Review of Palaeobotany and Palynology 252 (2018) 64–76

Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

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

Giuseppa Forte [a,b,*], Evelyn Kustatscher [b,c], Johanna H.A. van Konijnenburg-van Cittert [d,e], Hans Kerp [f]

[a] Dipartimento di Geoscienze, Via Giovanni Gradenigo 6, 35131 Padova, Italy
[b] Museo di Scienze Naturali dell'Alto Adige, Via Bottai 1, 39100 Bolzano, Italy
[c] Department für Geo- und Umweltwissenschaften, Paläontologie und Geobiologie, Ludwig-Maximilians-Universität and Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Straße 10, 80333 München, Germany
[d] Laboratory of Palaeobotany and Palynology, PO Box 80115, 3508 TC Utrecht, The Netherlands
[e] Naturalis Biodiversity Center, PO Box 9517, 2300 RA Leiden, The Netherlands
[f] Forschungsstelle für Paläobotanik, Institute for Geology and Palaeontology, University of Münster, Heisenbergstrasse 2, 48149 Münster, Germany

ARTICLE INFO

Article history:
Received 8 September 2017
Received in revised form 10 January 2018
Accepted 14 February 2018
Available online 20 February 2018

Keywords:
Cisuralian
Lower Permian
Southern Alps
Sphenopteris
Lake deposits

ABSTRACT

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

1. Introduction

During the late Carboniferous sphenopterids were common and diverse (e.g., Brousmiche, 1983), but they became much rarer in the Permian with a limited number of species. No less than 13 species of *Sphenopteris* (Brongniart) Sternberg, 1825 were reported from the Stephanian of Central France (Blanzy: Langiaux, 1982; Saint-Étienne Basin: Doubinger et al., 1995). In contrast, the number of species reported from the classical Rotliegend and Autunian sequences of Europe (Asselian–Sakmarian) is surprisingly low (e.g., Barthel, 2006, 2016; Šimůnek and Martínek, 2009; Fig. 1). They comprise two species that were first described from the Stephanian (*Sphenopteris mathetii* Zeiller, 1888 and *Sphenopteris picandetii* Zeiller, 1888), and one species (*Sphenopteris germanica* Weiss, 1869; Fig. 1), originally described from lower Permian strata of Radogosz, Silesia, Poland (Weiss, 1879). The latter species is very rare and in many European Rotliegend basins even absent. However, it has recently been recognized in the southwestern United States, where it can be locally abundant in the upper Pennsylvanian and may occur as low as the middle Pennsylvanian (Lucas et al., 2013; DiMichele et al., 2013, 2017). In addition, two species were recorded from the Collio Formation (Artinskian) in Val Trompia, northern Italy, i.e. *Sphenopteris suessii* Geinitz, 1965 and *Sphenopteris kukukiana* Gothan et Nagalhard, 1921 (Geinitz, 1869; Remy and Remy, 1978; Visscher et al., 2001). The first species was established on fossils from Val Trompia, whereas the latter was originally described from the Zechstein of the Niederrhein, Germany (Fig. 1). None of these species is really common, some are even known from a few localities only. Other species from the lower Permian originally assigned to *Sphenopteris* were later transferred to other genera, i.e. *Ovopteris*

* Corresponding author at: Dipartimento di Geoscienze, Via Giovanni Gradenigo 6, 35131 Padova, Italy.
E-mail addresses: giuseppa.forte@studenti.unipd.it (G. Forte), evelyn.kustatscher@naturmuseum.it (E. Kustatscher), J.H.A.vanKonijnenburg@uu.nl, han.konijnenburg@naturalis.nl (J.H.A. van Konijnenburg-van Cittert), kerp@uni-muenster.de (H. Kerp).

