TRIASSIC MACRO- AND MICROFLORAS OF THE EASTERN SOUTHERN ALPS

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ABSTRACT

In this paper, we provide an overview of the historically known Triassic floras from the Eastern Southern Alps (e.g., Raibl and Recoaro), as well as the newer macro- and micro-plant assemblages that have been recorded during the 20th and 21st centuries. This includes some specimens stored in various European museums. The plant assemblages are presented here in chronostratigraphic order, starting with the Early Triassic, an interval of which only very few plant fragments are known from the area, whereas palynological data are available. In contrast to the Early Triassic, the Anisian floras (e.g., Kühwiesenkopf/Monte Prà della Vacca) are quite diverse, in both macrofloras – including *in situ* spores – and palynological assemblages. Similarly, the Ladinian of the Eastern Southern Alps is well known from the flora of Monte Agnello, which is outstanding in terms of both diversity and in total number of specimens, with additional information being derived from a large number of smaller macrofloral collections. The Carnian flora of the Eastern Southern Alps is also represented by a wide range of plant fossils, in contrast to the Norian/Rhaetian floras, which are represented only by a low number of macroremains and dispersed pollen and spores findings. A special subject of interest is the presence of amber in some of the Triassic sediments of the Southern Alps. Between the Wengen/La Valle and Heiligkreuz formations, the Dolomites represent the largest Triassic amber deposit known to date.

In addition to macrofossil collections, the palynological data from many localities permits the reconstruction of environmental conditions during the various stages of the Triassic in the Southern Alps. They provide evidence for at least three shifts from xerophytic to hygrophytic palynoassemblages. Moreover, (chrono-)stratigraphic revision of the various localities enables a better understanding of the geographic and temporal distribution of the various taxa.

Focusing on the overview picture of Triassic flora in the Eastern Southern Alps, only one necessary systematic aspect is highlighted herein. We transfer the material described as *Sphenozamites wengensis* to the genus *Macropterygium* as *Macropterygium wengensis* (Wachtler et Van Konijnenburg-van Cittert, 2000) Kustatscher et Van Konijnenburg-van Cittert comb. nov. The genus *Macropterygium* has been redefined for species with pinnate leaves with wedge-shaped segments that do not yield any cuticles and, thus, cannot be assigned to either the Cycadales or the Bennettitales, thereby distinguishing it from *Apoldia* and *Sphenozamites*.

KEY WORDS

Dolomites, fossil plants, palynomorphs, Werfen Formation, Dont Formation, Wengen Formation, Dolomia di Forni, Anisian, Ladinian, Carnian, Norian

1. INTRODUCTION

The Triassic successions of the Southern Alps are historically famous for two plant fossil sites. Both were well-known already in the 19th century; these were found at Raibl (now Cave del Predil) in the Julian Alps and at Recoaro in the Venetian Prealps (e.g., Schauroth, 1855; Bronn, 1858; De Zigno, 1862; Schenk, 1866–67; Stur, 1868a, 1868b; Schenk, 1868; Gümbel, 1879). Plant and fish fossils from the Carnian Predil Limestone of Raibl/Cave del Predil, stored today mostly in Vienna at the Natural History Museum and the Geological Survey of Austria, were donated or sold by local miners (e.g., Bronn, 1858; Schenk, 1866–67). The historical fossil plant collection of Recoaro comes from the Anisian successions cropping out in the area around Recoaro (Catullo, 1846; Massalongo, 1857; De Zigno, 1862) and is today stored mainly in the palaeontological collections of the natural history museums of Verona, Padova and Venice. Several important plant collections were recovered from the Dolomites (mostly 20th and 21st century) and the Carnic and Julian Alps (20th–21st century). From the Western Southern Alps, only a few floras are known so far, such as the Carnian flora from Monte Pora in the Bergamasc Alps and the Ladinian plants from the UNESCO World heritage site Monte San Giorgio (e.g., Passoni, 1996, 1999; Passoni & Van Konijnenburg-van Cittert, 2003;

Stockar & Kustatscher, 2010). There are also isolated historical reports about plant fossils from the Ladinian sediments of Besano, Brembana Valley, Seriana Valley, Valsassina and the surroundings of Lake Como (Schenk, 1889; Sordelli, 1896).
More recent studies include palynological analyses. Their results show that palynomorph assemblages reflect the climatic fluctuations that affected the main floristic groups during the Triassic, when the area of the Southern Alps was positioned in low northern latitudes, at about 20–35° N, on the north-western coast of Pangaea. They evidence a series of shifts to more humid climatic conditions that were partly of regional (late Anisian, late Longobardian) and partly of worldwide scale (e.g., Carnian Pluvial Episode). Furthermore, palynological analyses led to one of the most detailed biostratigraphic scales for this region, with biostratigraphic zones and distinct palynological assemblages based on the appearance of characteristic taxa, correlated with the ammonoid biozonation (e.g., Visscher & Brugman, 1981; Van der Eem, 1983; Brugman, 1986; Jadoul et al., 1994; Roghi, 1995; Carulli et al., 1998; Hochuli et al., 2015).
The aim of this paper is an integrative overview on the historically known Triassic floras in the frame of current (chrono-)stratigraphy, combined with new data that have been recorded during the 20th and 21st century. This also includes some single fossil specimens and small collections stored in various European museums.

2. MATERIALS AND METHODS

The Southern Alps as considered herein correspond to the part of the Eastern Alps lying south of the Periadriatic Seam. They are mainly located in Northern Italy and adjacent areas of Austria and Slovenia. In contrast to the austroalpine nappes in the Central Alps, the sediments of the Southern Alps document the history of the southern Tethys and the microcontinent Adria (e.g., Schmid et al., 2008). To the south, the Southern Alpine successions are overlain discordantly by the sediments of the Po Basin. The outcropping successions comprise mainly Permian to Cretaceous sediments, with limestones and dolomites being the most prominent types. This paper discusses the Eastern Southern Alps, i.e., East of the Giudicarie Line, including the Dolomites, the Venetian Prealps, the Julian Alps and Prealps and the Carnic Alps. This area is where almost all plant fossil localities of Triassic age in the Alps are located (Figs. 1, 9, 12) and can be considered in a coherent stratigraphic context (Figs. 2, 3, 5).
The fossils discussed here are stored in the palaeontological collections of several local and international museums and universities (Appendix 1). These include the Museum of Nature South Tyrol in Bozen/Bolzano (collection number prefix "NMS PAL"), the Museum de Gherdëina (prefix "MDG"), the Museo delle Regole of Cortina d'Ampezzo (prefix "MDR"), the Museo

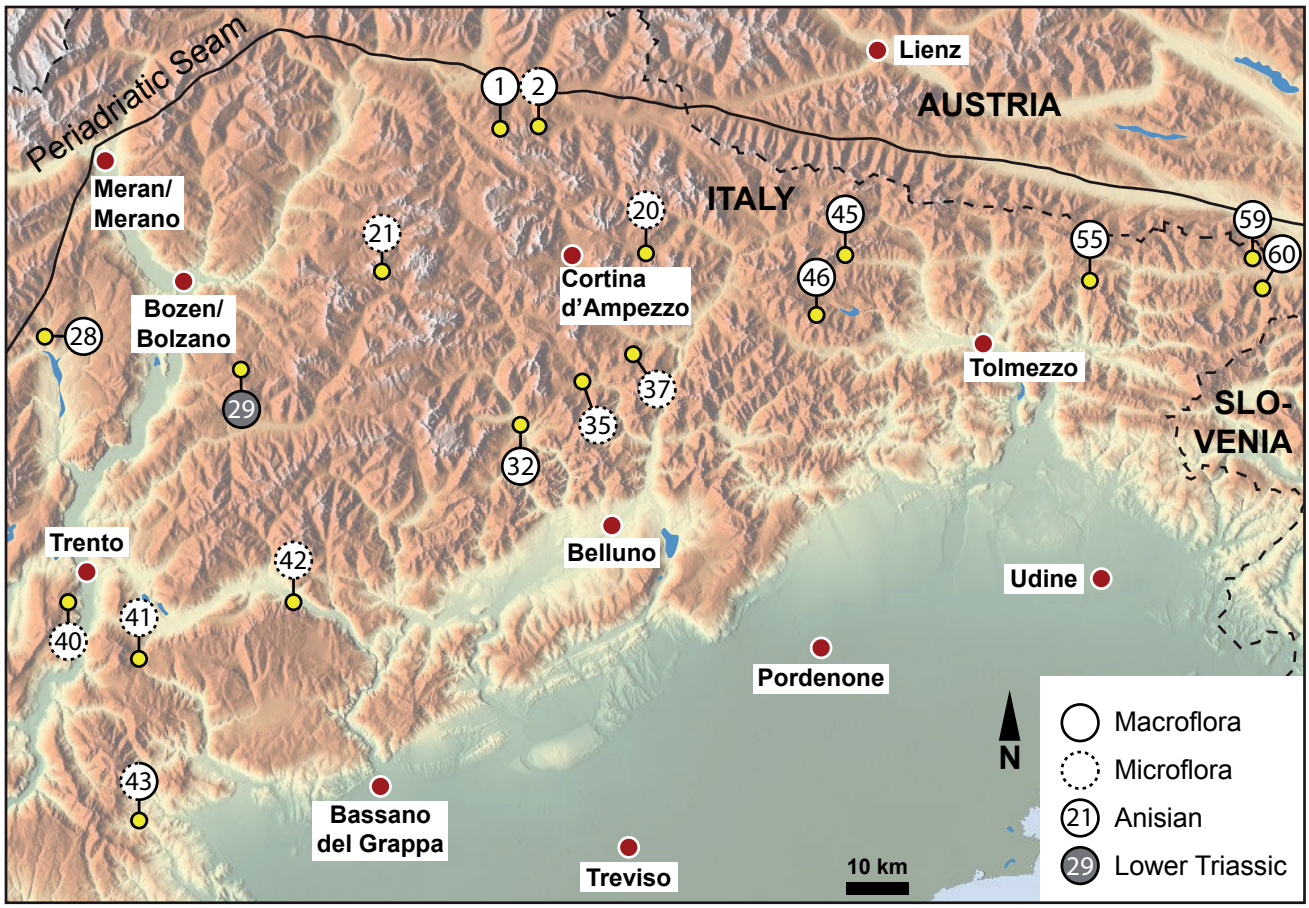

Figure 1: Map of the Eastern Southern Alps with the localities from which Lower Triassic and Anisian plant macrofossils and/or microfossil assemblages have been reported. **1.** Piz da Peres; **2.** Kühwiesenkopf/Monte Prà della Vacca; **20**. Palus San Marco; **21.** Plattkofel/Sasso Piatto, Grohmannspitze/Punta Grohmann (Rif. S. Pertini, Rif. T. Demetz, Gabia), Val Duron; **28.** Val di Non; **29**. Bletterbach Gorge; **32.** Valle di San Lucano, Agordo; **35.** Valle di Zoldo, Dont; **37.** Monte Rite; **40.** Val Gola, Margon; **41.** Val di Centa; **42.** Rio dei Carrari; **43.** Recoaro Terme, Monte Rove; **45.** Culzei, Prato Carnico, Val Pesarina; **46.** Monte Bìvera; **55.** Val Aupa (Moggio Udinese); **59.** Rio Tschofen, Tarvisio; **60.** Canale Prasnig, Rio Freddo/Kaltwasser.

Ladino Fodom (prefix "PL"), the Museo Geologico delle Dolomiti of Predazzo (prefix "MPP"), the Museo Friulano di Storia Naturale of Udine (prefix "MFSNgp"), the Museo di Storia Naturale of Venice (prefix "MSNV"), the Museo Civico di Storia Naturale, Verona (prefix "MCSNV"), the Museum für Naturkunde Berlin (prefix "MB.Pb"), the Natural History Museum of Vienna (prefix "NHMW"), the Goldfuss Museum Bonn (prefix "STIPB-PB"), the Staatliche Sammlung für Naturkunde Dresden (prefix "ItTr"), the Staatliches Museum für Naturkunde Stuttgart (prefix "SMNS"), the National Museum Prague (NMP), the Bayerische Staatssammlung für Geologie und Paläontologie (prefix "BSPG"), the Geologisches Landesamt München (prefix "GLA"), the palaeontological collections of the universities of Ferrara (prefix "MPL"), Padova (prefix "MPP"), Göttingen (prefix "GZG"), Halle-Wittenberg (prefix "MLU"), Innsbruck (prefix "GII"), Utrecht (prefix "UU") and Tübingen (prefix "GPIT"), as well as the botanical institute of the University of Innsbruck (prefix "BII"). Additional specimens described in the 19th and early 20th centuries are partly lost (e.g., Schauroth, 1855; Catullo 1846; Massalongo, 1857; Bronn, 1858; De Zigno, 1862; Schenk, 1866–67, 1868; Stur, 1868a, 1868b; Gümbel, 1879; Mojsisovics, 1879; Arthaber, 1903; Ogilvie Gordon, 1927, 1934; Mutschlechner, 1932). For the sake of overview, localities are grouped in the geographic maps (Figs. 1, 9, 12) and tables (1, 3, 4). Details on individual localities are provided in Appendix 1.

3. THE EARLY TRIASSIC FLORAS OF THE EASTERN SOUTHERN ALPS

3.1. THE EARLY TRIASSIC MACROFLORA OF THE EASTERN SOUTHERN ALPS

There are so far no identified plant remains from the Early Triassic successions of the Eastern Southern Alps, although several small fragments were collected, e.g., in the Bletterbach Gorge ([29] in Figs. 1, 2, pers. observ. EK and HN). This scarcity in plant fossils may be related to the fact that the depositional environment of the Early Triassic Werfen Formation with its coastal sand-, silt- and limestones was not favorable for plant preservation.

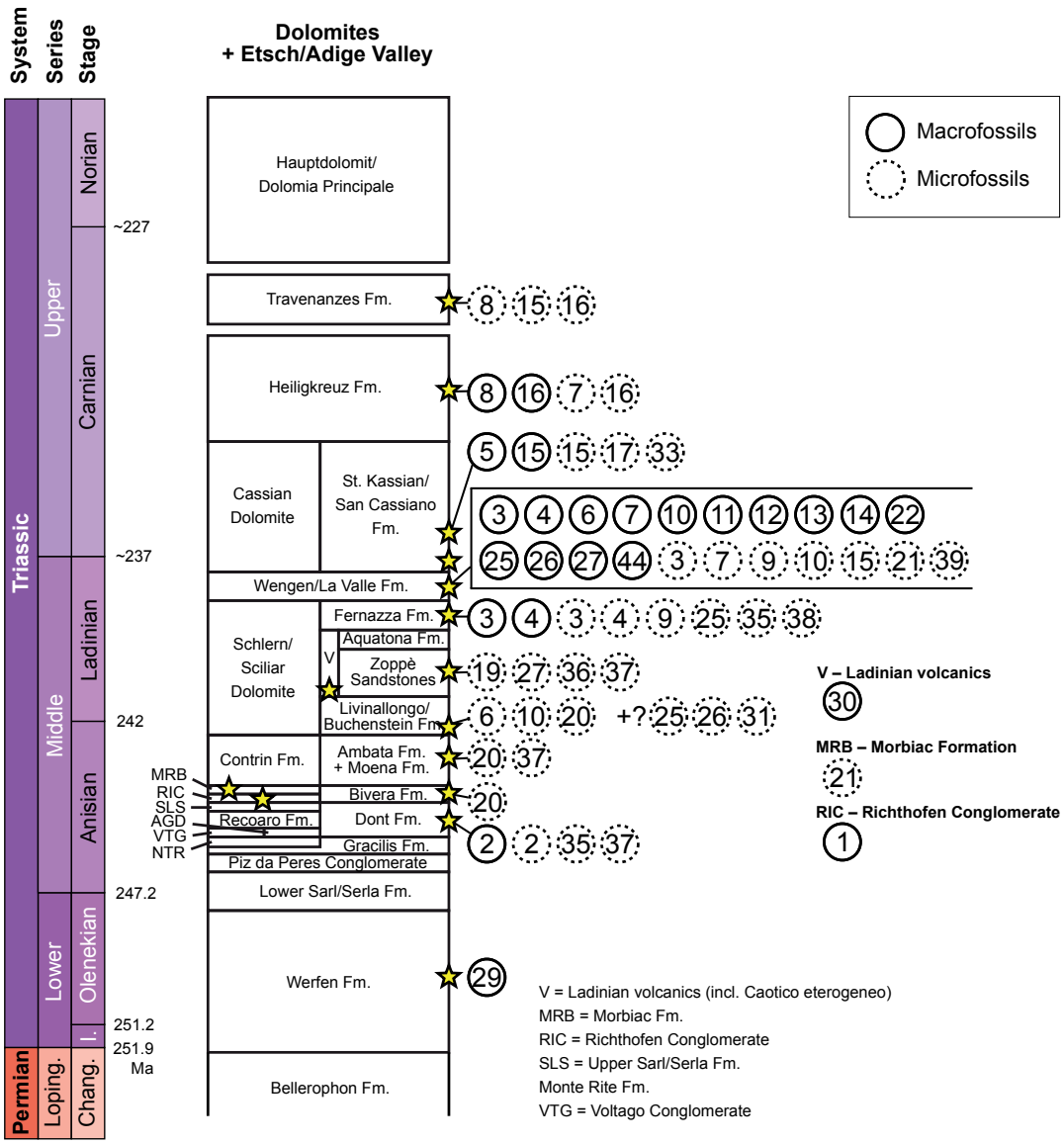

Figure 2: Stratigraphic distribution of plant macro- and microfossil assemblages in the Dolomites and the Etsch/Adige Valley. Encircled numbers refer to the localities in Figs. 1, 9, 12. Loping. = Lopingian; Chang. = Changhsingian; I. = Induan.

