-folded leaves. The leaves are up to 2.5 wide on each side, delicate and densely arranged; never forking veins arise in a right angle from the main rachis. The concentration of the veins is very high (35 per cm). The apex of the frond on TRE 2 is slightly U-shaped.

Discussion

Permian cycad or cycad-like fossils are rare, and therefore, for a long time, it was thought that the first true cycads evolved in the Triassic. Now, based on findings all around the world, from the United States (in Early Permian sediments cycad-like Dioonitocarpidium-fructifications (DI MICHELE ET AL., 2001) to China (Permian-Carboniferous *Pseudoctenis*-foliage (POTT ET AL., 2010), we could assume that the first true cycads evolved just in the Permian or even on the Carboniferous-Permian boundary. Also, from the Upper Permian Gröden-Formation, recently a fair amount of cycadalean material has cropped out (WACHTLER, in press), among them Nilssonia-leaves and suggested cycad-like cones.

In this context, we have seen the new cycad-discoveries in the Val di Non. *Nilssonia perneri* with its attached fronds on the trunk is interesting because, for the first time, we have unequivocal evidence that a low-growing bulb-like stem is to be found in the first Permian cycads. Although Lower Permian cycadophyte foliage described as *Pseudoctenis samchokense* (formerly *Pterophyllum*) (KAWASAKI, 1934; POTT ET AL. 2010) have some superficial affinities with *Nilssonia perneri*, its clearly divided pinnate fronds could not be confused with them.

From the Italian Dolomites, in the last decades, abundant Early Triassic cycadremains, and all parts of the plant from bulbs and fronds to male and female strobili were found (WACHTLER 2010). Feather-like fertile leaves bearing cones (*Dioonitocarpidium*) – like recent *Cycas* – as well the cone-like structure from the Zamiaceae and Stangeriaceae are encountered in these Early Mesozoic layers. It could be stated that most ancestors of the different cycad-lines evolved at the same time. Therefore, the genus *Cycas*, which is usually regarded as the most primitive and as a living fossil, with its loosely organised female sporophylls lacking a central axis, has not necessarily evolved earlier than the others.

There are enough parental affinities to regard Early Permian *Nilssonia perneri* as the precursor of Early-Middle Triassic cycadophyte material from the neighbouring Dolomites. It could also give rise to some debate around whether *N. perneri* could be left in the group of Nilssoniaceae or have more similarities with the Bjuviaceae, as well as a massive presence in the Anisian layers of Dolomites.

Anisian Bjuvia olangensis, as well as Ladinian Bjuvia dolomitica, differs from Nilssonia perneri in having much bigger fronds, with fewer veins (B. olangensis 20-30, N. perneri 35) and being more irregularly segmented. However, Nilssonia braiesensis from Anisian of Dolomites, with its clearly segmented fronds, does not completely satisfy a close relationship with N. perneri, with its poorly spanned leaves. All Nilssonia species have, like Pseudoctenis, clearly and geometrically segmented pinnas, whereas Nilssonia perneri only sometimes show this. Clearly, there is a distinction from *Taeniopteris* foliage, with their also never forking, densely arranged veins, nevertheless having an entire leaf-character.

Division: Cycophyta Order: Cycadales (DUMORTIER, 1829) Genus: *Bjuvia* (FLORIN, 1933)

Bjuvia tridentina (WACHTLER, 2012)

Holotype

TRE 44

Material

TRE 47, 177

Etymology

Named after the province of Trentino (Southern Alps) where this Cycadophyta was found for the first time.

Diagnosis

Cycadalean-like plants with oblong sometimes irregularly lacerated extraordinary big leaves. Delicate secondary veins rise almost perpendicularly – parallel and unforked – from the rachis.

Description

Leaves: The incompletely preserved holotype TRE 44 clearly shows the concept of the Bjuviaceae. The leaves are oblong and sometimes segmented, as seen in the upper part of the leaf. The apex varies from U-shaped to V-shaped. Unforked secondary veins arise at right angles from the rachis. It was not possible to count the veins per centimetre because of its densely contracted nature, but it is estimated that there are around 30 to 40. Also, the petiole is consistent. TRE 177 represents a more lacerated leaf, also with the basal part, re-entering the normal visual structure of Bjuvia.

Cones: Male cones of *Thetydostrobus* type. Some possible pollen organs of *Bjuvia* (or *Nilssonia perneri*) are shown in TRE 47. The preserved parts are 12 cm long with a petiole that is 1 cm long, and the width is 6 cm, which is on the larger side. The sporophylls are 2 cm long and hold their pollen sacs on the lower surface. Due to its poorly conserved character, other information is difficult to establish.



Bjuvia tridentina n. sp. a) Single frond (TRE 44), b) Reconstruction of the whole plant.



1) TRE 44. Bjuvia tridentina. Designed holotype. Single leaf.

2) TRE 47. Thetydostrobus sp. Suggest pollen cone of a cycadealean-like plant (Bjuvia, Nilssonia).

3 + 4) TRE 177 *Bjuvia tridentina.* Frond and detail.

Discussion

Consistently, typically segmented or lacerated foliage often belongs to the common flora elements from Early Permian to Triassic and Jurassic. Thus, superficially, today's banana leaf-resembling leaves are inserted in the family of Bjuviaceae, and testified by accompanying female cycadalean cones in the Triassic (*Dioonitocarpidium*) ancestors of extant cycads (WACHTLER, 2010, 2011). They can reach consistent sizes, with measurements of 50 cm to 1 m, especially in the Tri-



5) TRE 409. *Dioonitocarpidium sp.* Suggested isolated megasporophyll belonging to *Bjuvia* or *Taeniopteris* (*Ladinia*).

assic (Bjuvia olangensis, Bjuvia dolomitica). Permian Bjuviaceae usually are a little smaller, probably growing between 20 and 30 cm, with much more densely arranged secondary veins (30-40 per cm against 20-30 in the Triassic form). Therefore, Bjuvia tridentina fits well in the evolving concept starting with Bjuvia (Taeniopteris) multinervis known from the Lower Permian Rotliegend to Anisian Bjuvia olangensis, Ladinian Bjuvia dolomitica from the Dolomites and extending to the Jurassic (Bjuvia simplex, (Bjuvia) Taeniopteris gigantea) (FLORIN, 1933; POTT ET AL. 2009; REMY & REMY, 1975). Also, in the Upper Permian (Wuchiapingian) of the Dolomites Bjuvia-leaves were recently recovered (WACHTLER, in press).

Bjuvia tridentina cannot be confused with Nilssonia perneri from coeval layers. Bjuvia bears large only sometimes lacerated foliage, whereas Nilssonia holds nearly evolved sometimes clearly defined cycad fronds. Less confounding problems are seen with Wachtleropteris valentinii, which is a several leaf-forking bushy plant with much smaller leaves. However, it cannot be disregarded completely that all of these cycadalean plants (Bjuvia, Nilssonia, Taeniopteris, Wachtleropteris) have a Carboniferous common ancestor, although in the Permian they simply evolved to completely different lines. Surprisingly, in the Triassic and perhaps in the Permian, we have identified fully evolved fertile organs that differ little from today's Cycas, Zamia or Dioon (SCHUSTER, 1932, DELEVORYAS, 1982).

Both cycadophyta fill a gap in palaeobotany. We can state that, at least from the Early Permian, and potentially just before, there were real cycads occurring in Tregiovo such as *Nilssonia perneri* or *Bjuvia tridentina* and in almost the same manner, enigmatic plants with the same cycadalean aspects, but also manifesting significant features of bennettitaleans, other gymnosperms, and possibly proto-angiosperms were present. Division: Cycadophyta Order: Taeniopteridaceae (WACHTLER, 2012)

Genus *Taeniopteris* sp. (KURTZE, 1839)

1978 *Taeniopteris (Lesleya) eckardtii,* Remy & Remy 1999 *Taeniopteris (Lesleya) eckardtii,* Visscher 2012 Taeniopteris eckardtii, Wachtler, p. 37

Description

Some leaves (TRE 70), with their lanceolate form, their sometimes restricted structure on the base, and their clearly evidenced collateral secondary veins, resemble *Taeniopteris eckardtii*, as seen for the Upper Permian German Kupferschiefer. However, not until the real nature of this cycadalean foliage is known, can it be classified as *Taeniopteris* sp.