https://doi.org/10.1016/j.revpalbo.2018.02.006
0034-6667/

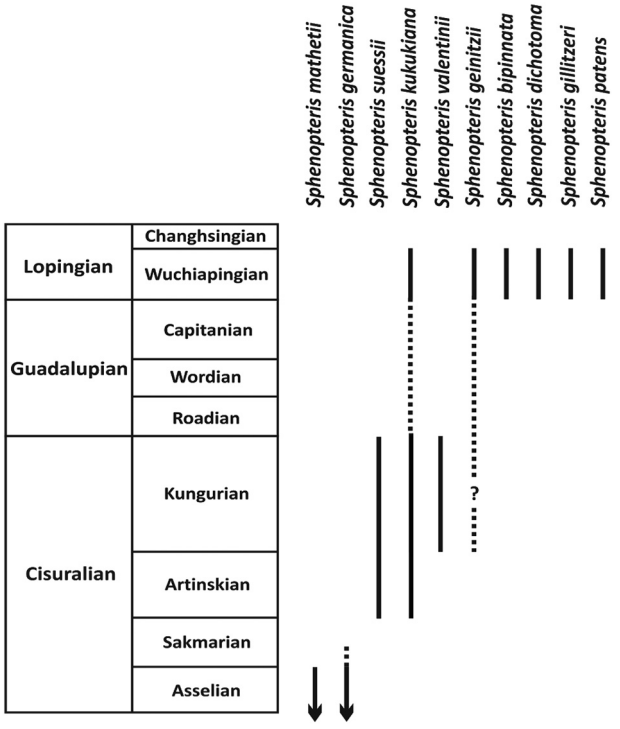


Fig. 1. Distribution of the genus *Sphenopteris* in the European area during the Permian.

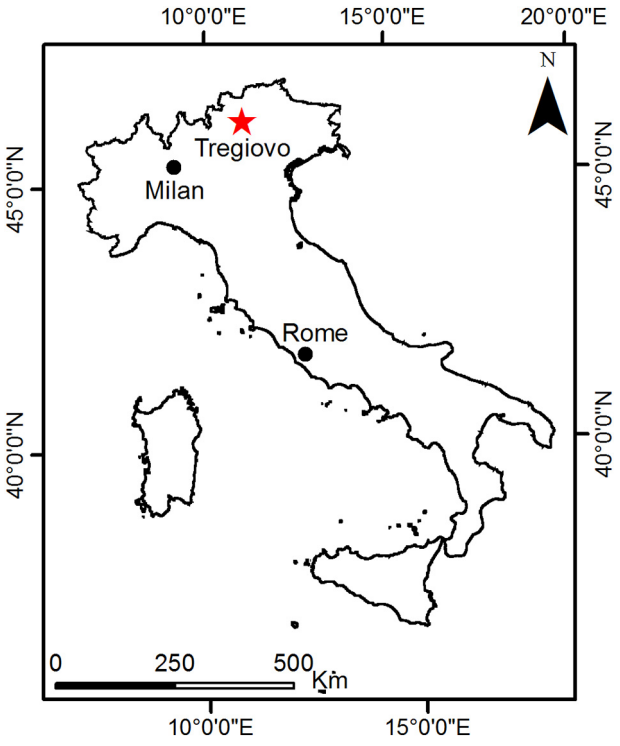


Fig. 2. Location of the Tregiovo village.

dechenii (Weiss) Potonié, 1893 and *Ovopteris lebachensis* (Weiss) Archangeli, 1895. Sphenopterids were quite diverse in the upper Permian, and Schweitzer (1960) listed seven *Sphenopteris* species from the German Zechstein although some are known from small fragments only. The preservation is generally poor to very poor and all species are from the Kupferschiefer. However, the number of species per locality is limited; from some localities only a single species is known. The discovery of a middle Kungurian flora in Tregiovo, Val di Non, northern Italy, with five species of *Sphenopteris*, including one new species, *Sphenopteris valentinii* sp. nov., is therefore of great interest. The Tregiovo Formation is one of the few fossil-bearing localities in Kungurian strata in Euramerica (see also Forte et al., 2017).