3.2. THE EARLY TRIASSIC MICROFLORA OF THE EASTERN SOUTHERN ALPS

The palynological record of the Early Triassic sediments gives better insights into the floral composition of this time interval. Several palynological analyses of the Permian–Triassic boundary (PTB) have been carried out in recent years (e.g., Cirilli et al., 1998; Looy et al., 2005; Spina et al., 2015; Nowak et al., 2019). The studied sections are mainly located in the Dolomites, such as Seres (Cirilli et al., 1998), Tesero (Spina et al., 2015), Tramin (Looy et al., 2005; Bernardi et al., 2018) and the Laurinswand in the Rosengarten/Catinaccio Massif (Nowak et al., 2019). The Early Triassic biotic recovery flora after the Permian–Triassic crisis is characterized by quantitatively poor palynological assemblages, with bisaccate pollen typical of Permian sediments, as well as trilete and monolete spores (cingulate and zonate). The spores show a notable increase in relative abundance and in the frequency of spore tetrads around the PTB (Looy et al., 2005; Nowak et al., 2019), probably correlative to the so-called "spore spike" that has been reported elsewhere from this interval.

A mass occurrence of *Reduviasporonites* (al. *Tympanicysta*, *Chordecystia*) has also been observed close to the PTB in the Southern Alps, most pronounced in the Tesero Member (Werfen Formation) at the Tesero section (Eshet et al., 1995; Visscher et al., 1996; Foster et al., 2002). Similar observations have been made in other parts of the world in approximately coeval strata (e.g., Eshet et al., 1995; Steiner et al., 2003; Sandler et al., 2006; Rampino & Eshet, 2018; Hochuli, 2016). This phenomenon has been called a "fungal spike" and led to theories about the role that this taxon might have played in the end-Permian mass extinction as a saprophyte or pathogen. This phenomenon is, however, not restricted to the disaster level as previously supposed. In the Laurinswand section, *Reduviasporonites* is present in almost all palynological assemblages from the upper Bellerophon and lowermost Werfen formations, but with the highest relative abundance in the lower Mazzin Member of the Werfen Formation (Nowak et al., 2019). The "fungal spike" normally pre-dates the spore spike, whereas at the Laurinswand section, the peak in abundance of *Reduviasporonites* lies stratigraphically above the onset of the spore spike (Nowak et al., 2019).

Palynological associations of Olenekian age (Val Badia and Cencenighe members, Werfen Formation) are characterized by abundant lycophyte spores and acritarchs (Visscher, 1974). The sudden spread of gymnosperms, evidenced in Hungary at the end of the Spathian and corresponding to the restoration of the equatorial semi-arid conifer forests in Europe, has also been recorded in the Recoaro area (Aegean–Bithynian) with an important increase in bisaccate pollen grains (alete, monolete, trilete), especially of the *Triadispora* group (Brugman, 1986; Looy et al., 1999 and references therein).

The Lower Triassic of the Alpine Realm is palynostratigraphically divided into an unnamed interval and two phases (Fig. 4); the nejburgii-heteromorphus phase and the heteromorphus-conmilvinus phase (Kustatscher & Roghi, 2014). The older phase ranges from the upper part of the Induan to the lower part of the Spathian, the younger one corresponds to the middle-upper Spathian (Brugman, 1986; Visscher & Brugman, 1986; Nowak et al., 2018). The nejburgii-heteromorphus phase is characterized by the first occurrence of *Voltziaceaesporites heteromorphus* and is subdivided into the late Dienerian-Smithian heteromorphus-papillatus subphase (Brugman, 1986) and the early Spathian heteromorphus-leschikii subphase. The heteromorphus-papillatus subphase shows a dominance in *Densoisporites nejburgii* and abundant *Endosporites papillatus* and *Punctatisporites* spp. The heteromorphus-leschikii subphase is dominated by *D. nejburgii* and, in the upper part, by abundant grains of *V. heteromorphus* and *E. papillatus.* Taeniate pollen grains are rare. Acritarchs are dominant in both subphases (Brugman, 1986).

The heteromorphus-conmilvinus phase starts with the first occurrence of *Jugasporites conmilvinus*. *Densoisporites nejburgii* continues to be dominant in the conmilvinus-cymbatus subphase, in correspondence with abundant *Voltziaceaesporites heteromorphus*, *J. conmilvinus* and trilete spores. The *Cyclotriletes-Convolutispora* complex has its first occurrence in this subphase. The conmilvinus-noviaulensis subphase corresponds to a decrease in abundance of *D. nejburgii* in conjunction with a dominance of bisaccate pollen grains such as *V. heteromorphus* and *J. conmilvinus* (Brugman, 1986).

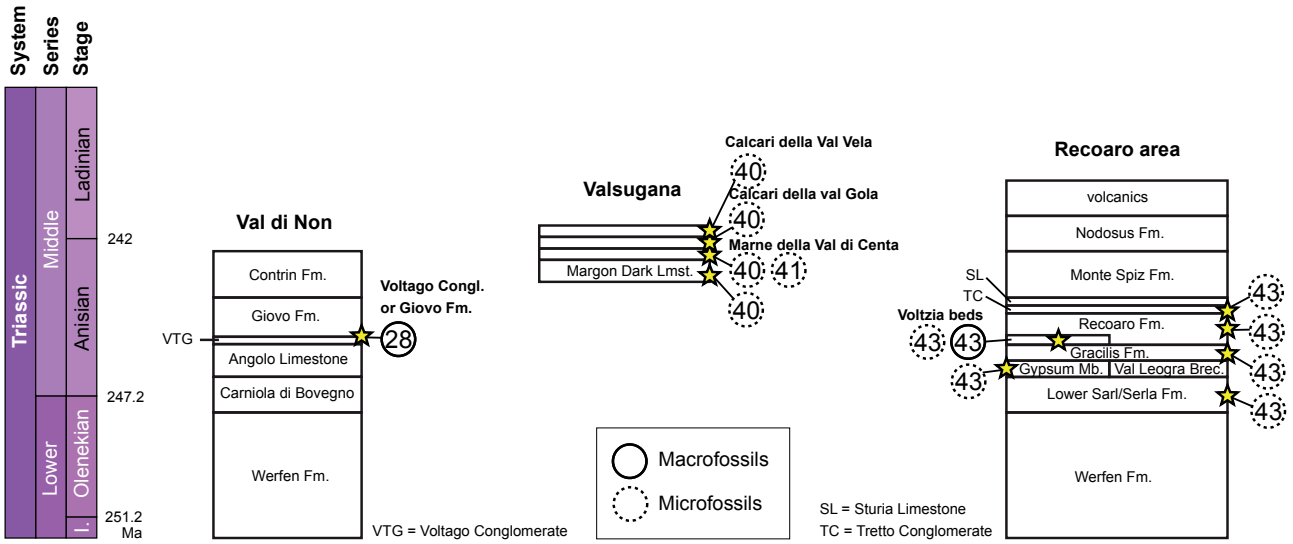

Figure 3: Stratigraphic distribution of plant macro- and microfossil assemblages in the Val di Non, Valsugana and Recoaro areas. Encircled numbers refer to the localities in Figs. 1, 9, 12. I. = Induan.

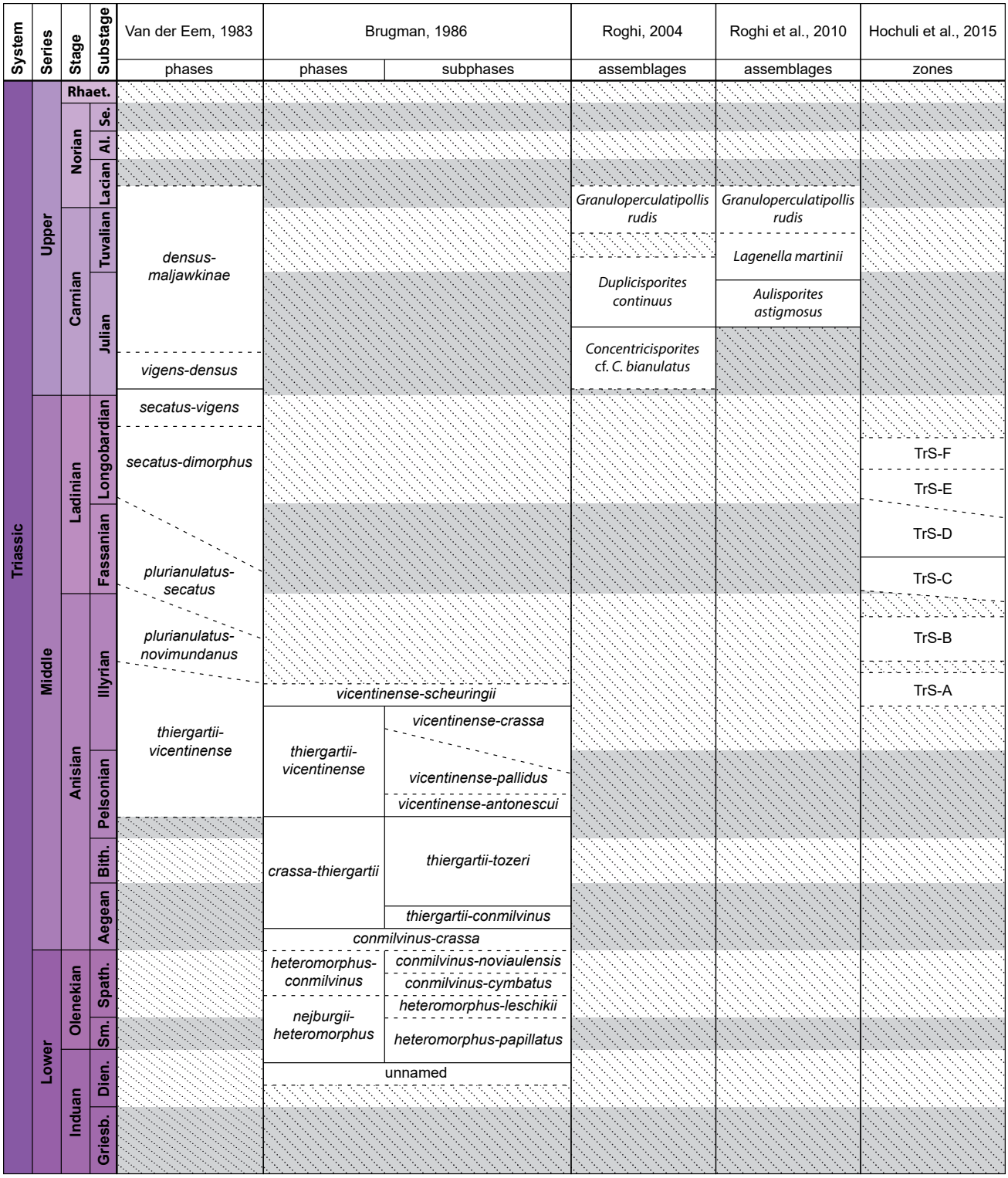

Figure 4: Palynostratigraphic schemes for the Triassic of the Southern Alps. Griesb. = Griesbachian; Dien. = Dienerian; Sm. = Smithian; Spath. = Spathian; Bith = Bithynian; Al. = Alaunian; Se. = Sevatian; Rhaet. = Rhaetian.

4. THE ANISIAN FLORAS OF THE EASTERN SOUTHERN ALPS

4.1. THE ANISIAN MACROFLORA OF THE EASTERN SOUTHERN ALPS

The most abundant, diverse and best-preserved plant assemblages of the Southern Alps come from Middle Triassic sediments (Fig. 1, 2, 3, 5). Grauvogel-Stamm & Ash (2005) described the Anisian flora (lower Middle Triassic) of the Northern Dolomites as one of the oldest examples of a full recovery of the ecosystems after the end-Permian crisis. The Anisian flora of the Eastern Southern Alps represents a highly diverse vegetation dominated by ferns, cycadophytes and conifers, while seed ferns and lycophytes are common and sphenophytes are rare. The diversity of the local assemblages may, however, vary noticeably. The most diverse and abundant Anisian plant assemblage comes from Kühwiesenkopf/Monte Prà della Vacca near Olang/Valdaora ([2] in Figs. 1, 2) in the Northern Dolomites (Broglio Loriga et al., 2002; Van Konijnenburg-van Cittert et al., 2006; Kustatscher et al., 2007, 2009, 2010a, 2010b). Less rich plant assemblages come from Piz da Peres ([1] in Figs. 1, 2; near Enneberg/Marebbe, also Northern Dolomites; Todesco et al., 2008), Agordo ([32] in Figs. 1, 2; Kustatscher et al., 2011b; Testa et al., 2013), Recoaro ([43] in Figs. 1, 2; e.g., Catullo, 1846; Schauroth, 1855; Massalongo, 1857; De Zigno, 1862; Schenk, 1868; Gümbel, 1879) and the Val di Non ([28] in Figs. 1, 3; Kustatscher et al., 2012a). Isolated plant fossil findings were collected from the surroundings of Rio Freddo/Kaltwasser ([60] in Figs. 1, 5; between Raibl/Cave del Predil and Tarvisio), Val Aupa ([55] in Figs. 1, 2; Moggio Udinese), Prato Carnico ([45] in Figs. 1, 5) and Tarvisio in the Udine Province ([59] in Figs. 1, 5; collection of the Museo Friulano di Storia Naturale). Our knowledge of the Anisian flora of the Eastern Southern Alps is, thus, strongly influenced by the plant assemblage of Kühwiesenkopf/Monte Prà della Vacca that was subjected to less taphonomic and preservation bias than other Anisian plant fossil localities, which show a more limited number of taxa (see Tab. 1). Lycophytes are represented by both herbaceous and sub-arborescent taxa (Broglio Loriga et al., 2002; Kustatscher, 2004; Kustatscher et al., 2010a, 2010b). *Lycopia dezanchei*, the most common form, is characterised by a dichotomising creeping prostrate rhizome (representing the primary shoot axis) from which arise aerial axes, apically bifurcated and covered with bundles of long microphylls. Isoetales are represented by two taxa. *Isoetites brandneri*, the more abundant form, is characterised by a short stem and long, helically inserted microphylls. *Lepacyclotes bechstaedtii* has a quadrilobed corm with proximally inserted macrosporophylls and distal microphylls that arise in a narrow spiral. Selaginellales are rare in the flora, with *Selaginellites leonardii* characterised by a strobilus yielding both micro- and megaspores, and some sterile fragments that have never been found in organic connection. Sphenophytes are represented by stem fragments, strobili and isolated sporangiophore heads of *Equisetites mougeotii*, as well as a few specimens of *Equisetites* sp. (Fig. 6A), *Neocalamites* sp. and *Echinostachys* sp. (Broglio Loriga et al., 2002; Kustatscher et al., 2007).

The ferns are a very diverse plant group represented, e.g., by several osmundaceous taxa, such as *Neuropteridium voltzii*, *N. elegans* and *N. grandifolium*, and their respective fertile fronds *Scolopendrites scolopendrioides* (fertile fronds of *N. voltzii*) and *S. grauvogelii* (fertile fronds of *N. elegans*). Another typical Anisian fern in European floras is *Anomopteris mougeotii* (Fig. 6B), whereas *Gordonopteris lorigae* is known so far only from the Southern Alps. The two marattialean taxa ?*Marattiopsis* sp. and *Danaeopsis* sp. are represented by small fragments (Van Konijnenburg-van Cittert et al., 2006; Kustatscher et al., 2012b). *Sphenopteris schoenleiniana*, *Cladophlebis remota*, *Cladophlebis* sp. and a fern described under gen. indet. sp. indet. by Van Konijnenburg-van Cittert et al. (2006) that resembles the specimens described as *Neuropteridium curvinerve* by Wang & Wang (1990) are of unknown botanical affinity. Some enigmatic fertile structures (*Lugardonia paradoxa*) consisting of an up to 20 cm long axis with helically arranged short stalks each carrying a cluster of 3–4 elongated microsporangia may also belong to the ferns or seed ferns (Kustatscher et al., 2009).

Seed ferns include the peltasperm foliage type *Scytophyllum bergeri* with sun and shade leaves and the associated reproductive organs *Peltaspermum bornemannii* (Kustatscher et al., 2007). Leaf fragments assignable to *Sagenopteris* sp. and *Ptilozamites* sp. are rare in the flora (Broglio Loriga et al., 2002; Kustatscher & Van Konijnenburg-van Cittert, 2007; Kustatscher et al., 2007, 2010a); these might each represent the oldest occurrence of their respective genera. Cycadophytes are well represented in this flora (Broglio Loriga et al., 2002; Kustatscher, 2004; Kustatscher et al., 2010a). *Bjuvia* sp. is characterized by large entire leaves (up to 50 cm long and 20 cm wide) with thin and brittle cuticles. *Taeniopteris* sp. has smaller leaves with an entire margin and parallel, undivided veins. Some dissected leaves with strap-like, regular or irregular leaf segments resemble *Pterophyllum robustum* from the Middle Triassic of Apolda (Germany; Kelber & Hansch, 1995). Moreover, several dispersed macrosporophylls and cones also belong to the cycadophytes. Each macrosporophyll has a finely pinnate apical part and carries two rows of seeds typical of the genus *Dioonitocarpidium* (Fig. 6C; Broglio Loriga et al., 2002; Kustatscher, 2004; Kustatscher et al., 2010a).