The form-genus Taeniopteris builds some of the most enigmatic plant-groups from Permian to Triassic. Although known in innumerable single-leaf findings, an understanding of their fertile parts or the habitat of the entire plant was never reached. With caution, it was sometimes inserted in the group of cycadales, the pteridosperms or even some proto-angiosperm flora elements. Only a few of the so-called compound-foliages found with more leaves attached together have been recorded from the northern hemisphere, mainly from the German Kupferschiefer. Therefore, every discovery of plant assemblages of Taeniopteris is interesting for research.



1) TRE 70. *Taeniopteris sp.* Single leaf with pointed apex, 2) TRE 70. *Taeniopteris sp.* Basal part of the leaf with the lateral arising parallel veins.

a) Taeniopteris sp.Leaf reconstruction.

Division: Pteridosperma? Order: ? Family: ?

Ozolia (WACHTLER, 2012)

2012 Ozolia franei, WACHTLER, p. 43

Generic diagnosis

Shrubby plant with heart-shaped to elliptical leaves attached opposite each other alternately on a primary rachis.

Etymology

Named after the overlying Monte Ozol in the Val di Non.

Ozolia frainei (WACHTLER, 2012)

Holotype

TRE 28

Material

TRE 15

Etymology

Named after the Le Fraine streamlet, where the Tregiovo plant deposit lies.

Diagnosis

Medium-growing plant consisting of a main stem with irregularly opposite to alternate arising foliage. Leaves leathery and cor-



TRE 28 *Ozolia fraineii*. Designed holotype. Specimen with heart-like leaf.
 TRE 15. *Ozolia frainei*. Other leaf.

date to ovoid in form, connected to the main stipe by a stalk.

Description

Whole plant: TRE 28 is 25 cm long, with an elegant stem with leaves more distant from each other.

Foliage: TRE 28 has a 3 cm long petiole linked to a heart-shaped leaf. Due to its leathery character, no mid-veins or lateral veins are visible. The leaf is 4.2 cm long, with a width of 3.5 cm. Another leaf or fructification is visible on the apex, but not preserved enough to diagnose it. The foliage of TRE 15 evidences only a short stalk attached to the main axis. It has lateral veins, but this could also be caused by the undulated structure of the slab. This leaf is 3.5 cm long with a maximum width of 3.5 cm. The main rachis is 0.8 cm, which is broader than in the other specimen.

Discussion

A positive classification of this enigmatic plant is difficult, but with caution it could be inserted into the group of seed-ferns or ferns. *Ozolia* could not be compared with any other Permian or Early Triassic plant of the vegetation-rich floras of the Alps or Europe. The xeromorphic character of the leaves is certain.



Ozolia valentinii. a) Whole frond (TRE 13)

SOME ENIGMATIC PLANT FOSSILS FROM THE ARTINSKI-AN/KUNGURIAN (EARLY PERMIAN) FLORA AT TREGIOVO (TRENTINO, NORTHERN ITALY)

by Thomas Perner Oregon Institute of Geological Research 32 SE 139th Ave Portland, OR 97233-1844

Abstract

The latest Artinskian/Kungurian Permian flora from Tregiovo-Le Fraine (Val di Non, Trentino, Northern Italy) holds some flora elements that can be inserted into groups of known plants with some difficulty. Therefore, the new *Wachtleropteris valentinii* nov. gen will be described, which holds some characteristics of the cycads but their expanding bifurcating growth distances it from them. At the same time, due to its ramifying leaves, analogies to the primitive ginkgophyta *Baiera* are evident, but are not sufficient to include them due to their distinguished midrib in this class. The cones have affinities with the cycdophyta, but only further findings can establish the real nature of this interesting plant.

Online: December 2013.

Key words: Permian floras, Cycadophyta, Ginkgophyta, Northern Italy

Division: ? Order: ?

Wachtleropteris gen. nov. (PERNER 2013)

Etymology

Named after Michael Wachtler who discovered new Permo-Triassic Fossil Floras in the Alps and described them extensively.

Diagnosis

Plant with bifurcating leaves holding a distinctive central rachis.

Wachtleropteris valentinii nov. comb. (WACHTLER) PERNER 2013

2012 Taeniopteris valentinii, WACHTLER, p. 39-41

Holotype

TRE 38

Paratype

TRE 39, TRE 1

Material

TRE 18, 40, 41, 65, 112, 113, 114, 131, 132,133, 134, 155, 179, 196, 256

Etymology

Dedicated to modest forest-man Fèro Valentini from the Val di Non, who discovered many plants on Tregiovo-Le Fraine and had a passion for the marvels of nature.

Repository

The holotypes and paratypes are stored at the Tridentine Museum of Natural Sciences (Trento, Italy). Their numbers are prefixed by "TRE" for Tregiovo.

Diagnosis

Shrubby plant with a ligneous stipe. Typically bifurcating leaves hold a distinct central rachis; lateral veins are usually hidden.

Description

Whole plant: Bushy low-growing plant with several times dichotomously-branched leaflets. Holotype TRE 38 shows a 13 cm part of a two times bifurcating plant. The peduncle is 1 cm wide and ligneous. Small adventitious roots are cognisable. The root system is better evidenced in TRE 155, whereas TRE 90 shows a mainly complete preserved adult plant with a young sprout growing from the same root basis. The leaves sprout out in a mainly seamless manner, without petiole,

from the rachis. A xeromorphic aspect of the plant is apparent. It is suggested that the whole *Wachtleropteris valentinii* plant can reach a size between 30 and 50 cm.

Leaves: Holotype TRE 38 shows four leaves branching from the knurl. The rachis-like stem is divided into ramifying segments, and the leaves hold a pronounced midrib, about 5 mm wide, from which arise lateral, nearly invisible, secondary veins at right angles to it and parallel to each other, which are closely crowded. The strap-shaped foliage is erected or obliquely spreading laterally, and is 2 cm wide in total. The rounded apex of the leaves is evident in the counter-plate of the holotype TRE 38 and also in TRE 39, TRE 91, TRE 134 and TRE 155. The preserved parts of the leaves on TRE 1 are 13 cm long, so an original length of 10 to 25 cm could be supposed. TRE 113 represents a leaf with suggested feeding traces of animals, as sometimes seen in Triassic Ladinia-leaves.

Male organs: TRE 39 is a good example of the aspect of a male fructification. The entire cone is 7 cm long and 3 cm wide and from a 1 cm long and 1 cm broad leaf-like petiole. Two bifurcating sterile leaves sprout on the right side, with one on the left side, whereas the other holds the fertile organ. The petiole continues without constricting in the cone, and the microsporophylls are spirally arranged on the main axis. The slightly pending sporophylls are 1 cm long, and pointed on the apex with the pollen densely covering the lower surface.

Female organs: A fertile specimen probably belonging to *Wachtleropteris valentinii* is TRE 70. The cone is 12 cm long, and also has a petiole 1 cm long. The sporophylls on

the basal part reach a length of 2.5–3 cm. They hang down under the weight of the fertile components. Elongated and rounded seeds are inserted on the lower part of the leaves. One to two seeds are embedded on the lower surface. However, whether several seeds on specimen TRE 18 on the lower part of *Wachtleropteris* leaves belong to this plant must be supported by further discoveries.

Discussion

When this plant was described for the first time in 2012 (WACHTLER, 2012) it was inserted as *Taeniopteris valentinii* with caution, which is a morphogenus assigned to many Late Carboniferous, Permian or Triassic foliage (TAYLOR ET AL., 2009) that is characterised by strap-shaped leaves, usually provided with a prominent mid-rib from which depart arching secondary veins at a right angle.