2. Geographical and geological setting

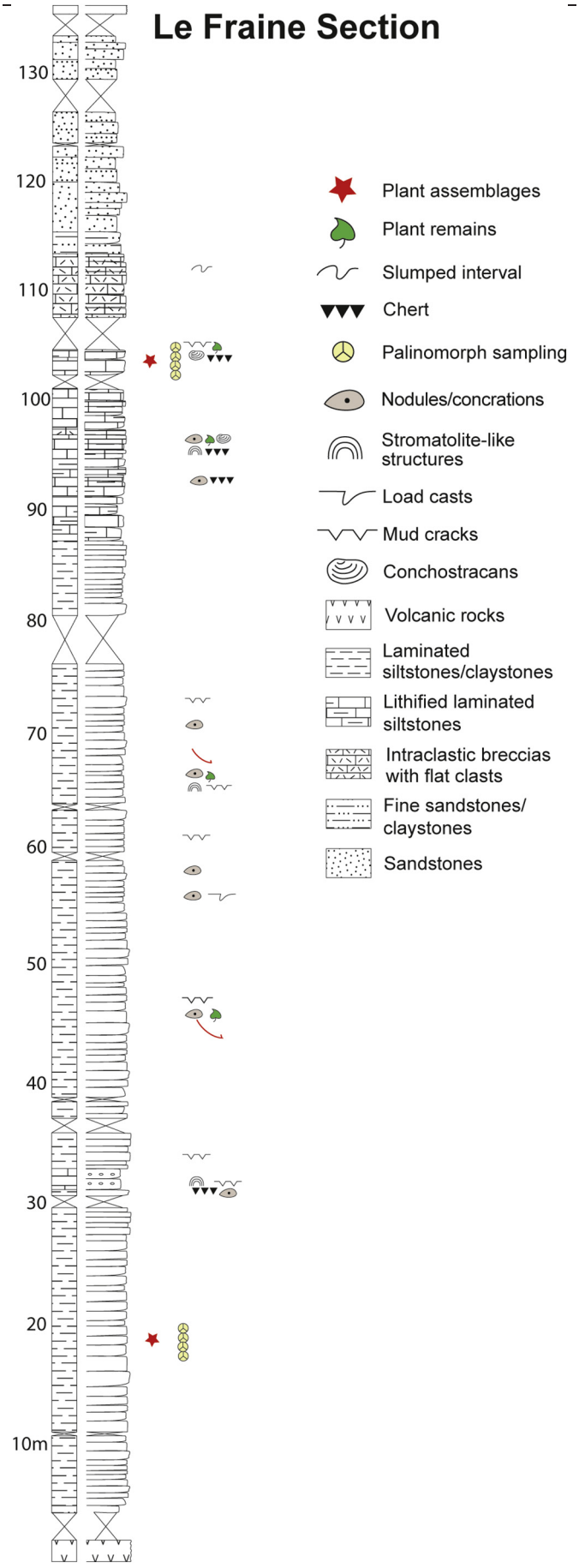
The Tregiovo Basin is a small sedimentary basin within the Athesian Volcanic Complex. The Tregiovo Formation is intercalated between two volcanic formations, i.e. the Auer/Ora Formation and the Gargazzon/Gargazzone Formation. Plant fossils from the Tregiovo Formation were described by Remy and Remy (1978), Visscher et al. (2001), Marchetti et al. (2015) and Forte et al. (2017). In addition, palynomorphs, conchostracans and vertebrate footprints were reported. Various ages were suggested based on palynomorphs, i.e. Artinskian–Kungurian (Mostler, 1966), Kungurian–Capitanian (Cassinis and Doubinger, 1991, 1992), and Kungurian–Ufimian (Barth and Mohr, 1994; Neri et al., 1999). Tetrapod footprints would support an Artinskian–Kungurian age (Conti et al., 1997, 1999), general palaeontological data suggest a middle Kungurian–early Roadian age (Cassinis et al., 2002). Recent radiometrical dating of the overlying Auer/Ora Formation and the underlying Gargazon/Gargazzone Formation attribute respectively 274.1 ± 1.6 Ma and 276.5 ± 1.1 Ma for the two formations (Avanzini et al., 2007; Marocchi et al., 2008), which confines the age of the Tregiovo Formation to the middle Kungurian.

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

3. Material and methods

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

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



remarkably complete including the base of the frond. All specimens were photographed with a Canon EOS 550D and were studied under a dissecting stereomicroscope (SZ-ST Olympus), measured with a calliper and also digitally with the free software ImageJ64®.

4. Systematic palaeontology

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

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

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

4.1.1. Sphenopteris kukukiana Gothan et Nagalhard, 1922

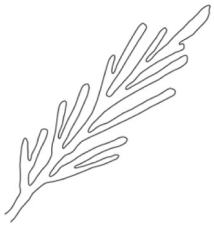
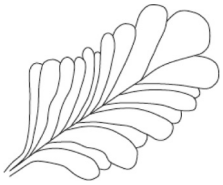
Plate I, 3, Plate II

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

Discussion: *Sphenopteris kukukiana* is the most common sphenopterid in the Tregiovo flora. The species is easily recognizable by its very regularly arranged pinnae and pinnules, both having a very stiff appearance. The lack of intercalary pinnules distinguishes *S. kukukiana* from callipterids with superficially similar pinnules, such as

Fig. 3. Simplified scheme of the "Le Fraine" section. (Modified from Marchetti et al., 2015).