At least five different conifer taxa have been distinguished (Broglio Loriga et al., 2002; Kustatscher, 2004; Kustatscher et al., 2010a). *Voltzia recubariensis* has robust, triangular, helically arranged leaves arising almost perpendicularly from the axis and male cones have been found as well (Fig. 6E). *Voltzia walchiaeformis* has fine, falcate needles inserted spirally on the shoots. The secondary shoots arise in one plane from the primary shoot. A third voltzialean taxon has heterophyllous leaves, ranging from short and falcate (1 cm long; Fig. 6D) with a pointed apex to long and strap-like (3–4 cm long) with a rounded apex, similar to those of *V. heterophylla* Brongniart. However, the female cones belonging to this conifer have ovuliferous scales divided into several lobes that are only slightly fused at the base, similar to *Pseudovoltzia*, a late Permian conifer (Clement-Westerhof, 1987). *Albertia* has multiply branched shoots, covered with spirally attached, elliptic leaves, whereas the leaves of *Pelourdea vogesiaca* are up to 25–30 cm long and lanceolate, slightly restricted at the base and with parallel veins.

Additional taxa have been recorded in less rich Anisian plant assemblages, including the sphenophytes *Equisetites arenaceus* and *E. conicus*, the fern *Cladophlebis leuthardtii* and the cycad macrosporophyll *Dioonitocarpidium pennaeformis* (Kustatscher et al., 2011b, 2012a). The conifer taxa *Aethophyllum foetterlianum*, *Araucarites massalongii*, *Araucarites pachyphyllus*, *Taxites massalongii*, *T. vincentinus* and *Taxodites saxolimpiae* were described from the flora of Recoaro (Tab. 1; De Zigno, 1862; Gümbel, 1879; Schenk, 1868), some were even mentioned only on labels in museum collections (e.g., *Araucarites agordicus* Anger, *Araucarites albuctenoides* Mass.). However, this taxonomy is partly outdated and needs a detailed revision with a modern approach. These taxa will therefore not be considered further on.

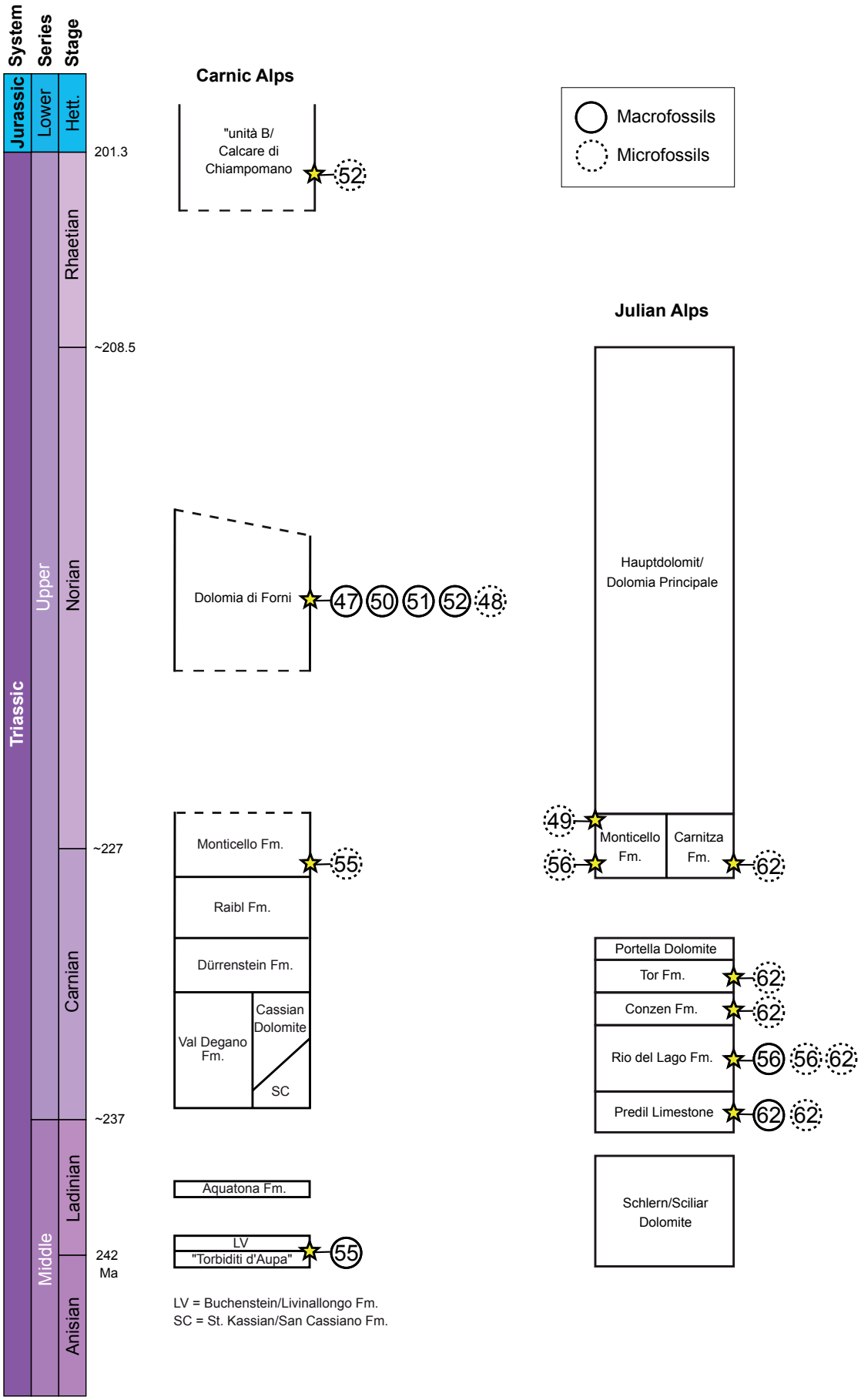

Figure 5: Stratigraphic distribution of plant macro- and microfossil assemblages in the Carnic and Julian Alps. Encircled numbers refer to the localities in Figs. 1, 9, 12. Hett. = Hettangian.

	Anisian	Kühwiesenkopf	Piz da Peres	Recoaro	Agordo	Val di Non	Prato Carnico	Rio Freddo/Kaltwasser	Moggio Udinese	Tarvisio	Monte Bivera
Lycophytes	*Isoetites brandneri*	x									
	Lepacyclotes bechstaedtii	x									
	Lepacyclotes sp.						x				
	Lycopia dezanchei	x									
	Selaginellites leonardii	x									
Horsetails	*Echinostachys* sp.	x		x							
	Equisetites arenaceus			x					x		
	Equisetites conicus					x					
	Equisetites mougeotii	x	?								
	Equisetites sp.			x	?		?		x		
	Neocalamites sp.	x				x					
Ferns	*Anomopteris mougeotii*	x	x		x				x		
	Cladophlebis leuthardtii		x								
	Cladophlebis remota	x			x						
	Cladophlebis sp.	x									
	Danaeopsis angustifolia	?	?								
	Gordonopteris lorigae	x	x			x					
	Marattiopsis sp.	?									
	Neuropteridium elegans	x	x			x					
	Neuropteridium grandifolium	x									
	Neuropteridium voltzii	x	x		x			x			
	Pteridophyta incertis sedis	x									
	Scolopendrites grauvogelii	x									
	Scolopendrites scolopendrioides	x									
	Scolopendrites sp.		x		x						
	Sphenopteris schoenleiniana	x									
	Symopteris sp.									x	
Seed ferns	*Peltaspermum bornemannii*	x	x								
	Peltaspermum sp.				x		x				
	Ptilozamites sp.	?									
	Sagenopteris sp.	x									
	Scytophyllum bergeri	x	x								
Cycads	*Bjuvia dolomitica*	x	x								
	Dioonitocarpidium pennaeformis					?					
	Dioonitocarpidium sp.	x	x								
	Nilssonia sp.	x									
Conifers	*"Aethophyllum foetterlianum"*			x							
	Albertia sp.	x		x	x		x				
	"Araucarites agordicus"			x							
	"Araucarites albuctenoides"			x							
	"Araucarites massalongii"			x							
	"Araucarites pachyphyllus"			x							
	Elatocladus sp.	x									
	Pagiophyllum sp.			x							
	Pelourdea vogesiaca	x					x				
	Pseudovoltzia sp.	?									
	"Taxites massalongii"			x							
	"Taxites vincentinus"			x							
	"Taxodites saxolimpiae"			x							
	"Voltzia heterophylla"	x		x			x				
	Voltzia recubariensis	x	x	x	x	x	x				
	Voltzia walchiaeformis	x				?					
	Voltzia sp.	x		x	x		x				x
Incertae sedis	*Carpolithes* sp.	x					x				
	Lugardonia paradoxa	x									
	Taeniopteris sp.	x	x		x						

Table 1: Occurrences of Anisian plant macrofossil taxa at the various localities in the Eastern Southern Alps.

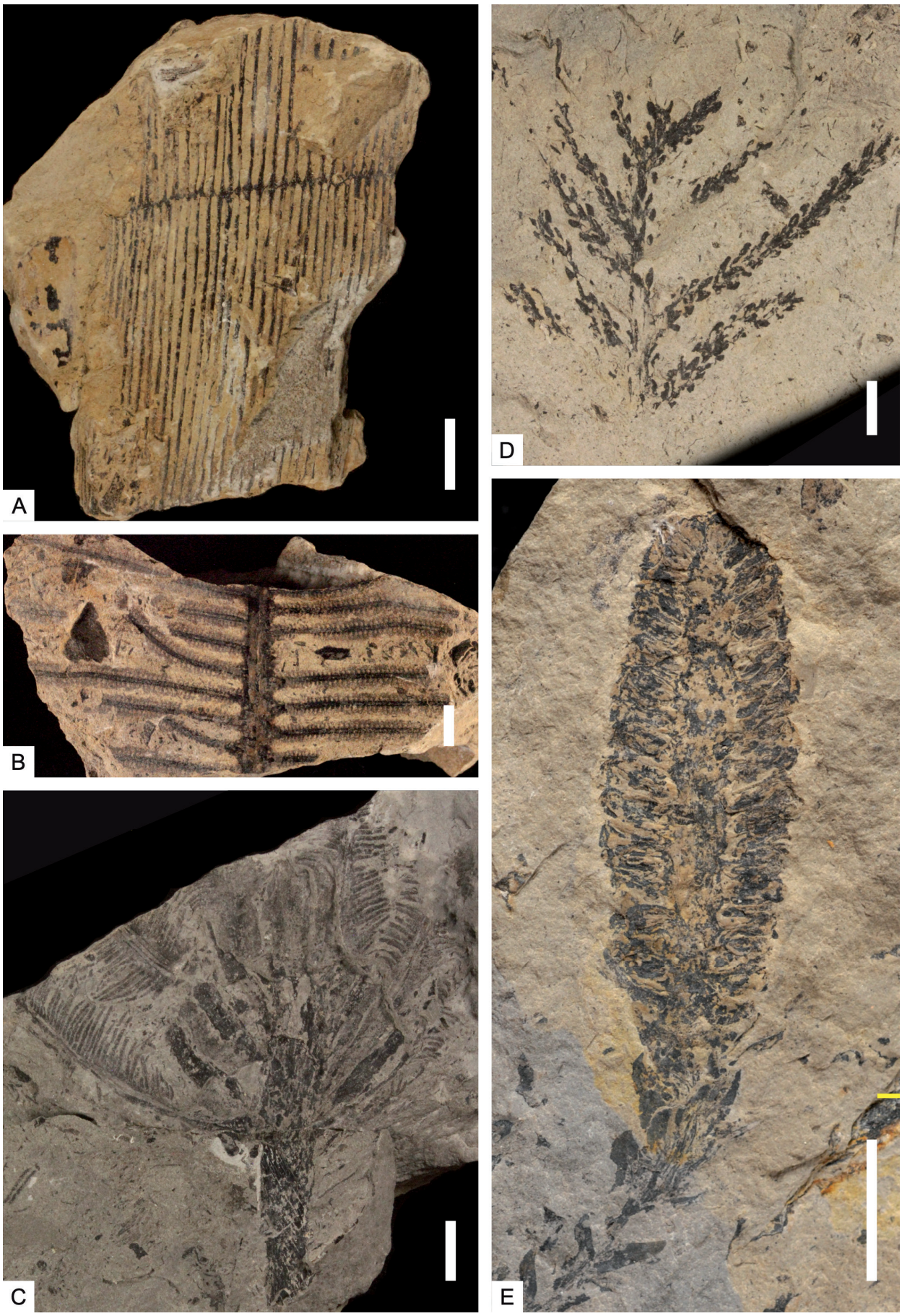

Figure 6: Plant macrofossils from the Anisian of the Eastern Southern Alps. Scale bars = 10 mm. **A.** stem fragment with vascular bundles of *Equisetites* sp., NMS PAL 808; **B.** Frond fragment of *Anomopteris mougeotii* Brongniart, 1828, NMS PAL 241; **C.** *Dioonitocarpidium* sp. from Kühwiesenkopf/Monte Prà della Vacca, NMS PAL 1669; **D.** shoot of *Voltzia* sp., NMS PAL 671; **E.** male cone of *Voltzia recubariensis* (De Zigno) Schenk, 1868, MPP.

4.2. THE ANISIAN IN *SITU* SPORES AND POLLEN OF THE EASTERN SOUTHERN ALPS

In situ spores have been isolated from the fertile organs of several macrofossil taxa of the Kühwiesenkopf/Monte Prà della Vacca plant fossil assemblage (Tab. 2). These include isospores of osmundaceous ferns (*Scolopendrites scolopendrioides*, *S. grauvogelii*, *Gordonopteris lorigae*; Van Konijnenburg-van Cittert et al., 2006) and microspores of the sphenophyte *Equisetites mougeotii* (Kustatscher et al., 2007), as well as both micro- and megaspores of selaginellalean (*Selaginellites leonardii*) and isoetalean (*Isoetites brandneri*) lycophytes (Kustatscher et al., 2010b; Zavialova et al., 2010). In addition, the problematic *Lugardonia paradoxa* has yielded *in situ* palynomorphs that may be either spores or pre-pollen (Kustatscher et al., 2009) (Fig. 7D).

So far, only the *in situ* spores of *Isoetites brandneri* and *Selaginellites leonardii* have been compared to dispersed sporomorph taxa. Kustatscher et al. (2010b) suggested that the possibly monolete microspores of *I. brandneri* (Fig. 7H) might relate to *Aratrisporites*. However, *Aratrisporites* is cavate, whereas the spores of *I. brandneri* have only one discernable wall layer. Considering also their lack of ornamentation and round to reniform shape, they correspond rather to *Laevigatosporites*, if they are monolete. The megaspores probably relate to *Verrutriletes* (Fig. 3G; Kustatscher et al., 2010b). The morphology and ultrastructure of both the micro- and megaspores of *S. leonardii* has been studied in detail by Zavialova et al. (2010). The microspores (Fig. 7J) were found to conform to *Uvaesporites* in ultrastructure, while no conclusion was reached on the correspondance of a dispersed taxon for the megaspores (Fig. 7I).

The spores of *Scolopendrites scolopendrioides* and *S. grauvogelii* (Fig. 7A, 7B) are both described as "trilete, circular in equatorial outline, with a diameter of 35–45 µm", and with a "scabrate to granulate" exospore (Van Konijnenburg-van Cittert et al., 2006, pp. 952–953). They could conceivably represent slightly immature versions of *Osmundacidites*. The exospore may also appear psilate with only pits around the proximal pole, thereby resembling *Todisporites*. Van Konijnenburg-van Cittert et al. (2006, p. 956) wrote about the spores of *Gordonopteris lorigae* (Fig. 7C) that they were "globose, trilete, 43–62 µm in diameter, with a finely punctate exospore". They can thus be compared to the dispersed genus *Punctatisporites*. The microspores of *Equisetites mougeotii* (Fig. 7E, 7F) have been briefly described as "slightly immature trilete spores, 30–45 µm in diameter" (Kustatscher et al., 2007, p. 1279). To this may be added that they show a dense, scabrate to verrucate ornamentation and that the laesurae can reach the equator.

Plant group	Macrofossil taxon	*In situ sporomorphs*				First description of *in situ* sporomorphs		
		Type	Short description	Corresponding dispersed taxa	Figure(s), this work	Reference	Page(s)	Figure(s)
Pteridophyta, Filicales, ?Osmundaceae	*Scolopendrites scolopendrioides*	isospores	trilete, circular in equatorial outline, diameter 35–45 µm, exospore psilate or scabrate to verrucate	*?Osmundacidites, Todisporites*	3A	Van Konijnenburg-van Cittert et al. 2006	952	pl. 1, figs. 1, 5–6
	Scolopendrites grauvogelii	isospores	trilete, circular in equatorial outline, diameter 35–45 µm, exospore psilate or scabrate to verrucate	*?Osmundacidites, Todisporites*	3B		952–953	pl. 1, figs. 4, 7
	Gordonopteris lorigae	isospores	trilete, globose, diameter ca. 45–60 µm, exospore finely punctate	*Punctatisporites*	3C		955–956	pl. 3, figs. 1–2
Sphenophyta, Equisetales, Equisetaceae	*Equisetites mougeotii*	immature spores	trilete, circular, scabrate to verrucate, diameter 30–45 µm, laesurae can reach equator	?	3E, F	Kustatscher et al. 2007	1279	pl. 1, figs. 6–7
incertae sedis	*Lugardonia paradoxa*	spores or pre-pollen	trilete, more or less circular, smooth inner wall, granulate-verrucate outer wall, diameter ~100 µm, laesurae 3/4 to 7/8 radius, no margo	?	3D	Kustatscher et al. 2009	91	pl. 2, figs. 3–10; pl. 3, figs. 1–11; text Fig. 1
Lycophyta, Selaginellales, Selaginellaceae	*Selaginellites leonardii*	microspores	trilete, diameter 42.5–50 µm, proximally punctate/?granulate or psilate and distally rugulate	*Uvaesporites*	3H	Kustatscher et al. 2010	597	pl. 1, figs. 6–8
		megaspores	trilete (aperture delicate or undeveloped, rare plicae), oval to circular, diameter 270–340 x 300–410 µm, spore wall 10 µm thick and psilate to punctate	?	3G		597	pl. 1, figs. 5, 9
Lycophyta, Isoetales, Isoetaceae	*Isoetites brandneri*	immature microspores	reniform (?monolete), longest diameter up to 35–40 µm, psilate, single wall layer	*?Laevigatosporites*	3J		602	pl. 2, fig. 4
		megaspores	trilete (aperture delicate, rare plicae), diameter 270–300 µm, thick spore wall, convolute to verrucate with proximally reduced ornamentation	*?Verrutriletes*	3I		602	pl. 2, fig. 5

Table 2: Overview on *in situ* palynomorphs from the Dont Formation (Anisian) from the Kühwiesenkopf/Prà della Vacca section.