Although having some affinities with other *Taeniopteris* leaves recovered from the Early Permian Rotliegend (*Taeniopteris jejunata, Taeniopteris abnormis*), as well as Late Permian *Taeniopteris eckardtii*, too many aspects emerged due to further findings to leave them in this morphogenus. First of all, it occurs frequently in the Tregiovo plant beds, and is sometimes encountered with attached fertile organs on the stems (TRE 39, TRE 132).

In the Early Permian Tregiovo, we have some cycadophyta, such as *Nilssonia perneri* or *Bjuvia tridentina*, which can be inserted without hesitation in a lineage with the Upper Permian and Triassic *Nilssonia* and *Bjuvia*-tribe. Whereas the male cones (TRE 39) have some analogy with recent cycad



Plant and leaf variability of *Wachtleropteris valentinii* n. sp. a) TRE 1, b) TRE 38 holotype, c) TRE 90, whole plant with young sprout, d) TRE 256, e) TRE 155, young plant.



TRE 38. *Wachtleropteris valentinii* nov. comb. Designed holotype. Part of the plant evidencing the bifurcating foliage.
 TRE 39. *Wachtleropteris valentinii* nov. comb. Holotype. Rounded apical part. Sometimes subtle hairs cover the leaves.

3) TRE 90. Wachtleropteris valentinii gen. nov. nov. comb. Leaf showing the extremely broad rachis.

4) TRE 1. Wachtleropteris valentinii nov. comb. Paratype. Compound found of five leaves.

5) TRE 39. Wachtleropteris valentinii nov. comb. Paratype. Male cone attached on the stem with leaves.

pollen organs, the arrangement on a several times bifurcating stem is unusual and has never been recorded from true cycads. Extant cycads are also characterised by a bulbous stem, which, in this case, we do not have (see TRE 38). It is indeed unique that this newly-described species represents a scrubby and ramifying bush.

In their growth habitat, they more closely resemble the bennettitalean group of Williamsoniaceae with their slender branched stems and *Nilssoniopteris* leaves. However, their fertile organs are completely different. Male cones of *Wachtleropteris valentinii* hold more and smaller sporophylls, whereas the female organs are characterised by their larger, but less numerous sporophylls.

We can also not find any correlation with Permian or Triassic seed ferns, especially the Peltaspermales, which are well represented in this area with *Peltaspermum meyeri* and *Autunia conferta*. Also, the group of Coniferophyta, Lycopophyta and Sphenophyta have to be discarded for their completely different foliage and cone arrangement.

One group with some affinities with this plant are surprisingly the Ginkgophyta.

Baiera pohli, from Tregiovo, with its slender bifurcating leaves, holds a mainly identical branching-concept. As in Wachtleropteris, it seems also to not be based on geometrical organisation but looks very incidental. Indeed, sometimes when the median rachis is not very well evidenced or obscured in Wachtleropteris and the leaves are relatively slender (in most cases they are wide enough to make a sure distinction), it can be confused with Baiera pohli. Otherwise, Baiera are characterised by their circular and often conjoined two seeds and, when present, also a collar on its leaf base. However, if the globular seeds from TRE 18 belong to Wachtleropteris, the possibilities of soma parental affinities grow.

Wachtleropteris valentinii therefore raises more questions than it resolves. The only way to understand this plant, especially its cones, is to accept some cycadalean affinities, but to agree in the same way that Early Permian ginkgophyta, especially those from Tregiovo, hold a similar ramifyingconcept.

In any case, this mysterious plant constitutes one of the most interesting and new flora elements of Permian Tregiovo.



Wachtleropteris valentinii n. sp. a) Whole plant (TRE 38) holotype, b) Male cone (TRE 39).



6) TRE 39. Wachtleropteris valentinii gen. nov. nov. comb. Paratype. Entire male cone attached on the stem with leaves.

7) TRE 39. Wachtleropteris valentinii nov. comb. Paratype. Detail of cone with the pollen on the lower surface.

8) TRE 48 Wachtleropteris valentinii gen. nov. nov. comb. Paratype. Entire female cone.

9) TRE 48. *Wachtleropteris valentinii* nov. comb. Paratype. Detail of the leaf-like sporophylls with the seeds attached on the lower surface.

10) TRE 132 Wachtleropteris valentinii nov. comb. Plant with young cone.

11) TRE 132. Wachtleropterisvalentinii nov. comb. Detail of sporophylls.



12) TRE 196. Wachtleropteris valentinii nov. comb. Big branched leave.

- 13) TRE 256. Wachtleropterisvalentinii nov. comb. Leave segment.
- 14) TRE 179 Wachtleropteris valentinii nov. comb. Adult cone.
- 15) TRE 180. Wachtleropteris valentinii nov. comb. Frond with isolated seeds on the lower part.
- 16) TRE 155. Wachtleropteris valentinii nov. comb. Young even ramifying leave.

Evolutionary trends in Early Permian Floras

by

Michael Wachtler P. P. Rainerstrasse 11, 39038 Innichen, Italy; E-mail: michael@wachtler.com

Abstract

This brief paper tries to provide some answers about the evolution of plants in the Early Permian. Two main floras are examined. One from the German Saar-Nahe area (Niederhausen), belonging to the Carboniferous-Permian boundary (Kasimovian-Gzhelian), and one younger, also Early Permian from the Tregiovo Flora in the Southern Alps (Artinskian/Kungurian). This will be a tentative paper to correlate the evolving trends in one plant kingdom, and to identify probable ancestors of the extant vegetation. From the Earliest Permian, a gradually increasing aridity is identifiable. If the Niederhausen Flora can be indicated with their richness of different conifer genera, seedferns (Peltaspermales) and ferns and sphenophyta as mainly humid, but just missing the typical Carboniferous giant flora-elements like lycophyta (Sigillaria, Lepidodendron), horsetail-communities (Calamites) and fern-associations (Neuropteris, Pecopteris, Alethopteris etc.), then the Tregiovo-Flora as well as other German Early-Middle Permian areas are just characterised by a distinct drought for most of the year, interrupted only by seasonal flooding. This could not be correlated with a catastrophic scenery but can be regarded as natural movement of the continents to drier zones, as is also reported now in the African Okavango-Delta. However, inside this hostile climate, we have the rising and expanding of almost all vegetation elements that also today dominate our planet, like conifers, cycadophyta, sphenophyta and filicales, or are present as some living fossils, like the ginkgophyta.

General discussion

In the Southern Alps, as well as in the German basin, we have the unique occurrence of mainly all of the most important developmental phases of the plant kingdom, with rich Late Carboniferous, Permian and Triassic deposits grouped together in a territory of a size that is easy to survey. Thus, we were able to determine whether flora-saltations occurred or not.

A mainly identical landscape in the European Permian

In many ways, the sediments of the German Rotliegend (Early Permian) and the Zechstein Sea (Upper Permian) and the mainly coeval Tregiovo Formation (Early Permian) and Gröden-Formation (Upper Permian) all have similarities: in lower Permian, both landscapes were affected by local but intense volcanic activities, which left traces everywhere (SCHWEITZER, 1984); and in Upper Permian, the evaporite rocks of the Zechstein formation were laid down by the Zechstein Sea, an epicontinental or epeiric sea that occupied a region of what is now the North Sea, plus lowland areas of Britain and the north European plain through Germany and Poland. The coeval Gröden-Formation was deposited from rivers flowing in the nearby Tethys Sea, even though this ocean was just very near and began to inundate the contiguous landscapes at that time.

An antithesis flora

The giant and enormous Carboniferous flora-elements like lycophyta (*Sigillaria, Lepidodendron*), horsetail-communities (*Calamites*) and fern-associations (*Neuropteris, Pecopteris, Alethopteris* etc.) moved in Europe, beginning from the late Carboniferous, to a coniferophyta-cycadophyta-pelatspermaceae-dominated landscape with some ginkgophyta, sphenophyta and pteriodophyta associations. Nevertheless, we have in the Permian, for almost fifty million years a never seen before decline of the plant kingdom, which recuperated only in the EarlyMiddle Triassic. Until that time, we once again experienced a life-explosion, developing almost the entire plant kingdom. Nowhere is the decline so pronounced as in the group of ferns. The xerophyte fern *Sphenopteris* is one of the few true ferns recovered in a fair amount; in the seed ferns, with the Peltaspermales, we have the only survivorgroup.