Table 1a
Comparison between the morphology, stratigraphy and distribution of some Permian species of *Sphenopteris* (continued in Table 1b).

		Sphenopteris suessii	*Sphenopteris kukukiana*	*Sphenopteris valentinii*	*Sphenopteris geinitzii*
					
Frond architecture		Pseudodichotomous, pinnate-bipinnate	Bifurcate, triangular in outline	Bifurcate, triangular in outline	Bifurcate, pinnate-pinnatifid
Pinnules	Shape	Narrow, linear and sometimes bi- or three-furcate	Varying from simple, bilobed, pinnately lobed, narrow stiff, segments with rounded apices	Pinnules long, narrow, simple or bifurcated near their base, rounded apices, remarkably stiff, free for all their length	Elongate, more or less tongue-shaped in outline with many lobes, only few lobes free until the base
	Spacing	Rather loose	Rather loose	Dense, often overlapping	Rather dense
	Venation	Unclear	Unclear	Unclear	With a clear midvein
	Length	4.5–12 mm	2–10 mm	0.5–38 mm	7–40 mm
	Width	0.5–1 mm	0.8–5.5 mm	1–1.5 mm	4–16 mm
Occurrence		Mt. Collio, Val Trompia, I; Tregiovo, Val di Non, I	Niederrhein, D; Val di Non, Val Trompia, I	Tregiovo, Val di Non, I	Tregiovo, Val di Non, I (?); Gera, Ilmenau, D
Stratigraphy		Collio Fm., Artinskian; Tregiovo Fm., Kungurian	Tregiovo Fm., Kungurian, Collio Fm., Artinskian; Zechstein, Wuchiapingian	Tregiovo Fm., Kungurian	Tregiovo Fm., Kungurian?, Zechstein, Wuchiapingian
Remarks			Thus far, this species was only known from the Niederrhein		

Morphology, distribution and stratigraphy of some Permian sphenopterids.

Gracilopteris bergeronii (Zeiller) Kerp, Naugolnykh et Haubold, 1991 and *Arnhardtia scheibei* (Gothan) Haubold et Kerp, 1988. Its forked rachis suggests an affinity with the seedferns.

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

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

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

4.1.2. Sphenopteris valentinii Forte et Kerp sp. nov.

Plates III, IV

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

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

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

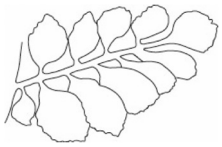
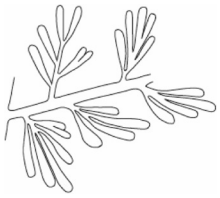
Stratigraphic type Horizon and age: Tregiovo Formation (middle Kungurian, Cisuralian, Permian).

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

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

Description: The available material consists of one complete frond (Plate III), several larger frond portions (Plate IV) and a number of smaller pinnae fragments. The frond fragment MGP-PD 31970 (Plate III) is more or less triangular in outline, 110 mm long and 75 mm wide at the tip. Pinnae are catadromically inserted at angles of 55° basally to 20° apically; pinnae are 14–81 mm long and 6–32 mm wide.

Table 1b
Comparison between the morphology, stratigraphy and distribution of some Permian species of *Sphenopteris* (continuation of Table 1a).

Sphenopteris sp.	*Sphenopteris bipinnata*	*Sphenopteris dichotoma*	*Sphenopteris gillitzeri*	*Sphenopteris patens*
				
Bifurcate, pinnate	Bifurcate, bipinnate	Bifurcate, pinnate	Bifurcate, pinnate	Bifurcate, pinnate
Laminar appearance, simple rounded/obovate shape or pinnately arranged lobes.	Pinnules spatulate, entire-margined, some with small lobes in the apical part	Pinnules with alternating obovate segments; segments usually entire-margined, sometimes lobed	Pinnules long, narrow, simple or bifurcated near their base	Flabellate, with deep, slightly club-shaped lobes, ±emerging from a single point
Rather dense	Dense, partly overlapping (?or partly fused)	Dense, partly overlapping	Rather loose	Loose to rather dense
Some pinnules show 2–3 ridges arising from the central part of the pinnule	Unclear	Pinnules with a clear, ±flexuous midvein/axis; venation of individual lobes palmate	Unclear	Unclear
1.5 mm	3–14 mm	20–45 mm	3–(?)15 mm	4–15 mm
0.5–1.5 mm	1.5–4 mm	12–20 mm	Up to 1 mm, usually less	1–4 mm
Tregiovo, Val di Non, I	Richelsdorf, D; Hilton, Eden Valley, Westmoreland, UK	Gera, Mansfeld, Richelsdorf, D	Mansfeld, D	Gera, Richelsdorf, D
Tregiovo Fm., Kungurian	Zechstein, Wuchiapingian	Zechstein, Wuchiapingian	Zechstein, Wuchiapingian	Collio Fm., Artinskian, Zechstein, Wuchiapingian
			Very similar to *S. patens*, but smaller and pinnules are more densely spaced. Some superficial similarity to *S. valentinii* but much smaller.	