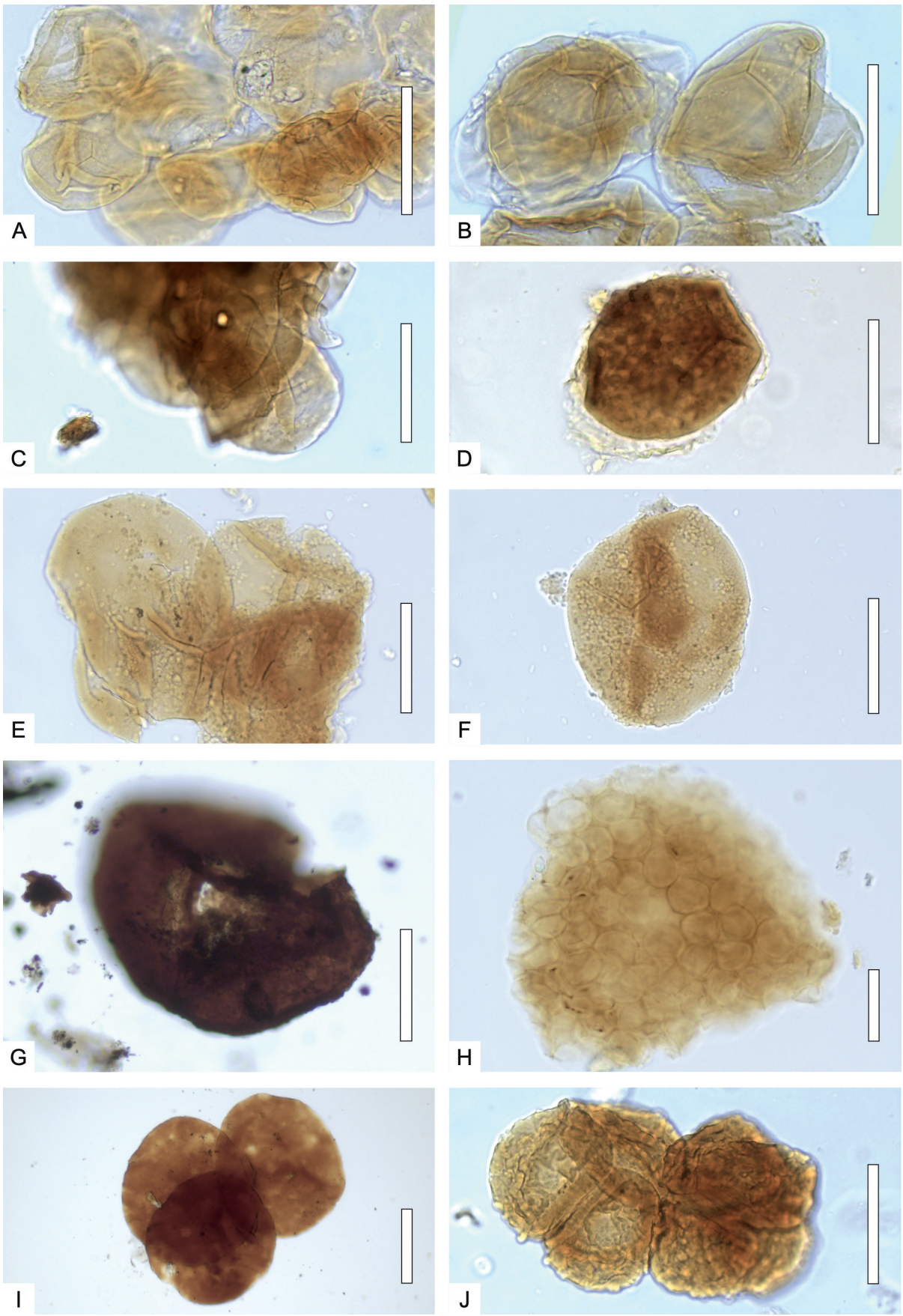

Figure 7: *In situ* palynomorphs from the Dont Formation (Anisian) at the Kühwiesenkopf/Monte Prà della Vacca section. Scale bars A–D, F, H, J = 50 µm; E, G = 100 µm; I = 200 µm. **A.** Spores of *Scolopendrites scolopendrioides* (Brongniart) Van Konijnenburg-van Cittert et al., 2006, NMS KÜH 204; **B.** Spores of *Scolopendrites grauvogelii* Van Konijnenburg-van Cittert et al., 2006, NMS PAL 379; **C.** Spores of *Gordonopteris lorigae* Van Konijnenburg-van Cittert et al., 2006, NMS PAL 259; **D.** Spores or prepollen of *Lugardonia paradoxa* Kustatscher et al., 2009, NMS PAL 1105; **E, F.** Spores of *Equisetites mougeotii* (Brongniart) Wills, 1910, NMS PAL 561; **G.** Megaspore of *Isoetites brandneri* Kustatscher et al., 2010, NMS PAL 1126; **H.** Cluster of microspores of *I. brandneri*, NMS PAL 1136; **I.** Megaspores of *Selaginellites leonardii* Kustatscher et al., 2010, NMS PAL 536; **J**. Two tetrads of microspores of *S. leonardii*, NMS PAL 536.

4.3. THE ANISIAN MICROFLORA OF THE EASTERN SOUTHERN ALPS

The palynofloras diversify noticeably during the Anisian. They contain a large abundance of different lycophytes, horsetails and fern spores, as well as seed fern, cycadophyte and conifer pollen (Fig. 8).

Biostratigraphically (Fig. 4), the Anisian has been divided by Brugman (1986) into at least four phases and five suphases: i) the conmilvinus-crassa phase, ii) the crassa-thiergartii phase (with the thiergartii-conmilvinus and the thiergartii-tozeri subphases), iii) the thiergartii-vicentinense phase (with the vicentinense-antonescui, the vicentinense-pallidus and the

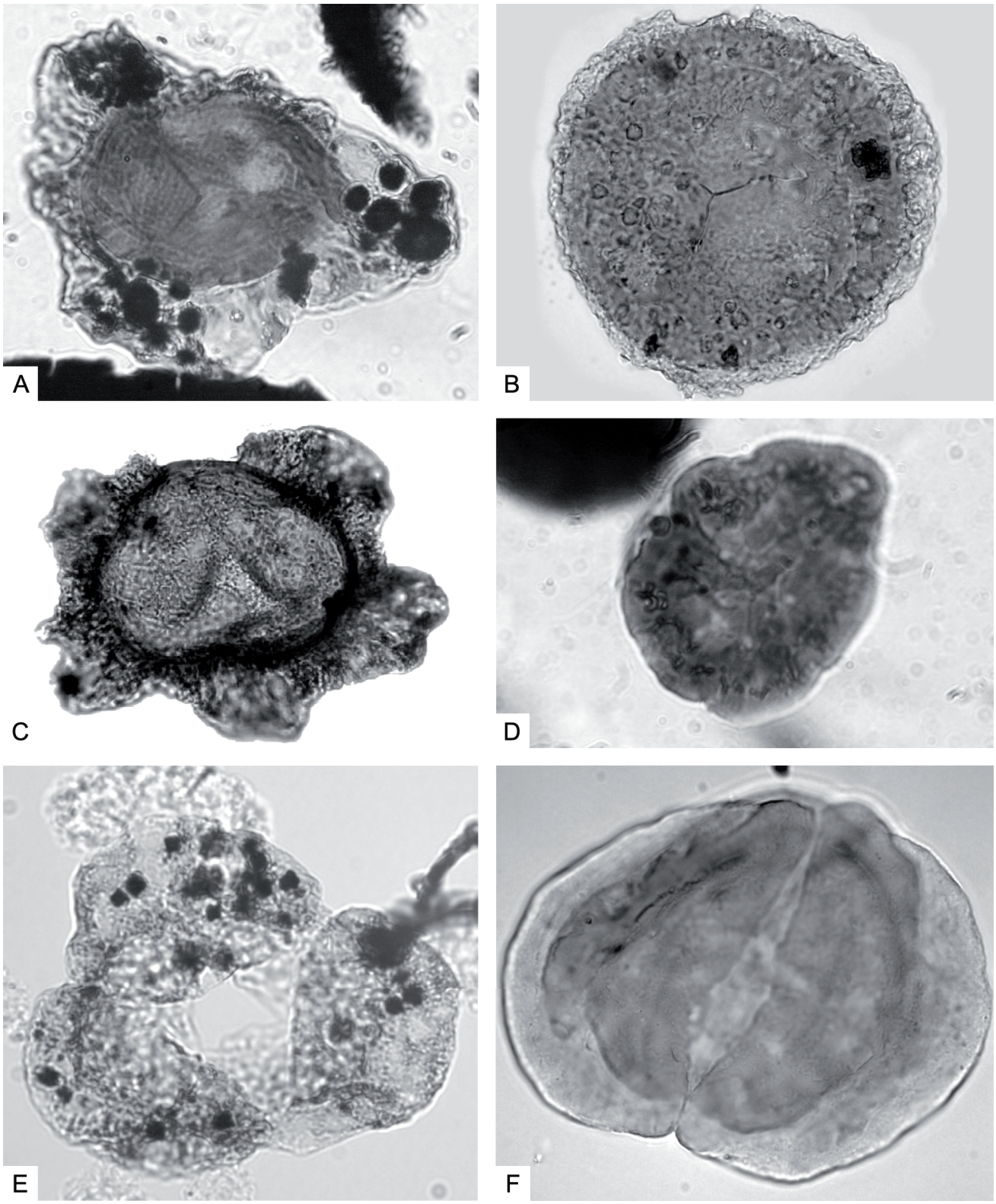

Figure 8: Palynomorphs of the Anisian of the Eastern Southern Alps. **A.** *Cristianisporites triangulatus*, 93 µm; **B.** *Cannanoropollis scheuringii*, 90 µm; **C.** *Dyupetalum vicentinense*, 160 µm; **D.** *Densoisporites variomarginatus*, 100 x 30 µm; **E.** *Stellapollenites thiergartii*, 70 µm; **F.** *Jugasporites conmilvinus*, 50 µm.

vicentinense-crassa subphases) and iv) the vicentinense-scheuringii phase. Previously, Van der Eem (1983) had distinguished the Fassanian (Early Ladinian) into the thiergartii-vicentinense (vicentinense-scheuringii phase in Brugman, 1986) and plurianulatus-novimundanus phases. In an unpublished PhD thesis, Roghi (1995) restudied the Middle Triassic of the Dolomites and distinguished at least three phases and eleven zones that are currently being revised. In all three studies, phases and zones are characterized by first and last occurrences of selected pollen taxa, while the subphases are generally referring to quantitative differences within the phase, thus representing primarily environmental and/or climatic signals that may be strongly diachronous (Van der Eem, 1983; Brugman, 1986; Roghi, 1995, 1997). The time calibration of these phases need revision after the definition of the GSSP for the base of the Ladinian (Brack et al., 2005). They are now considered to be of middle-upper Illyrian age (Hochuli et al., 2015). Finally, Hochuli et al. (2015) defined a succession of Anisian–Ladinian palynozones (TrS-A to TrS-F) from the Seceda drill core, of which the first two zones belong to the Anisian (TrS-A and TrS-B), specifically the Illyrian substage. The TrS-A zone corresponds to the thiergartii-vincentinense phase of Van der Eem (1983) and to the vicentinense-scheuringii phase of Brugman (1986).

Between the Early and Middle Triassic, a strong shift in dominance from trilete and monolete spores to bisaccate pollen with and without aperture is observed, although the initially common pollen species *Voltziaceaesporites heteromorphus* and *Jugasporites conmilvinus* (Fig. 8F) also decrease noticeably (Brugman, 1986; Kustatscher & Roghi, 2006; Kustatscher et al., 2006a, 2010a). The spore *Cristianisporites triangulatus* (Fig. 8A) and *Densoisporites variomarginatus* (Fig. 8D) and pollen monosaccate *Dyupetalum vicentinense* (Fig. 8C) and *Stellapollenites thiergartii* (Fig. 8E) are characteristic for the Anisian whereas monosaccate *Cannanoropollis scheuringii* (Fig. 8B) appear in the upper Anisian. Of particular importance is also the radiation and increase in abundance of the *Triadispora* group. An increase in and/or dominance of trilete spores is observed in the middle Pelsonian vicentinense-pallidus subphase of the thiergartii-vicentinense phase, especially with the genera *Concavisporites*, *Punctatisporites*, *Cyclotriletes*, *Verrucosisporites*, *Convolutispora* and *Uvaesporites*. *Vitreisporites* is also abundant in some levels. This shift from hygrophytic to xerophytic elements has been observed in several quantitative palynological analyses of the Southern Alps (Brugman, 1986; Kustatscher et al., 2010a; Dal Corso et al., 2015). These palynological data are further supported by changes in the associated abundant macroflora and indicate a warm and humid climate (e.g., Kühwiesenkopf/Monte Prá della Vacca; Kustatscher & Roghi, 2006; Kustatscher et al., 2006a), especially since they do not seem to be linked to specific depositional sequences and systems tracts (Dal Corso et al., 2015). This change in floral composition and precipitation regime is recognizable in other sections in the northwestern Tethys (e.g., Hungary, Recoaro; Brugman, 1986). The climatic change cannot be explained with a northward drift of the continents (Mangerud & Rømuld, 1991), since such a change in palaeolatitude would have caused a long-term trend rather than an episodic and short-term humid phase. Additionally, the Southern Alps were placed within the arid tropical belt (10–30°N) during the Middle Triassic and entered the humid climate belt (>30°N) only in the latest Triassic (Muttoni et al., 2013). The vicentinense-scheuringii phase is again dominated by xeromorphic elements (mainly bisaccate pollen grains) with a low percentage of hygromorphic elements (Dal Corso et al., 2015).

5. THE LADINIAN FLORAS OF THE EASTERN SOUTHERN ALPS

5.1. THE LADINIAN MACROFLORA OF THE EASTERN SOUTHERN ALPS

Many Ladinian localities throughout the Dolomites yielded small amounts of plant remains, often limited to a few taxa only (Tab. 3). The first record of plant fossils in the Dolomites belongs to these rare accounts of fossil plant remains; a fern frond fragment, probably *Cladophlebis leuthardtii*, figured by Wissman & Münster (1841). Other authors occasionally mentioned and figured plant fossils from the so-called "Buchensteiner Schichten" and "Wengener Schichten" of various areas in the Dolomites (Fig. 2, 9; Mojsisovics, 1879; Arthaber, 1903; Ogilvie Gordon, 1927, 1934; Mutschlechner, 1932; Leonardi, 1953, 1968; Calligaris, 1982–83, 1986; Jung et al., 1995) and from Sappada ([44] in Fig. 2, 9; Leonardi, 1964). Thus, by the end of the 20th century, a reasonably high number of different plant remains had been described from the Dolomites. Most of these remains, at least those that are accessible in public collections, come from the Wengen or Fernazza formations, the old "Wengener Schichten". So far, only one fragment belonging with certainty to the Buchenstein Formation has been identified (in the Zürich collection, pers. observ. EK).

Most plant fossil sites are situated in the South Tyrol area of the Dolomites, such as Seewald and Innerkohlbach near Prags/Braies ([3] in Fig. 2, 9), several localities in the Gadertal/Val Badia (Ritberg, Wengen/La Valle, [4] in Fig. 2, 9; St. Leonhard in Abtei/S. Leonardo in Badia, [7] in Fig. 2, 9; near Corvara, [13] in Fig. 2, 9; St. Kassian/San Cassiano, [14] in Fig. 2, 9; Grödner Joch/Passo Gardena, [12] in Fig. 2, 9) and the area of Gröden/Val Gardena and Seiser Alm/Alpe di Siusi (Pufels/Bulla, Puflatsch/Bullaccia, [10] in Fig. 2, 9; Schgaguler Schwaige/Malga Schgaguler, [11] in Fig. 2, 9; e.g., Kustatscher & Van Konijnenburg-van Cittert, 2005; Kustatscher et al., 2014). One of the richest and most diverse plant assemblages comes from Monte Agnello (near Pampeago, [30] in Fig. 2, 9) in the Trento Province (Kustatscher et al., 2014). Additional localities, in the Friuli-Venezia-Giulia region are Arabba, [24] in Fig. 2, 9; Forcella Giau and Corvo Alto/Monte Mondeval (Croda da Lago Group, [27] in Fig. 2, 9), Laste and Monte Sief (Livinallongo area, [26] in Fig. 2, 9); Cercenà ([22] in Fig. 2, 9), Spitz Zuel/Col d'Agnelessa (near Dont, [44] in Fig. 2, 9), Sappada ([10] in Fig. 2, 9), Val Aupa (Moggio Udinese, [55] in Fig. 5, 9), Monte Nebria (Malborghetto Valbruna, [58] in Fig. 2, 9), and Dierico ([54] in Fig. 2, 9; Kustatscher & Van Konijnenburg-van Cittert, 2005; Kustatscher et al., 2014; see also the collection database of the Museo Friulano di Storia Naturale, Udine).