No desertic scenery

In Permian, vast areas of the northern hemisphere have the same xerophytic vegetation. It is suggested that the mutation-rate at that time was the lowest in evolutionary history. Almost all of the plants are characterised by being poor in species, prickly in visual nature, and dwarfish in dimension. As large parts of Pangaea lies in the dry savannahs of the present, no universal catastrophic events were needed. Even though it was suggested that most of the Early Permian plants on the European continent could be defined as xerophytic, this is not as valid as previously believed. The relative abundance of the sphenophyta Neocalamites and Equisetites, beginning from the Early-Middle Permian, and the variegated cycadophyta flora (Bjuvia, Nilssonia, Taeniopteris) suggest a savannah-like climate with intense flooding in springtime and long-lasting dry seasons for most of the year, similar to what we see today around the tropics, where a manifold wildlife evolves only near the rivers and during intense rainy seasons.

A rich animal life

Inserted in the fossilised plant remains, we have frequent animal footprints from lacertoid reptiles (*Dromopus*), as well as pronounced insect and animal feeding in the German basin, originating from a lot of reptiles which found sufficient survival resources in this biocenosis.

The main vegetation elements in detail

Lycophyta: Astonishingly the archaic Lycopodiales – well represented in Carboniferous with the Sigillariaceae and the Lepidodendrales – disappeared in a relatively short time. *Sigillaria brardii*, recorded from the German basin until the Lower-Upper Rotliegend, seems to be the only apparent survi-

vor, along with some dwarfish *Selaginellites* (*zollwegii*). Nevertheless, they appear variegated but totally modified in the Early Triassic with *Pleuromeia sternbergii* (widespread from Europe to China), and in the Anisian strata of the Dolomites with the arborescent *Lycopia dezanchei*; also, they are in a relative abundance with the Isoetaceae like *Lepacyclotes bechstaedtii, Isoetites brandneri, Selaginellites leonardii* or *S. venieri*.

Sphenophyta: Gradually from the Earliest Permian, we have a decline of the true Calamitaceae (*Calamites gigas, Calamites multiramis* or dwarfish *Calamites wachtleri*) as well as several *Annularia* whorls thought to be the terminal foliage-parts of some *Calamites* species (*Annularia carinata, A. spicata, A. spinulosa, A. galioides* or *Asterophyllites equisetitiformis*) (BARTHELS, 2009). In that time, new horsetail-genera arose and developed, like *Neocalamites (tregiovensis*) and *Equisetites (siberi)* (WACHTLER, in press).

Pteridophyta: The filicales seemed to suffer most from an arid climate. Although they were relatively widespread in the Early Rotliegend, with important still now existing archaic ferns like the Marattiales (Todites muelleri) or the Osmundaceae (Scolecopteris lothii), along with also ferns of undefined classification like Nemejcopteris (feminaeformis), Senftenbergia, Scolecopteris (S. oreopteridae, S. cyathea, S. arborescens, S. densifolia, S. candolleana, S. polymorpha. S. pseudobucklandii), and some morphogenus (Pecopteris) (BARTHELS, 2009), they declined totally from the Lower to the Upper Permian in this area. Apart from the skeletonised pteridophyta Sphenopteris and some isolated Scolecopteris, they are completely on the fringes in comparison to the subsequent manifold Early Triassic habitat, where they largely began to dominate the continents.

Pteridosperma: Although they were relatively widespread in the Carboniferous and played an important role in the Triassic with the Peltaspermales (*Scythophyllum*) and the Caytonales (especially *Sagenopteris*), they were restricted in the Permian to the largely occurring group of Peltaspermaceae. Their characteristic peltate and umbrelliferous shields are easily recognisable. Probably the earliest representatives are to be seen in (*Odontopteris*) *Hurumia lingulata* and *Rhachiphyllum hauptmannii*, whereas the



Peltaspermum: Evolving and increasing trends of *Peltaspermum* ovuliferous organs. 1ab) *Peltaspermum dammannii*, (Earliest Permian, Kasimovian-Gzhelian); 2ab), Peltaspermum meyeri (Early Permian, Artinskian_Kungurian); 3ab) *Peltaspermum martinsii*, (Upper Permian Wuchiapingian) Courtesy Museum of Natural history Gera; 4ab) *Peltaspermum bornemannii* Early Triassic (Anisian). Note: The peltate shields in Permian were usually half the size as in Triassic

first true Peltaspermales can be identified in Autunia (conferta) or Lepidopteris (meyeri). However, from the Earliest Permian, their leaf-size declined considerably. Even though Autunia bear still just leathery but relatively large neuropterid leaflets, Lepidopteris meyeri and L. martinsii hold only minute nanoid leaves. Also, the size of their ovuliferous fructifications with their segmented shields does not exceed 10 mm (Peltaspermum dammannii, P. meyeri, P. martinsii). Astonishingly, just from the beginning Triassic, they considerably increased their peltate-shield-fructifications (Peltaspermum bornemannii) (KUSTATSCHER ET AL., 2007) and also their leaflets (Scythophyllum berqeri).

Gingkophyta: One of the most enigmatic and strange plant families consists of the ginkgoales. It is probable that the leaves recorded from the Niederhausen-Flora (*Baiera perneri*) are close to the crown group of Progymnosperms which unites Gingkophyta and Coniferophyta. As seen in the Early Permian Tregiovo ginkgophyta, the reproduction cycle today will be nearly the same as in the Permian era. Tregiovo *Baiera pohli* holds what is believed to be the reproduction-organs with apparently modern features. The one to two attached seeds are also common today, the catkin-like polliniferous cones changed little over time, and the basal collar from which the leaves and the fertile organs sprout were fully evolved in the Early Permian. *Spheno (Baiera)*-like lacerated leaves occurred until the Jurassic, and then they fused together to form the extant *Gingko biloba* leaves.

Cycadophyta: One of the surprises of the Tregiovo flora is its richness in cycads. With *Bjuvia tridentina* and *Nilssonia perneri*, which could be defined as true cycads due to their bulbous short stems and fertile structures, we have with *Wachtleropteris* other cycadophyllous plants. Also here we can trace a continuous line from Lower Permi-

an to the rich Triassic cycadophyta deposits in Europe, maintaining their two main lineages - *Bjuvia* resembling extant *Cycas* and *Nilssonia* probably correlating with all other present Cycad-lines. However, the cycadophyta in Niederhausen are otherwise poorly evolved, with only some doubtful *Nilssonia* and *Taeniopteris*-fragments recorded to date.

About the organisation of Permian conifers

Knowledge of the visual nature and the body structure of Permian conifers is to date now only rudimentary. Too much attention was given over decades to the aspect of foliage, whereas the organisation of the male and female cones, especially the seed scales and bracts due to their complexity and sometimes the bad condition of preservation in the background were moved.

An exception is the fantastic work about the Upper Permian Alpine fossil plants, written by Johanna CLEMENT-WESTERHOF (1984 and 1986). She introduced a totally new concept of understanding ancient conifers, mainly based on the knowledge of their seed scales, which varies considerably – like in extant - and are therefore the basis for recognising the origins and evolving stages of all extant needle trees.

Permian polliniferous cones were rather much simpler than the ovuliferous ones. Usually around a cone axis, they bear slightly overlapping, numerous spirally arranged subpeltate microsporophylls, and end with a more or less distal appendix. More difficult to decode is the interior arrangement of the pollen-chambers: whether they are of araucarian style, which are mainly characterised by several pollen sacs hanging on the abaxial side of their peltate shields, or have the aspect of extant Pinaceae, with only two pollen-chambers attached to the lower side of the microsporophylls. Dead-ending pollination-trends probably come from the conifer Albertia, which seems to have become extinct after the Triassic.