Morphology, distribution and stratigraphy of some Permian sphenopterids.

The lowermost ones are small but they rapidly increase in length and the longest ones are found about halfway to the apex, then the pinnae become progressively shorter, giving the frond apex a blunt appearance. Pinnules are also arising catadromically and are densely spaced, simple or once bifurcated near their base and with rounded apices. Pinnules, respectively pinnule segments are long, narrow and remarkably stiff, free down to their base but often overlying each other (Plates III, IV); they are 0.4–38 mm long and 1–1.5 mm wide. The longest pinnules are found in the middle of the pinnae, and then they decrease in length resulting in a blunt pinna apex.

Comparisons: *Sphenopteris valentinii* is easily recognizable by its blunt-ending pinnae and pinnules that are less regularly arranged and much longer than other species. In *Sphenopteris kukukiana* pinnae are ending acutely, and pinnae are more regularly arranged and evenly spaced, and pinnules and pinnule segments are often slightly club-shaped and all more or less of the same size. *Sphenopteris valentinii* resembles *Sphenopteris suessii* but can be distinguished by the shape of the pinnae, and the apices, which are blunt in *S. valentinii*, whereas they are acute in *S. suessii*. Moreover, *S. valentinii* fronds appear to be more compact with more densely positioned pinnae and pinnules, which may overlap. However, it should be noted that small, fragmentary specimens may be difficult to distinguish.

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

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

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

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

4.1.3. *Sphenopteris suessii* Geinitz, 1869

Plate I, 1

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

Discussion: The material from Tregiovo includes the best-preserved specimens of *Sphenopteris suessii* known to date (e.g., Plate I, 1; TREG