The late Ladinian flora of the Southern Alps has always been considered to be gymnosperm-dominated, due to the abundance and diversity of this group. However, the discovery of a (par-)autochtonous flora at Monte Agnello allows new insight into the composition of this flora, since the latter plant assemblage yielded a number of different fern taxa (see below) including some of the earliest representatives of the Matoniaceae and perhaps Dipteridaceae (Kustatscher et al., 2014).

Thus, the Ladinian flora of the Eastern Southern Alps, as presently known, is composed of representatives of almost all plant groups (Tab. 3). The lycophytes and sphenophytes are

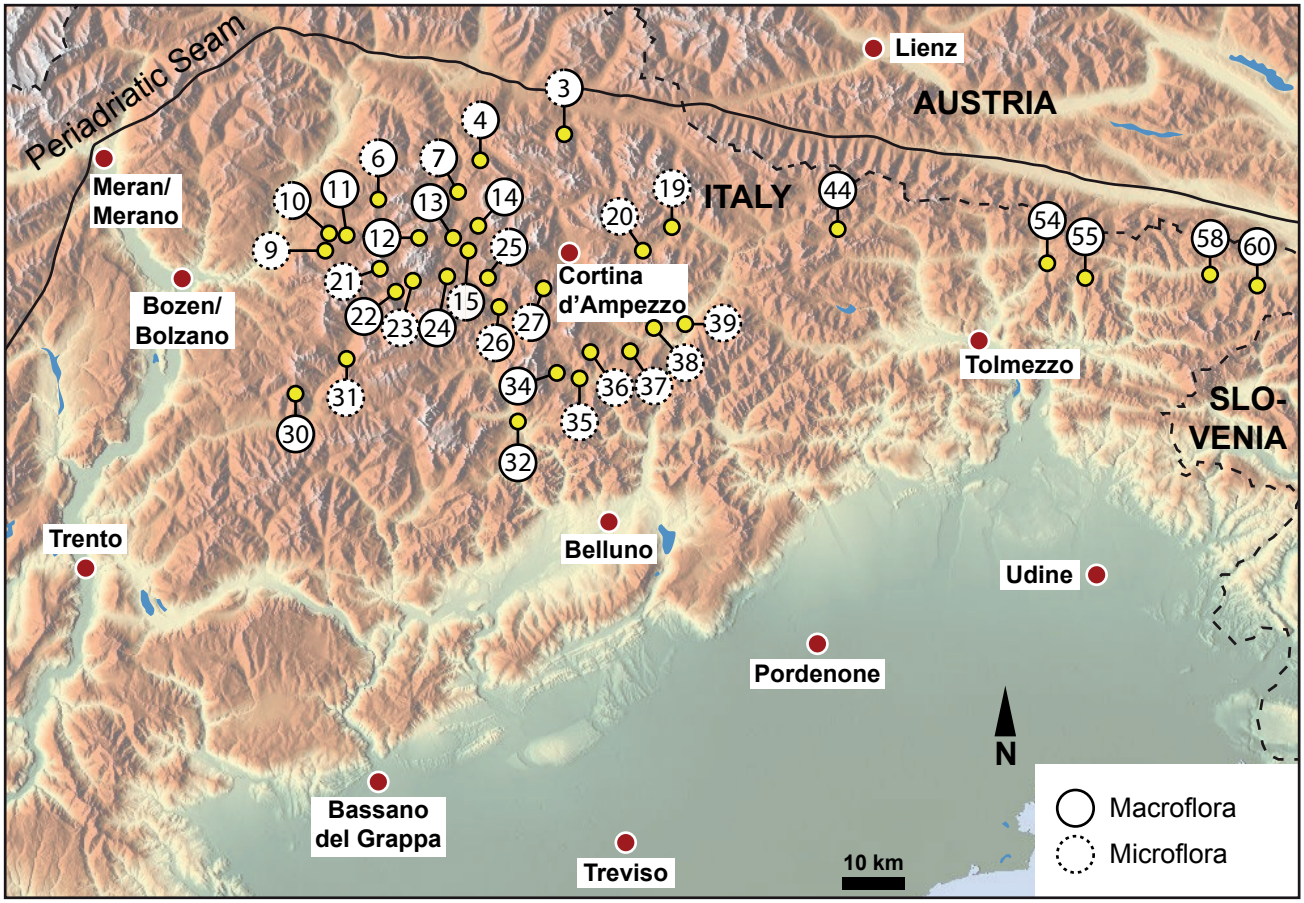

Figure 9: Map of the Eastern Southern Alps with the localities from which Ladinian plant macrofossils and/or microfossil assemblages have been reported. **3.** Prags/Braies (Seewald, Innerkohlbach); **4.** Ritjoch (Wengen/La Valle); **6.** Seceda (incl. Forcella di Pana/Panascharte, Aschkler Alpe/Alpe di Mastlé); **7.** St. Leonhard i. Abteital/San Leonardo in Badia; **9.** Seis/Siusi, Frommbach, Frötschbach; **10.** Pufels/Bulla, Puflatsch/Bullaccia; **11.** Schgaguler Schwaige/Malga Schgaguler; **12.** Grödner Joch; **13.** Col Alto, Corvara; **14.** St. Kassian/San Cassiano; **15.** Stuores Wiesen/Prati di Stuores; **19.** Val Ansiei, Cosderuoibe; **20.** Palus San Marco; **21.** Plattkofel/Sasso Piatto, Grohmannspitze/Punta Grohmann, Rif. S. Pertini, Rif. T. Demetz, Gabia, Val Duron; **22.** Cercenà; **23.** Pordoi, Pordoijoch/Passo Pordoi; **24.** Arabba; **25.** Livinallongo, Monte Sief, Col di Lana; **26.** Laste di Sopra, Caprile; **27.** Croda da Lago Group, Corvo Alto, Lastoni di Formin, Forcella Giau; **30.** Monte Agnello; **31.** Moena; **32.** Valle di San Lucano, Agordo; **34.** Spiz Zuel, Col d'Agnelessa; **35.** Valle di Zoldo, Dont; **36.** Zoppè di Cadore; **37.** Monte Rite; **38.** Vallesina di Sopra; **39.** Val Giaule, Pieve di Cadore; **44.** Sappada; **54.** Dierico; **55.** Val Aupa, Moggio Udinese; **58.** Monte Nebria, Malborghetto Valbruna; **60.** Canale Prasnig, Rio Freddo.

rare, with only a few sporophylls of *Lepacyclotes zeilleri* and some stem fragments of *Equisetites arenaceous* (Fig. 10A). The most abundant and diverse fern family is the Osmundaceae, with *Cladophlebis ladinica*, *C. leuthardtii*, *C. ruetimeyeri*, *Cladophlebis* sp., *Neuropteridium elegans*, *Scolopendrites* sp. and *Gordonopteris lorigae* (Kustatscher et al., 2004, 2014; Kustatscher & Van Konijnenburg-van Cittert, 2005). The Marattiales are represented by *Danaeopsis marantacea*, the Matoniaceae by frond fragments of *Phlebopteris fiemmensis*. Some frond pinna fragments resembling *Thaumatopteris* probably belong to the Dipteridaceae because of their typical venation (Kustatscher et al., 2014). The affinity of *Chiropteris monteagnellii* remains unclear, as well as the affinity of the whole genus *Chiropteris*. However, considering the leaf morphology and venation pattern, *Chiropteris* spp. might have belonged to the Dipteridaceae (Kustatscher & Van Konijnenburg-van Cittert, 2013; Kustatscher et al., 2014).

The seed fern group is dominated by *Ptilozamites sandbergeri* (Kustatscher & Van Konijnenburg-van Cittert, 2005), both leaf fragments and putative fertile structures and seeds are known. Peltaspermalean leaf fragments, such as *Scytophyllum bergeri*, are less common in this flora (Kustatscher et al., 2006b, 2007, 2014). The leaves of cycadophytes are assigned to the entire-margined *Bjuvia dolomitica* and *Taeniopteris* sp., the macrosporophylls to *Dioonitocarpidium moroderi* (Fig. 10B; Wachtler & Van Konijnenburg-van Cittert, 2000; Kustatscher et al., 2004, 2014; Kustatscher & Van Konijnenburg-van Cittert, 2005). The dissected leaves, previously assigned to *Pterophyllum*, yielded typical cycadalean cuticles and cannot be assigned to *Pterophyllum* anymore. They are here assigned to their corresponding fossil-taxon *Nilssonia* sp. (Fig. 10C) for these parallel-margined dissected leaves (Pott, 2013). *Sphenozamites wengensis* and *Sphenozamites* sp. cf. *S. bronnii* – the forms with club-shaped segments – are here assigned to a different genus (*Macropterygium*, see section 9) as no cuticles have been found so far, and *Sphenozamites* is nowadays reserved for bennettitalean leaves only (Zijlstra et al., 2013). The isolated macrosporophylls with a distal pinnate form and proximal two rows of seeds belong to the species *Dioonitocarpidium moroderi*. The genus *Voltzia* is dominant among the conifers with *Voltzia dolomitica* (Fig. 10D), *V. heterophylla*, *V. ladinica*, *V. pragsensis*, *V. zoldana* and *Voltzia* sp. Additional conifers are *Albertia* sp., *Pelourdea vogesiaca* (Fig. 10E) und *Elatocladus* sp. (Fig. 10F; Wachtler & Van Konijnenburg-van Cittert, 2000; Kustatscher et al., 2004; Kustatscher & Van Konijnenburg-van Cittert, 2005).

Ladinian		Wengen/La Valle	Monte Agnello	Prags/Braies	Seiser Alm/Alpe di Siusi	Gröden/Val Gardena	Hochabteiltal/alta Val Badia	Croda da Lago Group	Livinallongo	Col d'Agnelessa	Arabba	Cercenà	Sappada	Moggio Udinese	Malboghetto Valbruna	Dierico
Lycophytes	*Lepacyclotes zeilleri*	x														
Horsetails	*Equisetites arenaceus*	x											x			
	Equisetites sp.	?					?		?			?	?	?	x	
Ferns	*Anomopteris mougeotii*						x							x		
	Chiropteris monteagnellii		x													
	Cladophlebis ladinica		x													
	Cladophlebis leuthardtii	x		x	x	x	x	x	x			x	x			
	Cladophlebis ruetimeyeri				x		x					x				
	Cladophlebis sp.		x													
	Danaeopsis angustifolia			?												
	Danaeopsis marantacea						?									
	Gordonopteris lorigae	x						?				x	x			
	Neuropteridium elegans	x	x					x					x			
	Phlebopteris fiemmensis		x													
	Scolopendrites sp.						x									
	Thaumatopteris sp.		x													
	Dipteridaceae indet.		x													
Seed ferns	*Ptilozamites sandbergeri*	x		x	x	x		x								
	Scytophyllum bergeri		x				x									
Cycadophytes	*Bjuvia dolomitica*	x			x	x	x	x								
	Bjuvia sp.		?		?		?		?				?			
	Dioonitocarpidium moroderi				x											
	Macrotaeniopteris sp.		x													
	Nilssonia sp.		x						x							
	"Pterophyllum filicoides"						x					x				
	„Pterophyllum" sp.			x	x		x									
	„Zamites sp.*"*						x									
Conifers	*Albertia* sp.															x
	Elatocladus sp.				x											
	Pelourdea vogesiaca	x		x	x											
	Pelourdea sp.		x	x	?							?				
	Voltzia dolomitica	x		x	x								x	?		
	"Voltzia heterophylla"															x
	Voltzia ladinica	x		x	x	x								x		
	Voltzia pragsensis	x		x	x											
	Voltzia zoldana											x				
	Voltzia sp.	x	x	x	x	x						x	x	x	x	x
Incertae sedis	*Carpolithes* sp.	x											x	x		
	Macropterygium bronnii						?		?							
	Macropterygium wengensis	x		x												
	Macropterygium sp.		x													
	Taeniopteris sp.		x	x		x	x					x	x			

Table 3: Occurrences of Ladinian plant macrofossil taxa at the various localities in the Eastern Southern Alps.

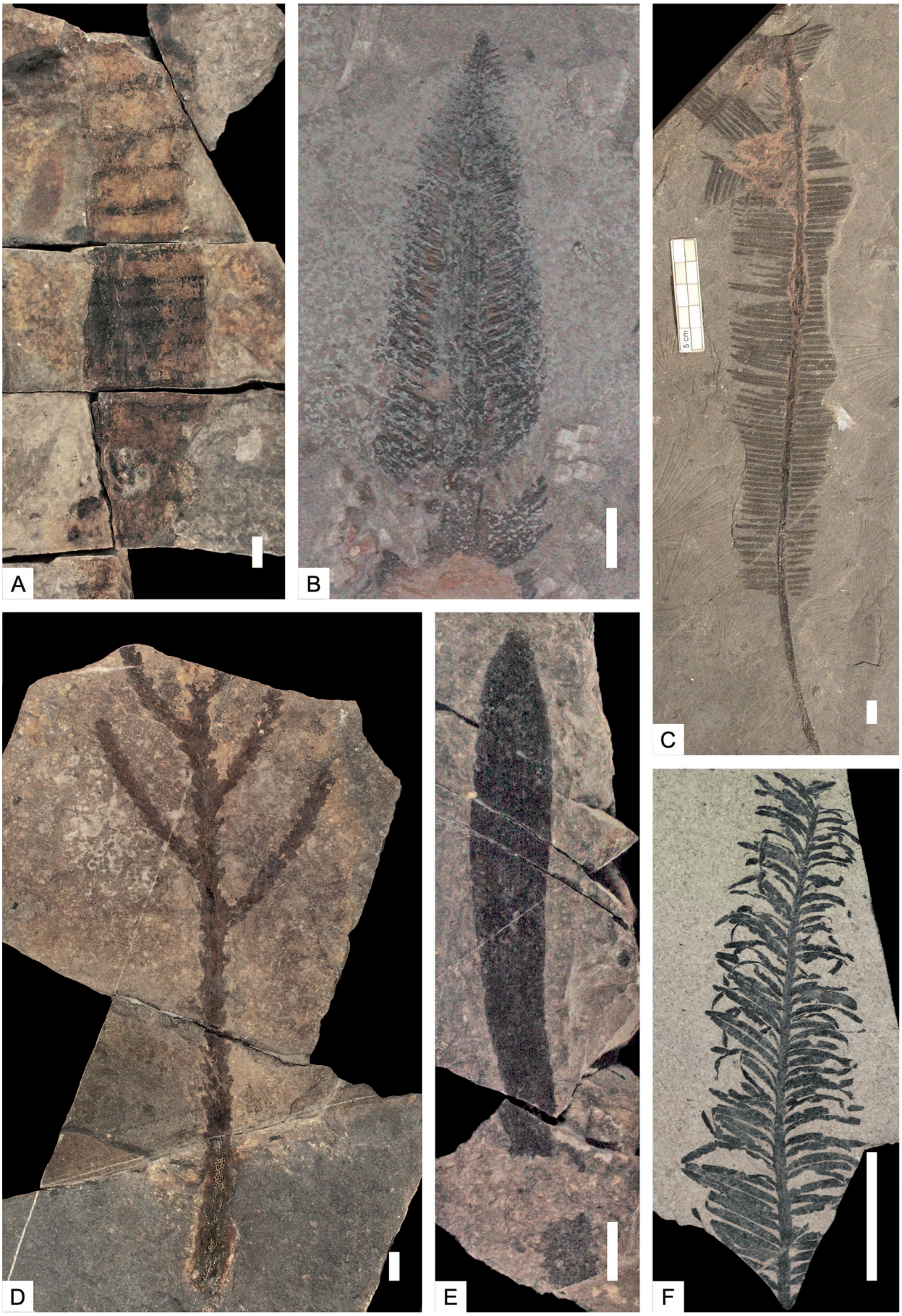

Figure 10: Plant macrofossils from the Ladinian of the Eastern Southern Alps. Scale bars = 1 cm. **A.** stem fragment of *Equisetites arenaceus* (Jaeger) Schenk, 1864 (Brongniart) Wills, 1910, NMS PAL 003; **B.** Megasporophyll of *Dioonitocarpidium moroderi* (Leonardi) Kustatscher et al., 2004, MDG M22; **C.** *Nilssonia* sp., GII P3775; **D.** shoot of *Voltzia dolomitica*, NMS PAL 032; **E.** *Pelourdea vogesiaca*, NMS PAL 556; **F.** *Elatocladus* sp., 1868, MDG 02.