Much more difficult to understand is the evolutionary lineage of the female cones and at least which origin the conifers are of? From the Westphalian B of Yorkshire originate the oldest reported to date (but only microscopic) leaf-remains of conifers, described as *Swillingtonia denticulata*. "*Most of the leaves are triangular-lanceolate with a den*- ticulate margin and single vascular strand; but a few of the leaves fork, with accompanying dichotomy of the vascular strand. ... The leafy shoots show superficial similarity to both conifers and lycopods" (SCOTT & CHALONER, 1983).

Therefore, it is suggested that Perneria thomsonii from Niederhausen, with its forking leaves and the dichotomsing vascular strand, has some affinities with Swillingtonia denticulata and the ancestor has to be looked for in one of the hinterland-progymnosperms which have been dormant and not conspicuous for many million years. The impulse to evolve and generate in the shortest time the main conifer lineages from wingseeded Majonicaceae (Wachtlerina bracteata of Lowest Permian or Majonica alpina in the Upper Permian), the seed/nuts bearing Walchiaceae (e. g. Walchia piniformis and Ortiseia daberi from Lower Permian, Ortiseia leonardii from Upper Permian) and probably to the Araucariaceae conducting Voltziaceae (Dolomitia nonensis from Lower Permian, Dolomitia cittertae and Pseudovoltzia liebeana from Upper Permian) constitutes a mystery. It can only be stated that most of the important conifer tribes from the present were just evolved, although in archaic forms, on the Carboniferous-Permina border. This is surprisingly valid also for Ginkgophyta and Cycadophyta.

We have to also leave the most accredited theory to date about the evolving scenery of conifers. Swedish palaeobotanist Rudolf FLORIN established in an immense work between 1938 and 1945 that the origin of the most archaic conifers has to be looked for in dwarf-shoots arising freely in the bractaxils, being provided with a more or less large number of independent sterile scales and varying from the conifer genera one or more fertile scales. Also, it was stated that by the constant fusing of their seed-scales and bracts, we arrive to all extant needletrees.

With this theory, however, it cannot be explained why just from the oldest known conifers we have aliform (*Wachtlerina*) and fused seed scales (*Seymourina*), which have fully evolved together, and why the number of sterile scales (or leaves) at the Carboniferous-Permian border was reduced or mainly non-existent, whereas two to fourfingered seed-scales were common.

Evolving concepts to the recent ginkgoales



1. *Baiera perneri*, Niederhausen, Earliest Permian, Niederhausen. 2. Baiera pohli, Leave and ovules, 3. Spur shoot, 4. Catkin-like polliniferous cone All: Early Permian, Tregiovo. Note the quadrilobed leave-structure till Triassic



5. *Psygmophyllum* Lower Permian. Locality Perm, Russia (Courtesy Natural History Museum Chemnitz). 6. *Sphenobaiera digitata*, Milbitz, Gera, coll. Bogenhard, Museum für Naturkunde Gera, Upper Permian - Zechstein, 7. *Schmeissneria microstachys*, leafy short shoots, in connection with ginkgo-leaves *Sphenobaiera spectabilis*. 8. Ginkgo-leaves *Baiera taeniata*, Collection Hauptmann. Liassic, Bayreuth.



9) Ginkgo adiantoides. Paleocene. Sentinel Butte Formation Morton Co., North Dakota, 10) Today's Ginkgo biloba with leaf, female seed and pollinferous cone.

The winged seed concept of conifers

Just from the Earliest Permian, we have fully evolved winged seeds. They modified only marginally till the present. This lineage brings us to extant Pinaceae and Cupressaceae.







Earliest Permian Niederhausen: Winged seeds from Perneria thomsoni or Wachtlerina bracteata, reconstruction



Upper Permian (Wuchiapingian) Recoaro, Italian Dolomites: Winged seeds and seed scales from Majonica alpina



Extant *Picea abies* (Norway spruce), Seed scale and seed. Reconstruction from Picea abies seed scale and seed, and Pinus sylvestris winged seed scale.

The Voltzialean seed scale concept through the time

Note: The connate three-lobed seed scale changed only a little from the Carboniferous-Permian boundary till the Triassic. The arrangement of the seeds is surprisingly different in similar appearing conifer seed scales.





Earliest Permian Niederhausen: Seymourina niederhauseni, seed scale abaxial view, adaxial, with bract, reconstruction.





Early Permian Tregiovo: Cassinisia ambrosii, seed scale abaxial view, adaxial view, reconstruction.



Upper Permian, Gera, *Pseudovoltzia liebeana*, seed scale abaxial view Coll. S. Brandt, Halle), adaxial view, with bract and seed, (Coll. M. Kahl, Gera) reconstruction.



Early Triassic, Dolomites, Voltzia agordica, seed scale abaxial view, adaxial view, small-sized seeds, reconstruction.

The embedded seed concept of conifers

Just from the Earliest Permian, we have fully embedded seeds. Some conifers hold only one (*Walchia, Ortiseia*), while others hold two or more (*Otovicia*). More or less sterile foliage - without reproduction-importance - covers the seed scales.



Walchiastrobus (Early Permian): lateral and adaxial view. Reconstructions: adaxial without bract, lateral without and with seed, Courtesy Museum Schleusingen



Ortiseiastrobus (Upper Permian, Seceda, Recoaro, Dolomites: Seed scale abaxial with seed, adaxial view; Reconstructions: Seed and sustaining scale, abaxial view; seed scale, adaxial view



Ullmannia (Upper Permian, Seed scale with seed, seed scale. Reconstruction of the scales. Courtesy Silvio Brandt, Halle and Matthias Kahl Gera



Extant Auracaria bidwillii with embedded seeds


Permian conifer cones: 1) *Walchiostrobus* Early Permian (Museum Schleusingen), 2) *Ortiseiastrobus* (Dolomites), 3) *Ullmannia frumentaria*, (Collection Matthias Kahl); 4) *Pseudovoltzia liebeana* (Natural history Museum Gera); (All Upper Permian

The multi-lobed seed concept

Note: In the Earliest Permian we have to the normal seed scales also some till now not specified multilobed seed scales. They change through rapprochement to the ginkgoales with their double-quadrilobed leaves could be suggested.



Niederhausen-Flora: 1) 187, 2) PER 01, 3) PER 102, 4) PER 327, Till now not specified double-quadrilobed seed scales belonging to some unknown conifer.

The quadrilobed evolutionary system in the gymnosperms



Surprisingly mainly all gymnosperms in the Early Permian can be conducted to a four-fingered construction concept: 1 - 2) Sterile leaves Perneria thomsonii (putative protoconifer), 3) Seed-scale Perneria thomsonii, 4) Baiera perneri, putative ginkgophyta, 5) Baiera pohli (ginkophyta), 6 + 7) Wachtleropteris valentinii, probably belonging to a cy-cadophyta ancestor.



Fèro Valentini at work in the Lower Permian site of Tregiovo-Le Fraine. Even in the winter time, he looked for new fossils and undiscovered plantspecies Foto courtesy Gerhard Eisenschink.



Permian Ortiseia, as well as Walchia, for example, held only one spherical seed inserted on a foliaceous megasporophyll and was surrounded by 20 to 30 sterile scales. The Permian Walchia-seed was attached on a bilobed megasporophyll, while Ortiseia was on an entire megasporophyll. Dolomitia can be inserted in a primitive Voltzia concept, with two to three seeds attached on a moderately connate and flattened seed scale. Others, like Early Permian Ernestiodendron, contains helically-arranged bifid bracts from Gomphostrobus-typus, while Otovicia, another Early Permian conifer, is also provided with bifid bracts incorporating two ovules in the dwarf-shoots. There are many conifertribes in the Permian, but for none could the amount of sterile leaves be deciding or having influences for the seed scale development. It is more likely that the sterile scales constitute only a protection collar, as in the spur shoots of the Ginkgoales.