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

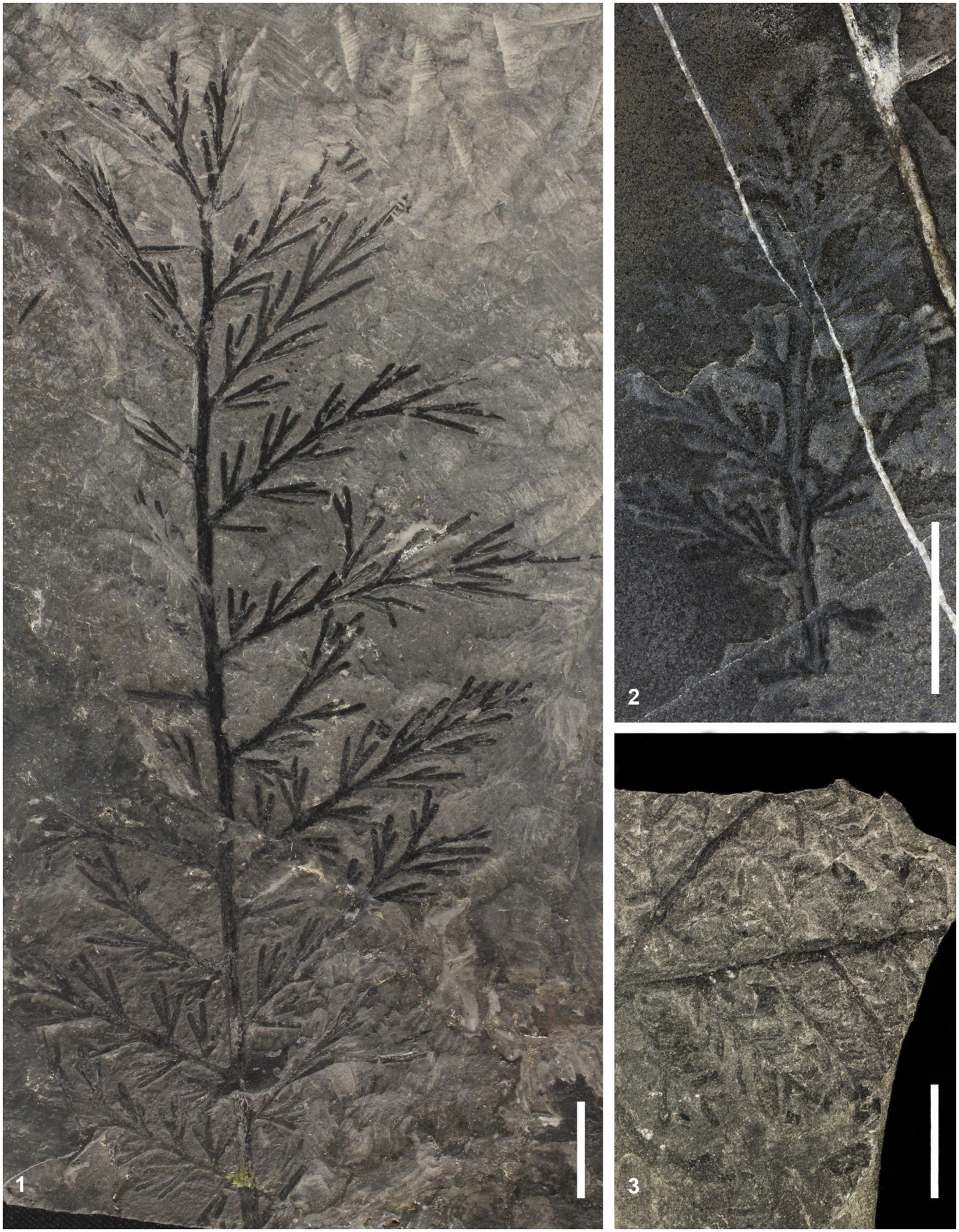


Plate I.

565). The species occurs in the upper assemblage only. Isolated pinnae are quite frequent. The species was originally described from the Collio Formation, Monte Colombine in Val Trompia, northern Italy (Geinitz, 1869; Remy and Remy, 1978). The very loose but regular appearance of the frond is typical with its rather widely spaced pinnae, widely spaced pinnules with narrow segments that are partly twice bifurcated (Table 1a).

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

Plate I, 2

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

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

4.1.5. Sphenopteris sp.

Plate V

Description: A single, largely complete but only partially well-preserved specimen was collected from the lower plant-bearing level (Plate V; TREG 328). It is a bifurcated, bipinnate frond, 85 mm long and 57 mm wide. The angle of bifurcation is c. 40°. The frond rachis varies in width from 3.3 to 4.4 mm. The first small pinnules are attached just below the bifurcation. Above the bifurcation pinnules rapidly increase in size and are then replaced by pinnae. Pinnae are widely spaced, alternating, 6–25 mm long and 3.8–6.7 mm wide, and arise at an angle of 40–60°; those in the interior portion of the frond being shorter than the exterior ones. Pinnules have a laminar appearance with small rounded to slightly obovate, pinnately arranged lobes. In some pinnules each lobe shows two or three conspicuous ridges arising from the central part of the pinnules (e.g., see enlarged pinnule in Plate V; TREG 328). The pinnules are up to 1.5 mm long and 1.5 mm wide. Unfortunately, the upper part of the frond is not well enough preserved to show details of the pinnule morphology. In addition, one specimen (part and counterpart) with two fragments of bifurcated fronds was recovered from the upper plant-bearing level. Also several smaller pinnae portions were found.