5.2. THE LADINIAN MICROFLORA OF THE EASTERN SOUTHERN ALPS

Several palynological studies have been carried out on Ladinian successions in the Dolomites during the last 25 years (Cros & Doubinger, 1982; Van der Eem, 1982, 1983; Blendinger, 1988; Roghi, 1995, 1997; Broglio Loriga et al., 1999; see also Fig. 2, 9). Palynological data were mostly used for biostratigraphy (Fig. 4; Blendinger, 1988; Roghi, 1995, 1997; Broglio Loriga et al., 1999). In several studies (i.e. Van der Eem, 1983; Kustatscher & Van Konijnenburg-van Cittert, 2005; Hochuli et al., 2014), the

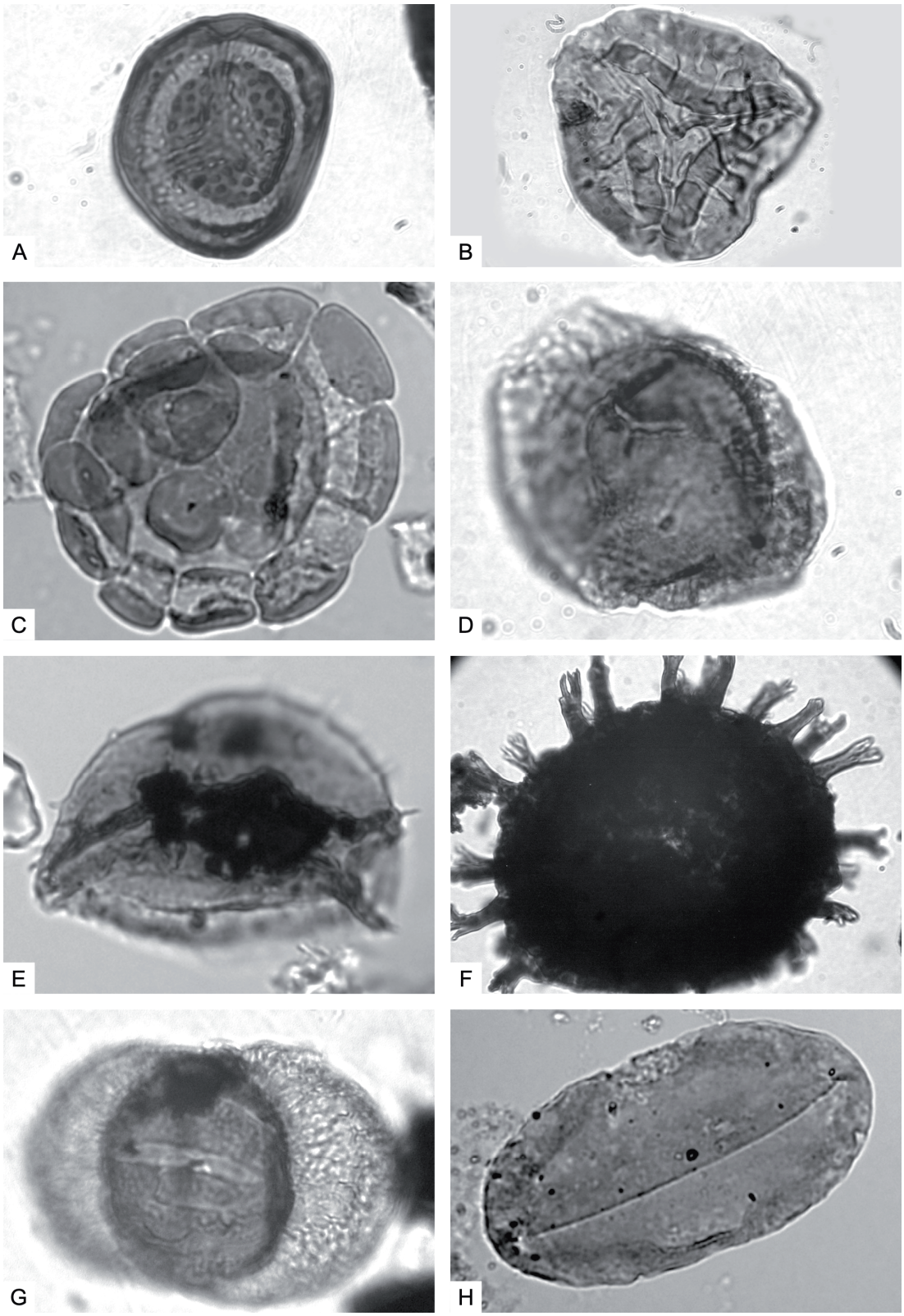

Figure 11: Palynomorphs of the Ladinian of the Eastern Southern Alps. **A.** *Gordonispora fossulata*, Ritberg section, 30 µm; **B.** *Kyrtomisporis ervii*, Ritberg section, 54 µm; **C.** *Camerosporites* secatus, 44 µm; **D**. *Triadispora* sp., Ritberg section, 40µm; **E.** *Aratrisporites* sp., 55µm; **F.** *Keuperisporites baculatus*, Ritberg section, 80µm; **G.** *Lunatisporites acutus*, Ritberg section, 70 µm; **H** *Ovalipollis pseudoalatus*, 71 µm.

palynomorphs are also considered as a source for paleoclimatic and paleoenvironmental data.Striate and taeniate bisaccate pollen (*Lunatisporites acutus* (Fig. 11G) decline gradually during the Ladinian, contemporaneous to a marked increase in bisaccate pollen such as *Triadispora* (Fig. 11D) and *Ovalipollis pseudoalatus* (Fig. 11H) (Van der Eem, 1983; Brugman, 1986; Roghi, 1995, 1997). The cavatomonolete *Aratrisporites* (Fig. 11E) is well represented during the Ladinian and Circumpolles (*Duplicisporites* spp.; *Camerosporites* secatus (Fig. 11C) and monosaccate pollen appear. The Ladinian Circumpolles from the Southern Alps were identified as ancestors of the "true" Circumpolles from the Late Triassic, which belong to the Hirmeriellaceae (Zavialova & Roghi, 2005). Also present in the uppermost Ladinian are: *Concentricisporites* sp. cf. *C. bianulatus Enzonalasporites vigens, Kyrtomisporis ervii* (Fig. 11B), *Keuperisporites baculatus* (Fig. 11F) and *Gordonispora fossulata* (Fig. 11A), together with *Nevesisporites vallatus*, *Todisporites marginalis*, *Calamospora* sp. A, *Apiculatisporites parvispinosus* and *Densosporites* sp. cf. *D. variomarginatus* (Mietto et al., 2012).

Van der Eem (1983) defined a sequence of at least four palynomorph phases for the Ladinian of the Western Dolomites (Southern Alps), correlated to regional ammonoid zones of Krystyn (1983). This includes the plurianulatus-secatus phase (p.p.), the secatus-dimorphus phase and the secatus-vigens phase (p.p.). Roghi (1995) revised the sequence of phases of Van der Eem (1983) in combination with the work of Brugman (1986) and proposed the scheuringii-pseudoalatus phase (with 5 zones, of which 3 belong to the Ladinian and one belongs partly also to the Anisian) and the pseudoalatus-baculatus phase (with 4 zones) based on different stratigraphic successions. These were correlated with ammonoid stratigraphy (Fig. 4). After the definition of the Ladinian GSSP (Brack et al., 2005), Hochuli et al. (2015) defined a succession of Anisian–Ladinian palynozones (TrS-A to TrS-F) from the Seceda drill core, of which the last four zones belong to the Ladinian (TrS-C to TrS-F).

Quantitative palynological analyses suggest that the Ladinian was generally dry and warm, but with a small humid event in the late Ladinian (e.g., Van der Eem, 1983; Kustatscher & Van Konijnenburg-van Cittert, 2005; Preto et al., 2010).

Megaspores have been reported from the Ladinian to Carnian at several localities in the Dolomites and have been assigned to the *Horstisporites selaginelloides* megaspore assemblage zone (Wierer, 1997; Marcinkiewicz et al., 2014).

6. THE CARNIAN FLORAS OF THE EASTERN SOUTHERN ALPS

6.1. THE CARNIAN MACROFLORA OF THE EASTERN SOUTHERN ALPS

One of the most important historical plant fossil collections comes from the Carnian flora of Cave del Predil/Raibl ([62] in Fig. 5, 12; Bronn, 1858; Schenk, 1866–67, Stur, 1868a, 1885; Dobruskina et al., 2001). Additional fossiliferous outcrops of Carnian age are Rifugio Dibona (Cortino d'Ampezzo area; [16] in Fig. 2, 12), Stuores/Pralongià (near Corvara, [15] in Fig. 2,

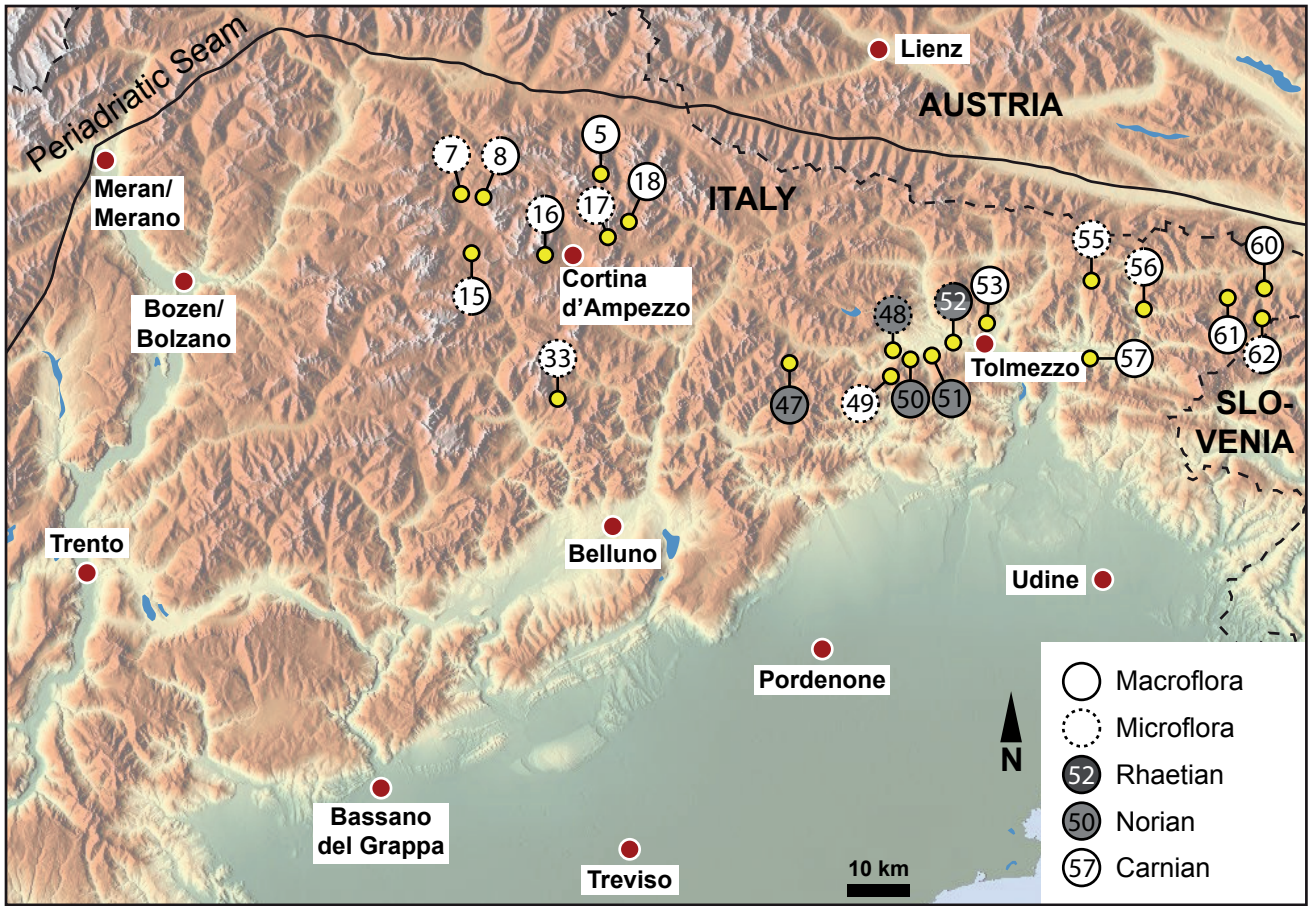

Figure 12: Map of the Eastern Southern Alps with the localities from which Upper Triassic plant macrofossils and/or microfossil assemblages have been reported. **5.** Seelandalpe, Plätzwiese/Prato Piazza; **7.** St. Leonhard im Abteital/San Leonardo in Badia; **8.** Heiligkreuz/Santa Croce; **15.** Stuores Wiesen/Prati di Stuores; **16.** Rifugio Dibona; **17.** Passo Tre Croci; **18.** Misurina; **33.** Passo Duran; **47.** Rio Rovadia; **48.** Priuso, Rio Canfoz; Caprizi, frana di Borta, Rio Molino; **49.** Monte Rest; **50.** Rio Torzulis, Socchieve; **51.** Preone, Rio Seazza, Valle di Preone, Enemonzo, Rio Spisulò; **52.** Villa Santina, Rio Plera, Rio Forchiàr, Rio Secco, **53.** Fusea, Cazzaso; **55.** Val Aupa, Moggio Udinese; **56.** Dogna, Val Dogna, Balador, Rio Pontuz; **57.** Rio Serai, Resiutta; **60.** Canale Prasnig, Rio Freddo/Kaltwasser; **61.** Val Saisera, Canale Placcia, Canale Klinken; **62.** Raibl/Cave del Predil, Rio dei Combattenti, Rio delle Cascate, Rio Conzen, Portella, Sella Ursic.

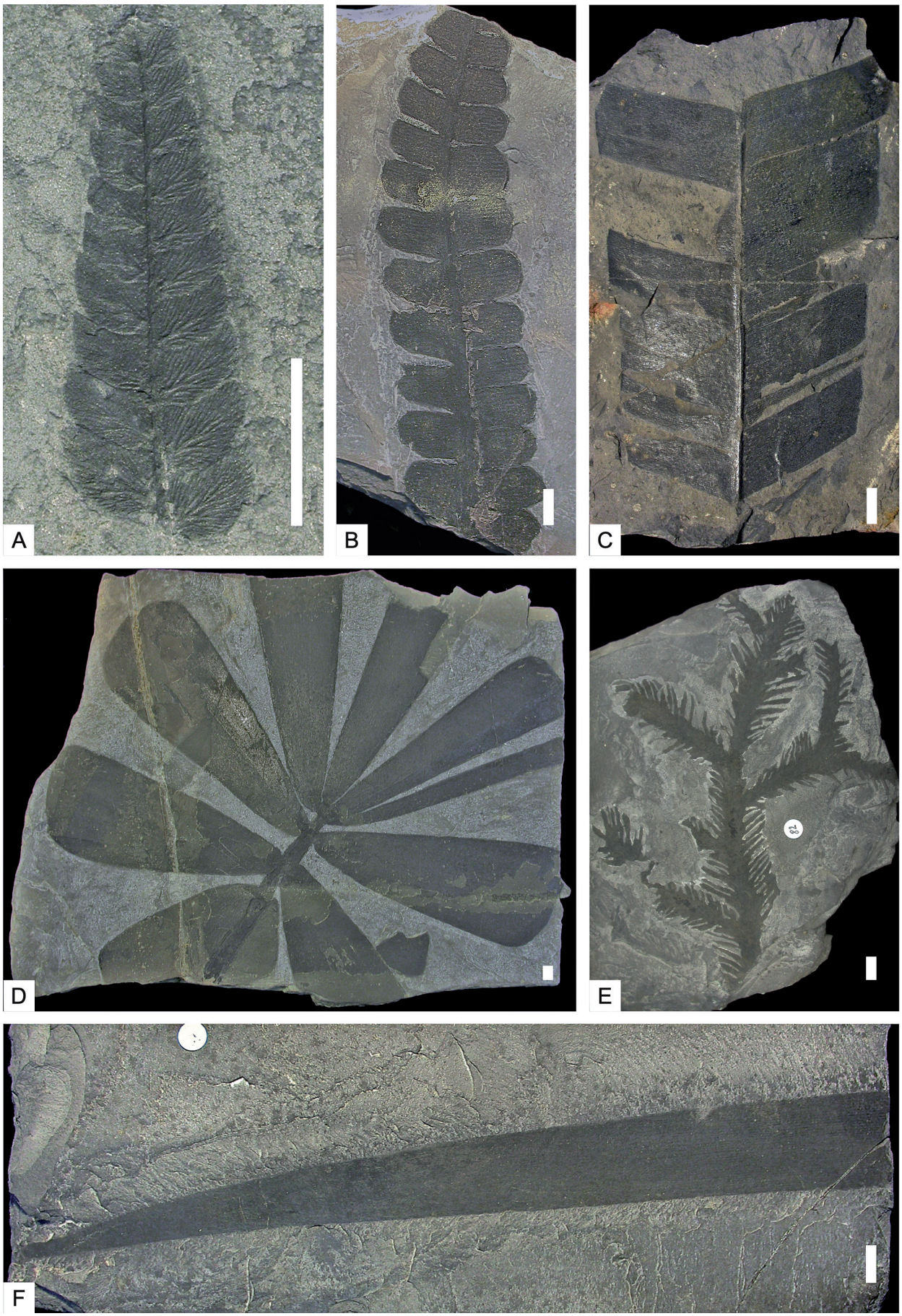

Figure 13: Plant fossils from the Carnian of the Eastern Southern Alps. Scale bars = 1 cm: **A.** frond fragment of *Cladophlebis leuthardtii* Leonardi, 1953, GBA 2007-072-0012; **B.** Leaf fragment of *Ptilozamites sandbergeri* (Schenk) Kustatscher et Van Konijnenburg-van Cittert, 2007, GBA 2005-0008-004; **C.** *Macrotaeniopteris* sp., GBA 2007-072-0070; **D.** *Macropterygium bronnii* (Schenk) Weber, 1996, GBA 2007-072-0053; **E.** *Voltzia haueri* Stur, 1885, GBA 1986-2-4; **F.** *Pelourdea vogesiaca* (Schimper et Mougeot) Seward, 1917, GBA 1986-2-128A.