Therefore, it can be proposed that the fourlobed leaves – fertile or sterile – as seen in Devonian progymnosperms, constitute the most primitive development-organ from conifers to ginkgophyta. Not resolved until now is the problem surrounding the origins of the Cycadophyta and where they are connected with the other Gymnosperms. Further studies are therefore required, with more attention being paid to the ovulestructure (if wing seeded or nut-like), the attachment of the ovules on the seed scale (if on the upper part and dorsiventrally or lower), the amount of ovules (currently ranging from one to probably at least eight), and the global evolving lines to the current Auracariaceae, Pinaceae or Cupressaceae or all other groups.

Acknowledgments

Silvio Brandt and Jürgen Meyer from Eastern German Saxony visited and gave me helpful information. The manuscript was greatly improved by the constructive remarks and considerations of Professor Giuseppe Cassinis from Department of Earth Sciences, University of Pavia. I also thank Francesco Angelelli, curator of the paleontological collections ISPRA for his support and encouragement. I thank the Naturhistorisches Museum. Schloss Bertholdsburg, Schleusingen especially Dr Ralf Werneburg, the Museum für Naturkunde Gera with Frank Hrouda, Matthias Kahl, Gera, Traute Hauptmann, Bayreuth.

I thank them gratefully.

Philosophies of the past

Due to a research ban in my country, my attention moved to the nearby Trentino mountains, where one day I met the forest man Fèro VALENTINI, who has spent much of his time in the woods around the lovely Tovel Lake, near Tuenno. He introduced me to the



The artist Egon Rusina near the fossil plant bearing mountains of the Seceda. Drawing for over thirty years "Samsāra", the "continuous flow", denoting the repeating cycle of birth, life and death in the wilderness.



art of collecting medical plants and on one occasion brought me to a place where he immediately quarried out fossilised plants from black-layered blocks. Fèro compared them to his herbs, like spruces or larches, from which he extracted substances to make fabulous unguents to heal lesions and skincomplaints. In return, I taught him about collecting and interpreting ancient plants.

From the day he led me to the Le Fraine streamlet, his passion for the evolution of life through the past arose, and he spent weeks and months in search of evidence of the changes made over time. After a short time he became a profound expert, whom I have since questioned often. I will forever remember the beautiful days spent experiencing nature with Fèro. He would bring out his self-pressed wild-living apples juice, and also his sausages, called "lucanica", from his rucksack. He also gave me his larch cream to heal my injured hands. As we looked around the ancient woods of the Val di Non, I felt that I was in the best restaurant of the world. When he explained to me his concept of nature, I was astonished with his profound knowledge of our lives and living through a "timeless" era.

Today, we do not live in a society where the discovery of a new ancient conifer or fern would be viewed with respect and gratitude. Excavators and bulldozers dug closer and

closer to "the territories of the native people and animals".

Also, in the extremely cold winters, he never interrupted his pilgrimage. Without gloves, in order to better feel the rock slabs, and with his long beard and hair iced up, he worked hard to discover new plant species. At night, he noted all of his observations in a diary. For 123 days a year he was collecting, bringing home 407 plant-fossils, only three per day.

Féro Valentini never did this for money and generously donated all of his specimens to museums. One day, the authorities confiscated all of Féro's discoveries, made by hand and using rudimental tools, and punished him with high penalties. I also received written communication that my researches were no longer allowed.

I was asked to attend personally in court to justify my discoveries. I was not allowed to further study my collected material and continue my researches. My computers, all of my annotations and my illustrations have also been sequestrated.

Together, we realised how the world around us has changed, with monster-buildings and enormous roads. We had to accept that we were studying a "lost time and world".

Fèro, the old man and I decided to fight, and to look for friends. One day in the Dolomites of Recoaro, we met the farming-family of Giuliano Pozza, popularly "Momi". At the





The family of Giuliano Pozza, "Momi" with the daughter Ilenia, adjacent to the plant-fossil site Ulbe (Southern Dolomites). Helping injured wild animals to survive.

same time as we collected beautiful Permian fossils, people from every part brought baby-roes and chamoises that were injured by cars and machines; we tried to understand the past, and he cared for the wild animals without legs and broken bones. While people were counting money and making plans to build bigger structures and destroy landscapes, we ate potatoes and apples from Momi's Garden whilst tired, but happy, between caring for "Bambis".

One day I moved to the hazardous abyss of the Seceda in the Dolomites. When night came, my life was at stake. Blind as a bat, I looked in the night for help. Finally, I recognised between the precipices a glooming light, and when I came closer, I met a bearded man. Egon Rusina was his name. In his youth, he was a celebrated artist, but now, for more than twenty years, he had been living in the wilderness to paint "Samsāra", the "continuous flow", showing the repeating cycle of birth, life and death. I told him about the eternal cycle of plants and animals fossilised in the rocks of Seceda. Sometimes the authorities made the long and exhausting journey to Egon Rusina to solicit him to leave, because, in their opinion and sustained by their laws, it was an illegal act to remain for all of his life "as a free man in the free nature". However, after a short time, they found that he was a hopeless case for humanity.

"I'm in the same way illegal as you", I told him; "society doesn't want free people in the wilderness, searching for deeper insights in the nature and our life." Together, we emptied a bottle of wine, being happy, he with his drawings about "Samsāra", and I with my million year-old Ortiseia-conifers.

But the circle of our friends amplified. If the knowledge about the fossil plants increases in the future, then it will be the work of humans who love nature. The common man in the street can in equally solve profound mysteries if he dedicates his fervour and life to his dreams. Professor Rudolf Daber, the former director of the venerable Natural History Museum of Berlin and one of the most accredited paleobotanists worldwide, but much more a great philosopher, wrote to me: "Nature doesn't speak to everybody!" He encouraged me to write down all of the observations which I made in my life in the mountains, and to not look for authorities, but to follow the sound of nature. Mandela, Voltaire, Diderot, and also Dolomieu, from which these mountains took their name, were in prison. Immanuel Kant, the great philosopher, wrote long abstracts that science must be free. Also, Rudolf Daber suffered during the Communism regime. Together, we wrote long essays. I thank you, Professor.



Prof Rudolf Daber, paleobotanist and former director of the Natural History Museum, Berlin

No researcher is bound to the authorities, but only to his own search of knowledge for all humans. No court and no judge can forbid this act of nature. Knowledge is power, but it owns all of mankind.

When I stand up for my research in front of the judge, I am not sure if I am the accused or the complainant against a society which wants to destroy nature.

References

AVANZINI, M., BARGOSSI, G. M., BORSATO, A., CASTI-GLIONI, G. B., CUCATO, M., MORELLI, C., PROSSER, G. & SAPELZA, A., (2007). Erläuterungen zur Geologischen Karte von Italien im Maßstab 1:50.000 Blatt 026 von Eppan. Servizio Geologico d'Italia.

BARTHEL, M., (2009). Die Rotliegendflora des Thüringer Waldes. Veröff. Naturhist. Mus. Schleus., Schleusingen.

BAUER, K., KUSTATSCHER, E. & KRINGS, M. 2013. The ginkgophytes from the German Kupferschiefer (Permian), with considerations on the taxonomic history and use of Baiera and Sphenobaiera. – Bulletin of Geosciences 88, 539–556.

BRANDT, S., (1997). Die Fossilien des Mansfelder und Sangerhäuser Kupferschiefers. - Schriftenreihe des Mansfeld-Museums (Neue Folge) Heft 2, S. 1- 68, Hettstedt.

BRAUN, C.F.W., (1843) Beiträge zur Urgeschichte der

Pflanzen", Münster, G.G. (Eds.), Beiträge zur Petrefactenkunde, vol. 6, 1843, p.5-25, Bayreuth; 7. BRONGNIART, A., (1849). Zeitschrift für geologische Wissenschaften Berlin, n. 16, pp. 865-876.