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

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

5. General discussion

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

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

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

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

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

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

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

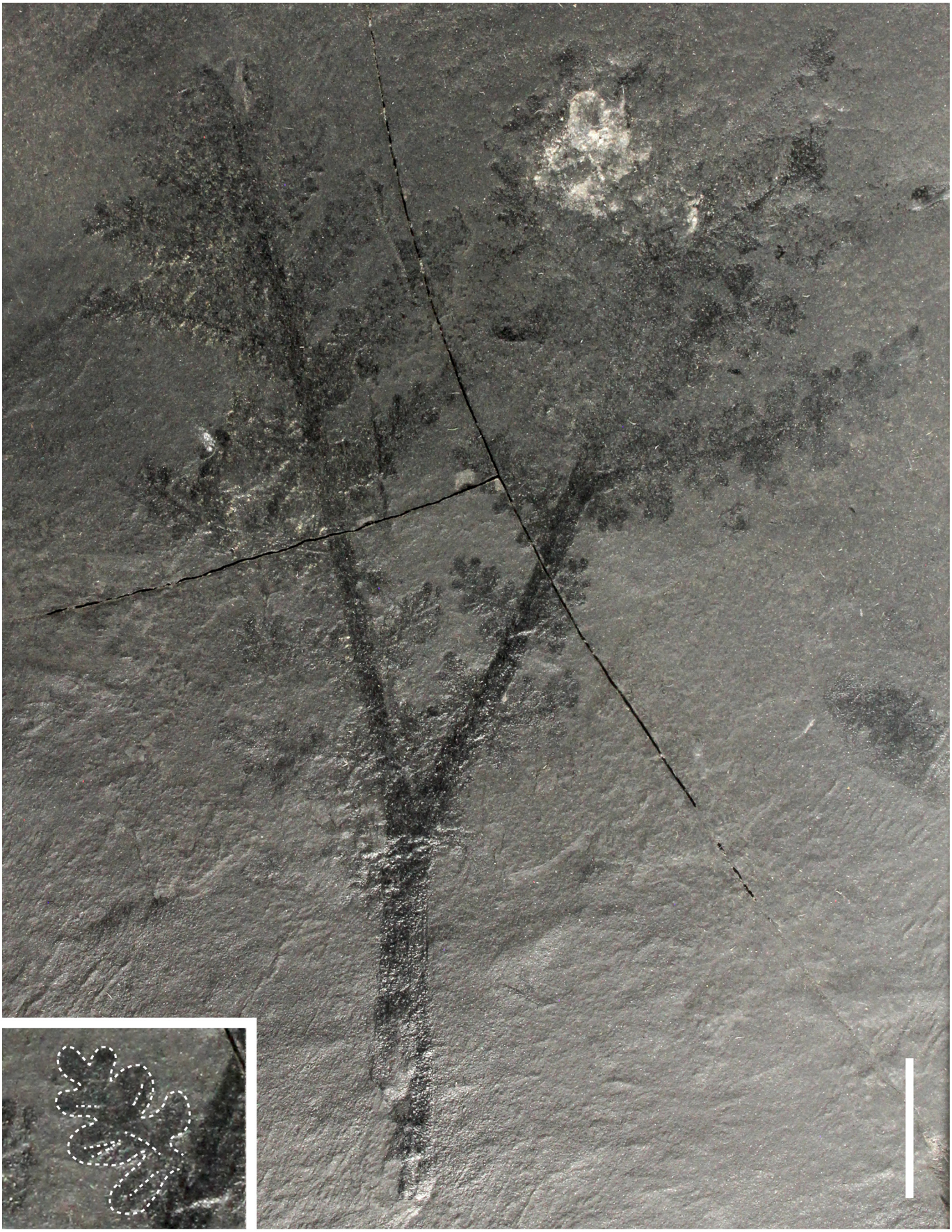


Plate V. Complete bifurcate frond of *Sphenopteris* sp. from the lower plant assemblage, TREG 328.

few specimens. The preservation of these Copper Shale plants is generally poor. For further details we refer to Tables 1a, 1b and to Schweitzer (1960).

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

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

Acknowledgements

Our thanks go to Mr. Ferruccio Valentini (Tuenno) who tirelessly collected in the last years the plant fossils discussed in this paper. Without his great enthusiasm and passion, we could never have carried out this paper. Thanks to the MUSE (Museo delle Scienze) of Trento and the Museum of Nature South Tyrol of Bolzano for making their collections accessible. We also would like to thank the Museum of Geology and Palaeontology of the University of Padova, and particularly the curator Dr. Mariagabriella Fornasiero for her assistance. This manuscript has been improved by the thoughtful comments of two anonymous reviewers. This work has been supported by funds from the Museum of Nature South Tyrol and funds from the PhD School of Earth Sciences of the University of Padova. This paper is also part of the IGCP 630 cooperation project "Permian-Triassic climatic and environmental extremes and biotic response".

References

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

Barth, S., Mohr, B.A.R., 1994. Palynostratigraphically determined age of the Tregiovo sedimentary complex in relation to radiometric emplacement ages of the Athesian Volcanic Complex. Neues Jahrb. Geol. Palaontol. Abh. 192, 273–292.