12), Heiligkreuz/Santa Croce (near St. Leonhard im Abteital/S. Leonardo in Badia, [8] in Fig. 2, 12) and Misurina ([18] in Fig. 2, 12; Kustatscher et al., 2011a) in the Dolomites, as well as Dogna in the Julian Alps ([56] in Fig. 5, 12; Roghi et al., 2006a). Other plant remains of Carnian age come from the Friuli area; the most important plant fossil localities are Val Saisera and Canale Placcia (both Malborghetto Valbruna, [61] in Fig. 5, 12), Fusea (near Tolmezzo, [53] in Fig. 5, 12), Rio Serai (Resiutto, [57] in Fig. 5, 12), as well as Rio Freddo/Kaltwasser and Canale Prasnig in the Tarvisio area ([60] in Fig. 5, 12; collection database of the Museo Friulano di Storia Naturale, Udine).

The Carnian flora of the Eastern Southern Alps is composed of a wide range of plant fossils (Tab. 4). These include, among the sphenophytes, internal stem casts and stem fragments

Upper Triassic		Carnian										Norian		
		Hochabteital/ alta Val Badia	Dogna area	Seiser Alm/ Alpe di Siusi	Plätzwiese/ Prato Piazza	Raibl/ Cave del Predil	Misurina	Rifugio Dibona	Malborghetto Valbruna	Fusea	Rio Serai, Resiutto	Rio Seazza	Rio Forchiar	Rio Secco di Villa Santina
Horsetails	*Equisetites arenaceus*	x		x										
	Equisetites sp.	?	x			x		x				x		
Ferns	*„Asterotheca“* spp.													
	Chiropteris lacerata					x								
	„Camptopteris“ sp.													
	Cladophlebis leuthardtii					x								
	Cladophlebis ruetimeyeri					x								
	„Clathropteris“ spp.													
	Danaeopsis angustifolia		?											
	Danaeopsis marantacea					?								
	Danaeopsis sp.		x											
	“Laccopteris lunzensis”													
	Neuropteridium elegans					x								
	Neuropteridium grandifolium					x								
	„Oligocarpia“ sp.													
	*„Rhacopteris“*sp.					x								
	“Rhacopteris raiblensis”					x								
	Rhacophyllum crispatum					x								
	„Speirocarpus“ sp.					x								
Seed ferns	*Ptilozamites sandbergeri*	x	x			x								
	Sagenopteris sp.					x								
Cycads	*Apoldia tenera*					?								
	“Cycadites suessi”					x								
	“Dioonites pachyrrhachis”					x								
	Dioonitocarpidium sp.					x								
	Macrotaeniopteris sp.					x								
	Nilssonia sp.					x								
Bennettitales	*“Pterophyllum filicoides”*					x								
	Pterophyllum giganteum					x								
	Pterophyllum sp.					x								
Conifers	*Albertia* sp.											?		
	Brachyphyllum sp.		x									x	x	x
	“Cephalotaxites raiblensis”					x								
	Pagiophyllum sp.											x	x	
	Pelourdea vogesiaca					x						x		
	Pelourdea sp.		x			x						x	x	x
	„Podozamites“ sp.					?								
	„Thuites“ sp.					x								
	Voltzia foetterlei					x								
	Voltzia haueri		x			x								
	“Voltzia heterophylla”					x								
	“Voltzia pachyphylla”					x								
	Voltzia raiblensis					x								
	Voltzia sp.	x	x		x	x	x	x	x	x	x	x	x	x
	“walchian-like” conifer		?											
Incertae sedis	*Carpolithes* sp.	x												
	Macropterygium bronnii	?				x								
	Phylladelphia strigata					x								
	Taeniopteris sp.					x								

Table 4: Occurrences of Late Triassic plant macrofossil taxa at the various localities in the Eastern Southern Alps.

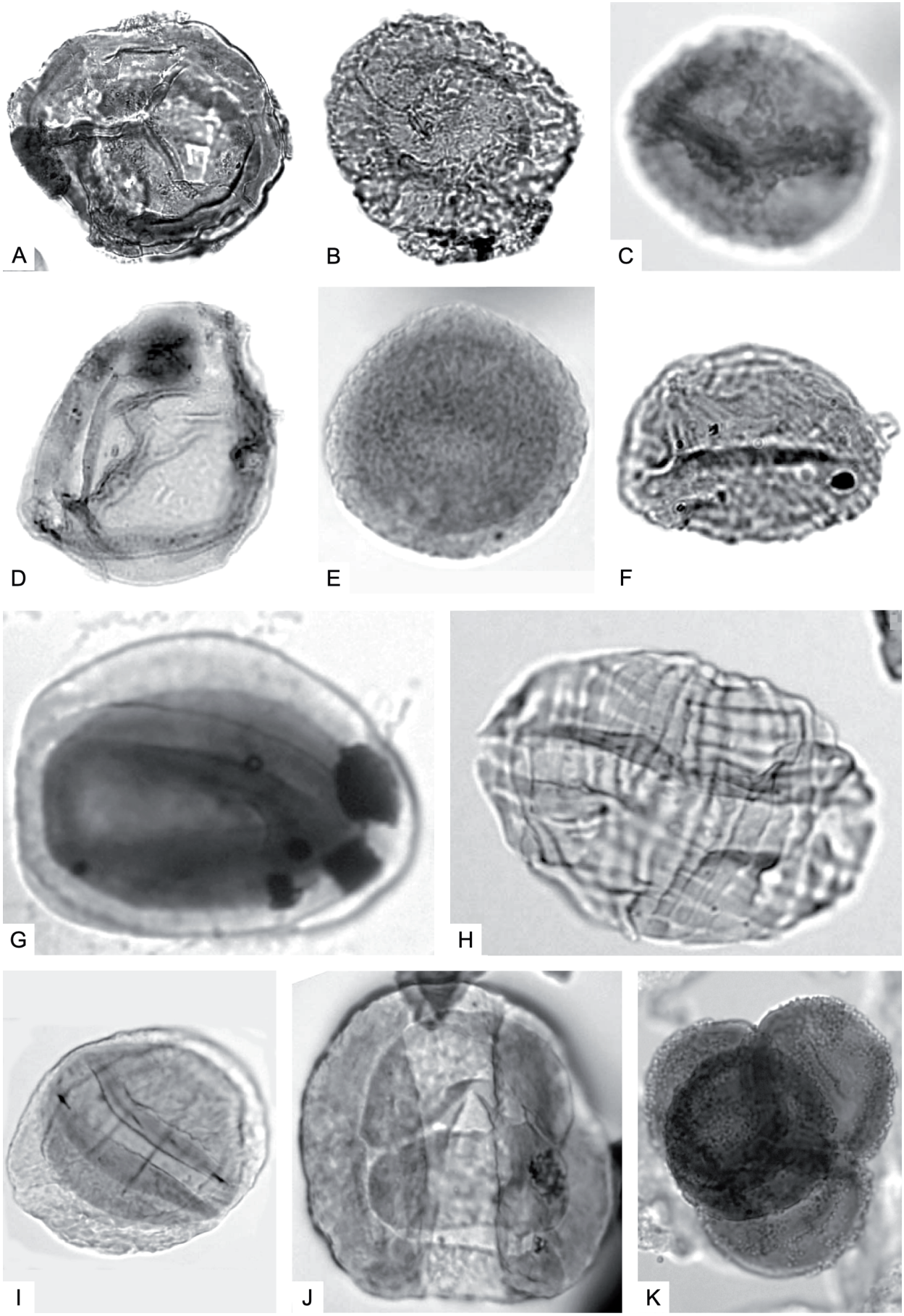

Figure 14: Palynomorphs of the Upper Triassic of the Eastern Southern Alps. **A.** *Concentricisporites* sp., 105 µm; **B.** *Patinasporites densus*, 62 µm; **C.** *Vallasporites ignacii*, 32 µm; **D.** *Aulisporites astigmosus*, 38 µm; **E.** *Enzonalasporites vigens*, 43 µm; **F.** *Lagenella martinii*, 35 µm; **G.** *Paracirculina* sp., 35 µm; **H.** *Equisetosporites chinleanus*, 50 µm; **I.** *Lueckisporites* cf. *L. parvus*, Rifugio Dibona, 65 µm; **J.** *Infernopollenites sulcatus*, 50 µm; **K.** *Granuloperculatipollis rudis*, 35 µm.

belonging to *Equisetites arenaceus* (Kustatscher et al., 2011a). The fern frond fragments belong to the Marattiales (*Danaeopsis lunzensis*, *D. angustifolia*, *Rhacophyllum crispatum*), Osmundaceae (*Cladophlebis leuthardtii*, (Fig. 13A), *C. ruetimeyeri*, *Neuropteridium elegans*, *N. grandifolium*), Matoniaceae (*Phlebopteris*), Dipteridaceae (*Clathropteris* sp.) and uncertain botanical affinity (*Chiropteris lacerata*, *Rhacopteris raiblensis*, *Rhacopteris* sp.). The seed ferns are dominated by simply pinnate leaves of *Ptilozamites sandbergeri* (Fig. 13B) and leaflets of *Sagenopteris* sp. The first undisputed Bennettitales (*Pterophyllum giganteum*, *Pt. longifolium*) appear in the fossil record of northern Italy during the Carnian. Historically mentioned are the cycadophyte leaves *Macropterygium bronnii* (Fig. 13D) and entire leaves belonging to *Macrotaeniopteris* sp. (Fig. 13C), as well as fragments of macrosporophylls assignable to *Dioonitocarpidium* sp. (e.g., Stur, 1885; Dobruskina et al., 2001; Kustatscher et al., 2012b).

Conifers are dominated by shoot fragments of *Voltzia*, such as *V. foetterlei*, *V. haueri* (Fig. 13E), *V. pachyphylla*, *V. raiblensis*. More rarely, *Brachyphyllum* sp. and *Cephalotaxites raiblensis* occur as well (Dobruskina et al., 2001). Long lanceolate leaves were historically assigned to the genus *Noeggerathia* but might belong to *Pelourdea vogesiaca* (Fig. 13F; Bronn, 1858). So far, leaf fragments with preserved cuticles were found only in Dibona, together with the amber drops that belong to the conifer family Hirmeriellaceae, and other conifers resembling the Permian walchian conifers (Roghi et al., 2006a, 2006b; for details see below). *Phylladelphia strigata* is of unknown botanical affinity (Kustatscher & Van Konijnenburg-van Cittert, 2008).

6.2. THE CARNIAN MICROFLORA OF THE EASTERN SOUTHERN ALPS

In the lowermost Carnian, several important types of vesicate and monosaccate pollen, (*Vallasporites ignacii* (Fig. 14C), *Patinasporites densus* (Fig. 14B), Circumpolles (*Duplicisporites verrucosus*, *Camerosporites secatus* (Fig. 11C), *C. pseudoverrucatus*), costate (*Weylandites magmus*) and bisaccate (*Samaropollenites speciosus*) pollen have their first occurrence (Mietto et al., 2012). Bisaccate pollen decline during the Carnian, whereas monosaccate, vesicate and the circumpollen forms show a noticeable diversification. Azonotrilete and monolete spores indicate the presence of ferns and cycads in cycadalean-dominated hygrophytic plant communities reflecting riverine, swamp or marsh environments (Roghi, 2004; Roghi et al., 2010; Kustatscher & Roghi, 2014).

In younger deposits, pollen of Bennettitales (*Aulisporites astigmosus*, Fig. 14D), as well as monolete (*Cycadopites* spp.) and costate forms (e.g., *Equisetosporites* (Fig. 14H), *Lagenella* (Fig. 14F) increase in abundance, indicating a flood plain vegetation characterized by moist soil conditions in a humid environment (Roghi, 2004; Roghi et al., 2010). This local humid event corresponds to the so-called "Carnian Pluvial Episode", a globally recorded climatic change (e.g., Simms & Ruffell, 1989; Gianolla et al., 1998; Roghi, 2004; Roghi et al., 2006b, 2010; Preto et al., 2010; Dal Corso et al., 2012, 2018). The abundant presence of cavatomonolete spores (*Aratrisporites* spp.) indicates mangrove-like ecosystems. The presence of bisaccate pollen (*Lunatisporites* spp., *Lueckisporites* cf. *L. parvus*; Fig. 14I) indicates influx of hinterland elements (Brugman et al., 1994). Circumpollen and monosaccate pollen represent xerophytic coastal pioneer vegetation, probably from saline mudflats.

Three main assemblages covering the Carnian Pluvial Episode in the Southern and Northern Calcareous Alps have been defined; the *Aulisporites astigmosus*, *Lagenella martinii* and *Granuloperculatipollis rudis* assemblages (Roghi et al., 2010). The *Aulisporites astigmosus* assemblage is late Julian in age and is found in the upper Conzen and lower Tor formations (Julian Alps), as well as in the lower Heiligkreuz Formation (Dolomites). It is characterized by the presence of *Calamospora lunzensis*, *Kraeuselisporites cooksonae*, *Distalanulasporites punctus*, *Leschikisporis aduncus*, *Tigrisporites halleinis*, *Duplexisporites* sp. 1, *Aulisporites astigmosus* and *Aratrisporites* spp.

The *Lagenella martinii* assemblage (Fig. 4) covers the middle–upper Tor and upper Heiligkreuz formations (late Julian to lower Tuvalian). Characteristic for this assemblage are spores such as *Conbaculatisporites mesozoicus*, *Leschikisporites aduncus*, *Raistrickia alpina*, *Baculatisporites comaumensis* and *Camarozonosporites*, as well as pollen grains such as *Lagenella martinii* (Fig. 14F), *Equisetosporites chinleanus* (Fig. 14H), *Araucariacites* spp., *Enzonalasporites vigens* (Fig. 14E), *Camerosporites secatus*, *C. pseudoverrucatus*, *Ovalipollis pseudoalatus* (Fig. 11H), *Duplicisporites* spp., *Patinasporites* spp., *Vallasporites ignacii*, *Cycadopites* spp. and *Doubingerispora filamentosa*.

The *Granuloperculatipollis rudis* assemblage has been found in the Carnitza Formation and in the Hauptdolomit/Dolomia Principale of the Julian Alps. It spans across the Carnian–Norian boundary and is characterized by the presence of *Infernopollenites sulcatus* (Fig. 14J), cf. *Brodispora* sp., *Granuloperculatipollis rudis* (Fig. 14K) and *Paracirculina quadruplicis* (Fig. 14G).

7. THE NORIAN FLORAS OF THE EASTERN SOUTHERN ALPS

7.1. THE NORIAN MACROFLORA OF THE EASTERN SOUTHERN ALPS

The Norian of the Eastern Southern Alps is generally rare in plant fossils. Almost all records so far came from the Dolomia di Forni in the Carnic Prealps (Figs. 5, 12; Dalla Vecchia, 2000, 2012). The most productive outcrops lie in the valley of the Rio Seazza near Preone ([51] in Figs. 5, 12). Other reported outcrops yielding plant fossils are Rio Rovadia and Rio Torzulis (both Socchieve; [50] in Fig. 5, 12), Rio Canfoz (Priuso; [48] in Figs. 5, 12), Rio Spisulò (Enemonzo; [51] in Fig. 5, 12), Rio Plera and Rio Forchiar (both Villa Santina, [52] in Figs. 5, 12; Dalla Vecchia, 2012). A few plant fossils from other localities in the same area, also belonging to the Dolomia di Forni, are listed in the collection database of the Museo Friulano di Storia Naturale. Most of the plant remains are conifer shoots, primarily shoot fragments assignable to the genera *Voltzia*, *Brachyphyllum* (Fig. 15E) or *Pagiophyllum* (Fig. 15B) and dispersed ovuliferous scales (Fig. 15C, 15D). Leaves and leaf fragments of *Pelourdea*, perhaps *Pelourdea vogesiaca* (Fig. 15A, 15F) are also present. Dalla Vecchia (2000) mentioned fragments of Bennettitales, whereas lycophytes, sphenophytes, ferns and seed ferns have so far not been observed.

Apart from the Dolomia di Forni, Dalla Vecchia (2000) also reported the presence of *Brachyphyllum* from a "bituminous" intercalation in the Dolomia Principale/Hauptdolomit at the Rio Serai near Resiutta in the collection of the Museo Friulano di Storia Naturale.