CASSINIS G., SANTI, G. (2001): Hanns Bruno Geinitz: A pioneer of the Permian stratigraphy of Eastern Lombardy (Southern Alps, Italy). In: "Intern. Hanns Bruno 5 Geinitz Symp.", Proceed. Symp. in Honour of Hanns Bruno Geinitz, Dresden, Saxony, January 28-30, 2000, Abh. des Museums für Mineral. und Geol. Dresden, Geologica Saxonica, n. 46/47, pp. 73-82, 2 pls., 4 figs., Dresden.

CASSINIS, G., NICOSIA, U., PITTAU, P. & RONCHI, A., (2002). Paleontological and radiometric data from the Permian deposits of the central Southern Alps (Italy), and their stratigraphic implications: Association Géologique du Permien, Paris, Mémoire n. 2.

CASSINIS, G. & RONCHI, A., (2001). Permian chronostratigraphy of the Southern Alps (Italy) – an update. – Contribution to Geology and Palaeontology of Gondwana in honour of Helmut Wopfner, Cologne p. 73-87.

CASSINIS, G., PEROTTI, C., (2007). A stratigraphic and tectonic review of the Italian Southern Alpine Permian. Palaeoworld 16, pp. 140- 172.

CLEMENT-WESTERHOF, J., (1984). Aspects of Permian Palaeobotany and Palynology. IV. The conifer Ortiseia from the Val Gardena Formation of the Dolomites and the Vicentinian Alps (Italy) with special reference to a revised concept of the Walchiaceae (GOEPPERT) SCHIMPER. - Rev. Palaeobot. Palynol., n. 41, pp. 51-166

CLEMENT-WESTERHOF, J., (1987). Aspects of Permian Palaeobotany and Palynology; VII, The Majonicaceae, a new family of Late Permian conifers. - Rev. Palaeobot. Palynol. 52 (4), pp. 375-402.

CLEMENT-WESTERHOF, J. A., (1988) Morphology and Phylogeny of Palaeozoic conifers, in BECK, C. B. (Hrsg.): Origin and evolution of gymnosperms. Columbia University Press, New York, pp. 298-337.

CONTI, M.A., MARIOTTI N., MANNI, R. & NICOSIA, U., (1999): Tetrapod footprints in the Southern Alps: an overview. In: CASSINIS, G., CORTESOGNO, L., GAGGE-RO, 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 September 1999. Earth Science Department, Pavia University, pp. 137–138.

DABER, R. (1970): Museum für Naturkunde an der Humboldt-Universität zu Berlin – 200 Jahre. Wiss.Z. Humboldt-Univ. math.-naturwiss.R. 19 (2/3); 123-328 Berlin

DELEVORYAS, T. 1982. Perspectives on the origin of cycads and cycadeoids. – Review of Palaeobotany and Palynology, 37: 115–132.

DIMICHELE, W. A., MAMAY, S. H., CHANEY, Dan S., HOOK, R. W. and NELSON, J. W., (2001). An Early Permian Flora with Late Permian and Mesozoic Affinities from North-Central Texas, Journal of Paleontology, n. 75, pp. 449-460.

FISCHER, T. C., MELLER, B., KUSTATSCHER, E., & BUTZMANN, R., (2010). Permian Ginkgophyte fossils from the Dolomites resemble extant O-ha-tsuki aberrant leaf-like fructifications of Ginkgo biloba L. BMC Evol Biol 10 (337) doi 10.1186/1471-2148-10-337.

FLORIN, R. 1933. Studien über die Cycadales des Mesozoikums (Bennettitales, pp. 12-30). – Kungliga Svenska Vetenskapsakademiens Handlingar 12: 4-134

FLORIN, R. (1938 - 1945): Die Koniferen des Oberkarbons und des unteren Perms. I. - Palaeontographica,

FLORIN, R., (1936): Die fossilen Ginkgophyten von Franz-Joseph-Land nebst Erörterungen über vermeintliche Cordaitales mesozoischen Alters. II. Allgemeiner Teil. Palaeontographica 1936, 82(B):1-72.

FLORIN, R. 1949. The morphology of Trichopitys heteromorpha Saporta, a seed-plant of Palaeozoic age, and the evolution of the female flowers in the Ginkgoinae. Acta Horti Bergiani 15:79-109.

FLORIN, R., (1964). Über Ortiseia leonardii n. gen. et sp., eine Konifere aus den Grödener Schichten im Alto Adige (Südtirol). - Mem. Geopaleont. Univ. Ferrara, 1(1), pp. 3-11, n. 41, pp. 51-166.

GAND, G. & DURAND, M., (2006). Tetrapod footprint ichnoassociations from French Permian basins, Comparisons with the Euramerican ichnofaunas. In: LU-CAS, S.G., CASSINIS, G. & SCHNEIDER, J.W. (Eds.), Non-Marine Permian Biostratigraphy and Biochronology. Geol. Soc. London, Special Publications 265. , pp. 157–177.

GEINITZ, H. B., (1869). Über Fossile Pflanzenreste aus der Dyas von Val Trompia. Neue Jahrbuch für Mineralogie Geologie Paläontologie: 456-461

GRAUVOGEL-STAMM, L. & GRAUVOGEL, L., (1973). Masculostrobus acuminatus nom. Nov., un nouvel organe reproducteur male de gymnosperme du Grès a Voltzia (Trias inférieur des Vosger (France). Geobios, 6 (2), pp. 101-114.

GRAUVOGEL-STAMM, L., (1978). La flore du Grès a Voltzia (Buntsandstein Supérieur) des Vosges du Nord (France), morphologie, anatomie, interprétations, phylogénique et paléogéographique. Sci. Geol., Mem. 50, pp. 1–225 (plates 1–54).

GRAUVOGEL-STAMM, L. & SCHAARSCHMIDT, F., (1979). Zur Morphologie und Taxonomie von Masculostrobus Seward und anderen Formgattungen peltater männlicher Koniferenblüten. Senckenb. Lethaea 60, pp. 1–37.

GUEMBEL, C. W., (1873). Geognostische Mitteilungen aus den Alpen. I, Das Mendel und Schlerngebirge, Sitzungsber. Akad. d. Wiss., pp. 13-88.

HAUBOLD, H., SCHAUMBERG, G. (1985). Die Fossilien des Kupferschiefers. Pflanzen- und Tierwelt zu Beginn des Zechsteins – eine Erzlagerstätte und ihre Paläontologie. – Neue Brehm-Bücherei, Bd. 333, 223 S., 139 Abb., 13 Tab., Wittenberg (A. Ziemsen-Verlag). ISSN 0138-1423

KERP, J. H. F., (1988). Aspects of Permian palaeobotany and palynology. X. The West- and Central European species of the genus Autunia KRASSER emend. KERP (Peltaspermaceae) and the form-genus Rhachiphyllum KERP (callipterid foliage). Review of Palaeobotany and Palynology, n. 54, pp. 249-360.

KERP, J.H.F. & HAUBOLD, H. (1988): Aspects of Permian palaeobotany and palynology. VIII. On the reclassification of the West and Central European species of the form-genus Callipteris BRONGNIART 1849. – Rev. Palaeobot. Palynol., 54: 135-150, Amsterdam.

KERP, H., PENATI, F., BRAMBILIA, G., CLEMENT- WEST-ERHOF, 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). Review of Palaeobotany and Palynolology, 91(1-4), pp. 63-84.

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, Freiberger Forschungshefte C 348, pp. 69–172.

KUSTATSCHER, E., VAN KONIJNENBURGH – VAN CIT-TERT, J. H. A. & WACHTLER, M., (2004). A number of additional and revised taxa from the ladinian Flora of the Dolomites, Northern Italy. Geo.Alp, vol. 1, p. 57-69 KUSTATSCHER, E., WACHTLER, M. & VAN KONIJNEN-

BURGH – VAN CITTERT, J. H. A., (2007). Horsetails and seedferns from the Middle Triassic (Anisian) locality Kühwiesenkopf (Monte Prà della Vacca) in the Dolomites (Northern Italy). Palaeontology, vol. 50, Part 5, Elsevier Publishing House, Oxford, pp. 1277-1298.