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

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

Brousmiche, C., 1983. Les fougères sphénopteridiennes du Bassin Houiller Sarro Lorrain (Systematique Stratigraphie). Soc. Géol. Nord Publ. 10, 1–477.

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

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

Cassinis, G., Nicosia, U., Pittau, P., Ronchi, A., 2002. Palaeontological and radiometric data from the Permian continental deposits of the Central-Eastern Southern Alps (Italy), and their stratigraphic implications. Mém. Assoc. Géol. Permien 2, 53–69.

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

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

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

DiMichele, W.A., Wagner, R.H., Bashforth, A.R., Álvarez-Vázquez, C., 2013. An update on the flora of the Kinney Quarry of central New Mexico (Upper Pennsylvanian), its preservational and environmental significance. N. M. Mus. Nat. Hist. Sci. Bull. 59, 289–325.

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

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

Forte, G., Kustatscher, E., Van Konijnenburg–van Cittert, J.H.A., Looy, C.V., Kerp, H., 2017. Conifer diversity in the Kungurian of Europe – evidence from dwarf-shoot morphology. Rev. Palaeobot. Palynol. 244:308–315. https://doi.org/10.1016/j.revpalbo.2017.01.004.

Geinitz, H.B., 1869. Über fossile Pflanzenreste aus der Dyas von Val Trompia. N. Jb. Mineral. Geol. Paläontol. 1869, 456–461.

Gothan, W., Nagalhard, K., 1922. Kupferschieferpfanzen aus dem niederrheinischen Zechstein. Jahrb. Preuss. Geol. Landesanst. 42, 440–459.

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

Kustatscher, E., Bauer, K., Butzmann, R., Fischer, T.C., Meller, B., van Konijnenburg-van Cittert, J.H.A., Kerp, H., 2014. Sphenophytes, seed ferns and taeniopterids from the Upper Permian of Bletterbach (Dolomites, N-Italy). Rev. Palaeobot. Palynol. 208, 65–82.

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

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

Lucas, S.G., Nelson, W.J., DiMichele, W.A., Krainer, K., Barrick, J.A., Voigt, S., Chaney, D.S., Elrick, S., Spielmann, J.A., 2013. Field guide to the carboniferous – Permian transition in the Cerros de Amado and Vicinity, Socorro Country, Central New Mexico. N. M. Mus. Nat. Hist. Sci. Bull. 59, 39–76.

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

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

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

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

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

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

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

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

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

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

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

Tabor, N.J., Montañez, I.P., 2002. Shift in late Paleozoic atmospheric circulation over western equatorial Pangea: insights from pedogenic mineral $\delta^{18}C$ compositions. Geology 30, 1127–1130.
Tabor, N.J., Montañez, I.P., 2004. Morphology and distribution of fossil soils in the Permo–Pennsylvanian Wichita and Bowie Groups, north-central Texas, USA: implications for western equatorial Pangean palaeoclimate during icehouse–greenhouse transition. Sedimentology 51, 851–884.
Van Amerom, H.W.J., 1975. Die eusphenopteridischen Pteridophyllen aus der Sammlung des Geologischen Bureaus in Heerlen, unter besonderer Berücksichtigung ihrer Stratigraphie bezüglich des südlimburger Steinkohlenreviers. Mededelingen Rijks Geologische Dienst, Serie C-III-1-No. 7. pp. 1–208.
Visscher, H., Kerp, H., Clement-Westerhof, J.A., Looy, C.V., 2001. Permian floras of the Southern Alps. Nat. Bresciana Mus. Civ. Sci. Nat. Brescia Monogr. 25, 117–123.
Weiss, C.E., 1879. Die Flora des Rothliegenden von Wünschendorf bei Lauban in Schlesien. Abh. Geol. Spec. Preuss. Thür. Staaten 3 (1), 1–39.
Zeiller, R., 1888. Études sur le terrain houiller de Commentry. 2. Flore fossile. I. In: Renault, B., Zeiller, R. (Eds.), (1888–1809), Bulletin de la Société de l'Industrie Minérale 2(2), pp. 1–366.
Zeiller, R., 1892. Bassin houiller et permien de Brive. II. Flore fossile. Études des Gîtes Minéraux de la France. pp. 1–132.
Zeiller, R., 1898. Contribution à l'étude de la flore ptéridologique des schistes permiens de Lodève. Bul. Mus. Hist. Nat. Marseille 1, 6–69.