LEONARDI, P., (1953). Orme di Tetrapodi nelle arenarie di Val Gardena (Permiano medio-inferiore) dell'Alto Adige sud-orientale. Mem. Ist. Geol. Univ. Padova, 17, pp. 1-23.

LOOPE, D. B. & ROWE, C. M., (2003). Long-lived pluvial episodes during deposition of the Navajo Sandstone. The Journal of Geology, vol. 111, pp. 223-232.

LOSS G. (1877) - L'Anaunia: saggio di geologia delle Alpi tridentine, Trento, p. 323.

MAROCCHI, M., MORELLI, C., MAIR, V., KLÖTZLY, 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, pp. 480-498.

MOSTLER, H., (1966). Sedimentäre Blei-Zink-Vererzung in den mittelpermischen "Schichten von Tregiovo". Mineralium Deposita, Vol. 1, Issue 2, pp. 89-103

PERNER T., WACHTLER M. (2013): Seymourina niederhauseni a new conifer from the Carboniferous-Permian (Kasimovian/Gzhelian) Niederhausen Flora (Rheinland-Pfalz, Germany) p. 74, DoloMythos, Innichen.

PERNER T., WACHTLER M. (2013): Pteridosperma from the Carboniferous-Permian (Kasimovian/Gzhelian) Niederhausen Flora (Rheinland-Pfalz, Germany) p. 24 DoloMythos, Innichen.

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 West and Central Europe and a reclassification of the species formerly assigned to Peltaspermum HARRIS. Review of Palaeobotany and Palynology, n. 63, pp. 197-225.

POTT, C., McLOUGHLIN, S. & LINDSTROEM, A., (2010). Late Palaeozoic foliage from China displays affinities to Cycadales rather than to Bennettitales necessitating a re-evaluation of the Palaeozoic Pterophyllum species. Acta Palaeontologica Polonica, n. 55, pp.157-168.

REMY, W., REMY, R., 1975. Beiträge zur Kenntnis des Morpho-Genus Taeniopteris Brongniart. Argumenta Palaeobotanica vol. 4, pp. 31–37.

REMY, W. & REMY, R., (1978). Die Flora des Perms im Trompia-Tal und die Grenze Saxon/Thuring in den Alpen. Argumenta Palaeobotanica, Münster, vol. 5, pp. 57-90.

RICHTHOFEN, VON F., (1874). Über Mendola und Schlern Dolomite. Zeitschr. Deutsch. Geol. Gesell., n.

26, pp. 225-256.

SCHIMPER, W. P. & MOUGEOT, A., (1844). Monographie des Pantes fossiles du Grès Bigarré de la Chaine des Vosges. Ed. Englmann, Leipzig, p. 83.

SCHIMPER, W. P., (1869). Traité de Paléontologie Végétale Paris: J. B. Bailliere et Fils.

SCHUSTER, J. 1932. Cycadaceae. In: H. G. A. Engler, ed. 1900-1953. Das Pflanzenreich. Berlin. Vol. 99[IV,1], pp. I-168.

SCHWEITZER, H.-J., (1960). Die Sphenopteriden des Zechsteins. Senckenbergiana Lethaea, 41, pp. 37-57, Frankfurt.

SCHWEITZER, H.-J., (1984). The land flora of the German and England Zechstein sequences. [In HARWOOD, G.M. & SMITH, D.B., (eds.). The English Zechstein and related topics.]. Geological Society Special Publication 22, pp. 31-54.

SCOTT A.C., CHALONER, W.G. (1983):. The earliest fossil conifer from the Westphalian B of Yorkshire // Proc. Roy. Soc. London. -- Vol. B220. - P. 163-182.

SUESS, E., (1869). Über das Rotliegende im Val Trompia. Sitzg. d. Akad. Wiss. Wien. Math.-Naturwiss. Klasse, 1. Abt., vol. 59.

TOWNROW, J., (1960) The Peltaspermaceae, a pteridosperm family of Permian and Triassic age. Palaeontolgy, 1960, 3: 333–361

UHL, D. & KERP, H., (2003). Wildfires in the Late Palaeozoic of Central Europe - The Zechstein (Upper Permian) of NW-Hesse (Germany). Palaeogeography, Palaeoclimatology, Palaeoecology, 199, pp. 1-15.

ULLRICH, H., (1964). Zur Stratigraphie und Paläontologie der marin beeinflußten Randfazies des Zechsteinbeckens in Ostthüringen und Sachsen. Freib. Forsch.-H., C169, pp. 1-163.

VACEK, M., (1882) Vorlage der geologischen Karte des Nonsberges, Verh. k. k. geol. R. A., Wien, pp. 42-47.

VACEK, M., (1894) Über die geologischen Verhältnisse der Umgebung des Nonsberges, Verh. k. k. geol. R. A., n. 16, Wien, pp. 431-466.

VOERDING, B. & KERP, H., (2008). Stomatal indices of Peltaspermum martinsii (Pteridospermopsida, Peltaspermaceae) from the Upper Permian of the Bletterbach Gorge and their possible applicability as climate proxies. Neues Jahrbuch für Geologie und Paläontologie, n. 248, pp. 245-255.

VISSCHER H., KERP J.H.F., CLEMENT-WESTERHOF J.A. AND LOOY, C.V., 1999. Permian vegetation in the Southern Alps. In: Cassinis G., Cortesogno L., Gaggero L., Massari F., Neri C., Nicosia U. and Pittau P. (Eds). Stratigraphy and facies of the Permian deposits between eastern Lombardy and the western Dolomites, Earth Science Department Pavia, p. 139-147.

VISSCHER, H., KERP, H., CLEMENT-WESTERHOF, J. A. & LOOY, C. V., (2001). Permian floras of the Southern Alps. In : CASSINIS, G., ed., Permian continental deposits of Europe and other areas. Regional reports and correlations: "Natura Bresciana", Annali del Museo Civico di Scienze Naturali n. 25 p. 117-123.

ZIEGLER, PA., STAMPFLI, GM., (2001). Late Paleozoic ? Early Mesozoic plate boundary reorganisation: collapse of the Variscan orogen and opening of Neotethys In: CASSINIS, G. (ed.), The continental Permian of the Southern Alps and Sardinia (Italy). Regional reports and general correlations. Annali Museo Civico Science Naturali, Brescia, Monografia 25, pp. 17-34.

WACHTLER M., VAN KONIJNENBURGH – VAN CITTERT, J. H. A., (2000). The fossil flora of the Wengen Formation (Ladinian) in the Dolomites (Italy). Beiträge zur Paläontologie, Wien No. 25, pp. 105-141.

WACHTLER, M., (05/2010) About the origin of Cycads and some enigmatic Angiosperm-like fructifications from the Early-Middle Triassic (Anisian) Braies Dolomites (Northern Italy). Dolomythos, Innichen, n. 1, pp. 3-55.

WACHTLER, M., (06/2011). Evolutionary lines of conifers from the Early-Middle Triassic (Anisian) Piz da Peres (Dolomites - Northern Italy), Dolomythos, Innichen , pp. 3-72.

WACHTLER, M., (01/2011) Ferns and seed ferns from the Early-Middle Triassic (Anisian) Piz da Peres (Dolomites - Northern Italy), Dolomythos, Innichen, pp. 57-79.

WACHTLER, M., (01/2011). Seed ferns from the Early-Middle Triassic (Anisian) Piz da Peres (Dolomites -Northern Italy). Dolomythos, Innichen, pp. 88-104.

WACHTLER, M. 2012. The Genesis of Plants. Preliminary researches about the Early-Middle Triassic Fossil Floras from the Dolomites. A Compendium. DoloMythos – Innichen. ISBN 978-88-904127

WACHTLER, M. (2012). The latest Artinskian-Kungurian (Early Permian) Flora from Tregiovo - Le Fraine in the Val di Non (Trentino - Northern Italy) - Preliminary researches, Dolomythos, 3-56 Innichen. ISBN 978-88-904127

WACHTLER, M., (2013a): Ursprünge und Entwicklung der Cycadeen. Dolomythos, 3-62 Innichen. ISBN 978-88-904127