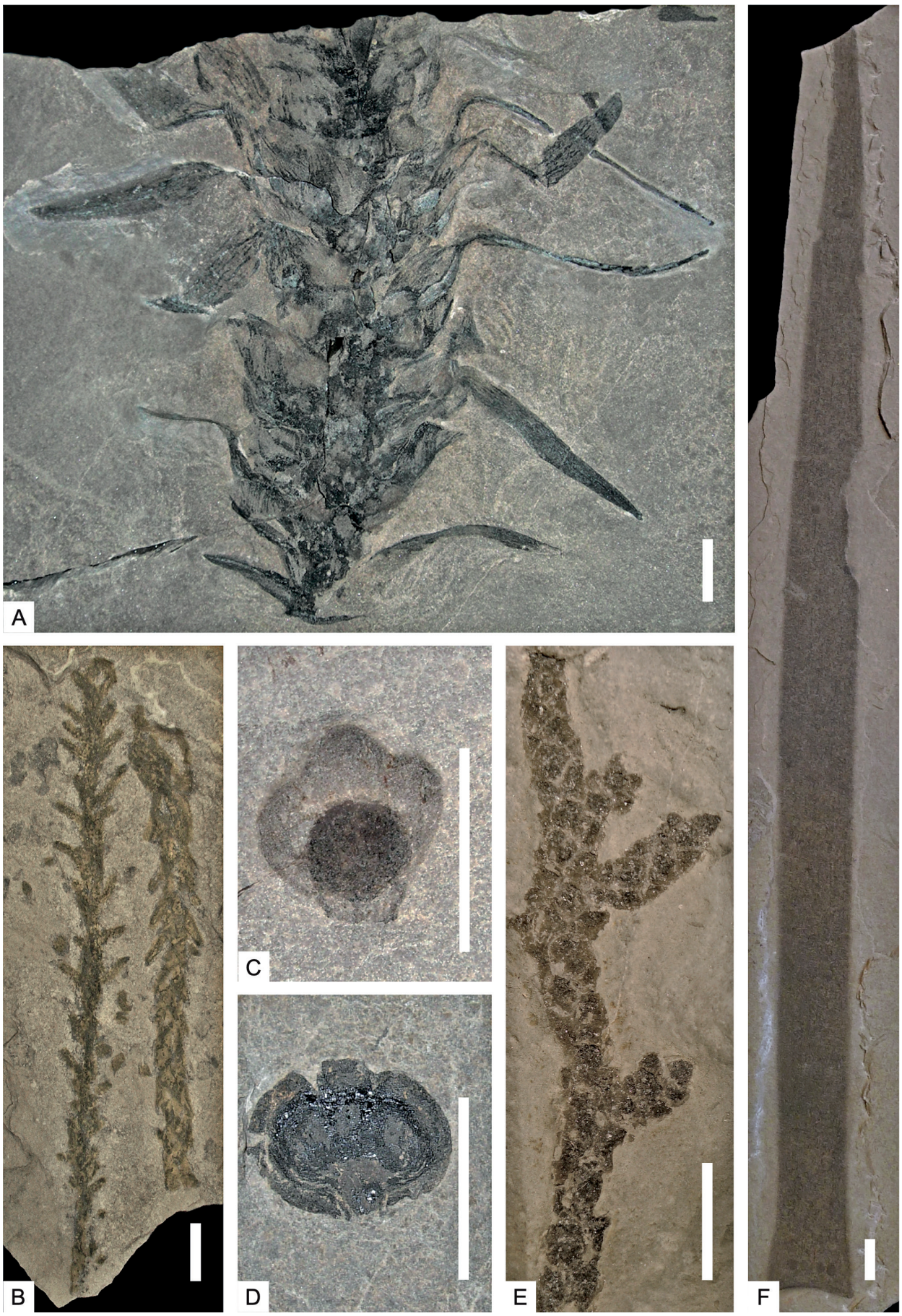

Figure 15: Plant fossils from the Norian of the Eastern Southern Alps. Scale bars = 10 mm: **A.** putative stem fragment of *Pelourdea vogesiaca* (Schimper et Mougeot) Seward, 1917, MFSN 40305; **B.** shoot fragments of *Pagiophyllum* sp., MFSNgp 40292; **C.** female scale of unknown affinity, MFSNgp 44397; **D.** female scale bar of cheirolepidaceous affinity, MFSNgp 44429; **E.** shoot fragments of *Brachyphyllum* sp., MFSNgp 50365; **F.** *Pelourdea vogesiaca* (Schimper et Mougeot) Seward, 1917, MFSNgp 1826.

7.2. THE NORIAN-RHAETIAN MICROFLORA OF THE EASTERN SOUTHERN ALPS

The Monticello Formation, Dolomia di Forni and Chiampomagno Limestone yielded abundant Norian and Rhaetian palynological associations in the Carnic and Julian Alps (Figs. 5, 12). They represent sediments of the intraplatform basins heteropic to the Dolomia Principale/Hauptdolomit and Dachstein Limestone (Dalla Vecchia, 2012; Carulli et al., 1998). These assemblages are dominated by trilete spores, monosaccate and bisaccate pollen and Circumpolles typical for the middle part of the Norian. During the late Norian, an increase in trilete spores and Circumpolles, along with a decrease of bisaccate pollen can be observed (Kustatscher & Roghi, 2014). The Rhaetian associations are characterized by trilete spores with fern, sphenophyte and lycophyte affinities and pollen grains belonging to the Circumpolles (*Corollina*), as well as pollen of uncertain botanical affinity, such as *Rhaetipollis germanicus* (Carulli et al., 1998).

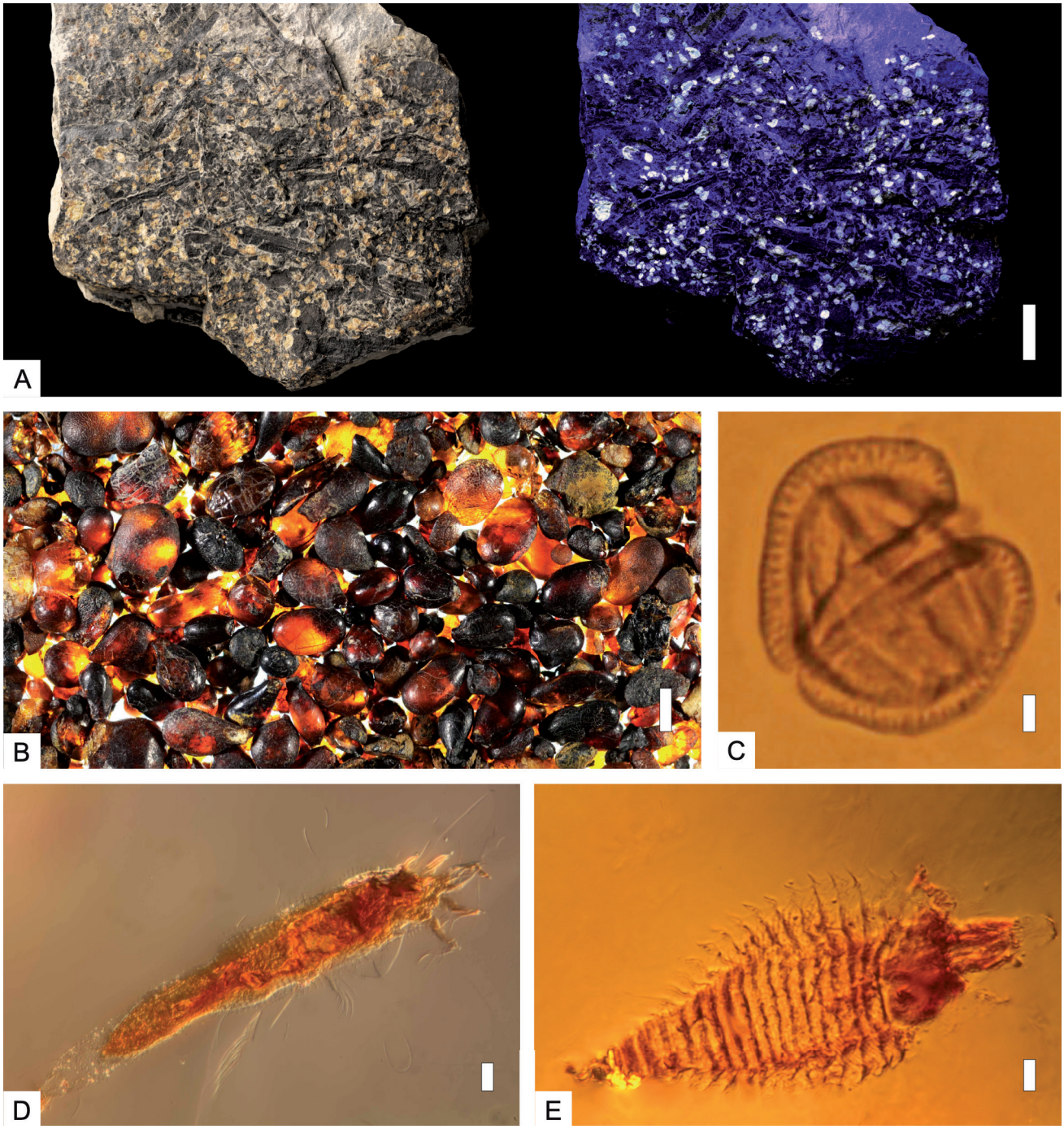

Figure 16: Triassic amber from the Dolomites. **A.** Sandstone with amber drops, fossil wood and charcoal (Heiligkreuz Fm., Dibona Section). The right image shows the sample under UV light, scale bar = 2 cm; **B.** Amber drops from the main palesols (Heiligkreuz Fm., Dibona section), scale bar = 5mm; **C.** Bisaccate taeniate pollen grain (*Lunatisporites* sp.) inside fossil resin, scale bar = 10µm; **D.** Plant-feeding mite inside Triassic amber: *Triasacarus fedelei* Lindquist et Grimaldi in Schmidt et al., 2012, scale bar = 10µm; **E.** Plant-feeding mite inside Triassic amber: *Ampezzoa triassica* Lindquist et Grimaldi in Schmidt et al., 2012, scale bar = 10µm.

8. THE AMBER

Triassic amber (Fig. 16) is very rare and occurs concentrated in a specific time interval in the Upper Triassic. Koken (1913) was the first to mention amber from the Triassic of the Southern Alps, specifically from the Heiligkreuz Formation around Cortina d'Ampezzo. This fossil resin is associated with conifer shoots and cuticle fragments, partly in palaeosoils. It was rediscovered almost 100 years later near the Rifugio Dibona (Fig. 16A, 16B) and subjected to a detailed study that also reported various inclusions (Fig. 16C–E); Roghi et al., 2006b, Schmidt et al., 2012, Sidorchuk et al., 2015; Seyfullah et al., 2018). More findings of amber together with plant fossils came from the Carnian of Dogna in the Julian Alps (Roghi et al., 2006a). Carnian amber is found in many different localities in Europe, North America and Southern Africa (Schmidt et al., 2012) and is linked to stressed conditions triggered by the Carnian Pluvial Episode (Gianolla et al., 1998; Roghi et al., 2006b). The Dolomites represent the largest Triassic amber deposit known to date.

Older Triassic amber was found in only one sample each from the Anisian in the Recoaro area and from putatively Ladinian sediments in the Dolomites (Roghi et al., 2017). The Anisian amber was found in a small collection of fossils, originally belonging to the botanist Abramo Massalongo (who lived from 1824 to 1860), which is presently housed at the Museum of Natural History of Venice. It pertains to the so-called "*Voltzia* beds" (lower Anisian) of the Recoaro area. Palynologically, these beds correspond to the vicentinense-antonescui subphase of the thiergartii-vicentinense phase (Fig. 4), which is characterized by the dominance of conifer pollen (Brugman, 1986). The amber was found in association with a conifer shoot fragment that was identified by Massalongo as "*Araucarites athrotanoides* Msslg" (*nomen in schedis*), which nowadays would correspond to *Voltzia recubariensis*. The Ladinian amber is associated with a shoot of *Voltzia ladinica* that was found, according to its label at the Museum of Natural History of Vienna, in the "Wengener Schichten" of Wengen/La Valle (Gadertal/Badia Valley). Based on the lithology, the sample corresponds to the uppermost part of the Wengen/La Valle Formation (latest Ladinian; Roghi et al., 2017). The Carnian amber of the Southern Alps has been mainly recovered from the Heiligkreuz Formation in the eastern Dolomites and in (marginal) marine sediments of the Rio del Lago Formation in the Julian Alps (Koken, 1913; Zardini, 1973; Gianolla et al., 1998; Roghi et al., 2006a, 2006b). In all cases, the amber was associated or in physical connection with conifer shoots and/or leaves, which permits the assignment to their respective resin-producing plant species. The Anisian and Ladinian amber of Northern Italy was produced by representatives of the Voltziales (*Voltzia recubariensis* and *V. ladinica*, respectively).

Although rare, the presence of the fossil resin in the Recoaro area and in the Wengen/La Valle area suggests it may be coeval with two Triassic humid shifts detected during the Bithynian/Pelsonian and Longobardian, respectively (Preto et al., 2010; Stefani et al., 2010). A transgressive phase could also have created stressed conditions for the forest habitat, leading to increased resin production while at the same time creating favorable conditions for the preservation of fossil plants and resin.

9. TAXONOMIC REMARKS

Genus *Macropterygium* Schimper, 1870
Type: Macropterygium bronnii (Schenk) Schimper, 1870

Remarks. Schimper (1870) attributed leaves to his new genus *Macropterygium* that had previously been assigned to *Pterophyllum bronnii* by Schenk (1866–67). *Macropterygium* was originally a junior synonym of *Sphenozamites* Brongniart, 1849. Wesley (1958) reserved the name *Sphenozamites* for leaves of bennettitalean affinity, and erected the new genus *Apoldia* Wesley, 1958 for macromorphologically similar leaves with a cycad affinity. The species *Sphenozamites tener* Compter, 1883 was assigned to *Apoldia* because of its cycadalean cuticle (Linnell, 1932, p. 251). However, that combination was invalid, since it lacked a full and direct reference to the basionym of the type species (Zijlstra et al., 2009). Moreover, the new combination was not in general use and new species with oblanceolate to spatulate segments were still assigned to the genus *Sphenozamites*.

During a revision of various *Pterophyllum* and *Zamites* species, Weber (1996) re-discussed *Macropterygium* and proposed *M. bronnii* (Schenk) Schimper, 1870 as type species and the specimen figured by Bronn (1858, pl. 4, fig. 1) as holotype of the species. Within the genus, he proposed three new subgenera – *Macropterygium* (Schimper) Arber, 1907, *Glandulozamites* (Bock) Weber, 1996 and *Indozamites* Weber, 1996 – and assigned *M. bronnii* to the first subgenus. The author suggested also to assign *Macropterygium* putatively to the Bennettitales, based on the finding of a syndetocheilic stoma apparatus in *Macropterygium rogersianum* (Fontaine) Weber, 1996. However, no cuticles have been described for the type species.

Zijlstra et al. (2009, 2013) proposed the conservation of the genus *Sphenozamites* for fossil bennettitalean leaves only. As a consequence, the genus *Macropterygium* Schimper, 1870 in its original diagnosis by Schimper is not considered a junior synonym of *Sphenozamites* anymore, since the former genus was created to include leaf fragments belonging to *Pterophyllum bronnii* Schenk, 1866–67, for which so far no cuticle has been described and which can, therefore, not be assigned with certainty to any plant group. Here we propose to use *Sphenozamites* (Brongniart) Miquel, 1851 for leaves with a clear affinity with the Bennettitales, *Apoldia* Wesley, 1958 for leaves clearly belonging to the cycads and *Macropterygium* Schimper, 1870 for those with unknown botanical affinity.

Macropterygium wengensis (Wachtler et Van Konijnenburg-van Cittert, 2000) Kustatscher et Van Konijnenburg-van Cittert comb. nov.
Basionym: Sphenozamites wengensis Wachtler et Van Konijnenburg-van Cittert, 2000, The fossil flora of the Wengen Formation (Ladinian) in the Dolomites (Italy), pp. 109–110, pl. 3, fig. 1–2.

Holotype: The specimen figured by Wachtler et Van Konijnenburg-van Cittert, 2000, pl. 3, fig. 1.

References

2000 *Sphenozamites wengensis* Wachtler et Van Konijnenburg-van Cittert, p. 109–110, pl. 4, fig. 1–3, pl. 5, fig. 1–5.
2004 *Sphenozamites wengensis* Wachtler et Van Konijnenburg-van Cittert – Kustatscher, p. 36.
2013 *Sphenozamites wengensis* Wachtler et Van Konijnenburg-van Cittert – Petti et al., p. 465.

Description. The rachis of the leaf fragments is thick (2–6 mm), the segments are inserted (sub-)oppositely and slightly to the upper side of the stout rachis, without covering it significantly. The segments are oblanceolate, slightly asymmetric with the posterior margin longer than the anterior margin, a slightly restricted base and a rounded apex. The segments are 30–45 mm long with a maximum width of 11–15 mm. The veins originate from the attachment area, fork in the lower and middle part of the segments and reach the outer margin at a concentration of 16/cm.

Remarks. The epidermis of *Macropterygium wengensis* has not been found preserved so far. Petti et al. (2013) suggested that the leaf fragments of *Sphenozamites wengensis* Wachtler et Van Konijnenburg-van Cittert, 2000 should be considered as cycadalean and thus transferred to the genus *Apoldia*. However, the missing cuticles make it impossible to assign this taxon to any higher plant group; consequently, an assignment to the genus *Macropterygium* Schimper, 1870 is proposed here.

Geographic and stratigraphic distribution. The species is so far restricted to the Ladinian of the Dolomites.

10 STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION OF THE MACRO PLANT REMAINS

The Triassic flora of the Eastern Southern Alps is a diverse flora with at least 95 different taxa. However, the stratigraphic record of these taxa is still scattered. Some plant assemblages, such as those from the Kühwiesenkopf/Monte Prà della Vacca (37 taxa) and the Raibl/Cave del Predil area (34 taxa), are important not only in comparison with other localities from the Southern Alps, but are also among the most diverse and abundant of their respective time slices in Europe. Relatively abundant and diverse assemblages are Piz da Peres (14 taxa), Recoaro (12 taxa; this plant assemblage is in need of a modern revision), Wengen/La Valle (15 taxa), Monte Agnello (15 taxa), Seiser Alm/Alpe di Siusi (12 taxa), Prags/Braies (11 taxa), and Agordo (10 taxa). All other localities yielded less than 10 taxa each. As a general overview, considering each of the stages, the Anisian flora of the Southern Alps is composed of 52 taxa, the Ladinian one of 39 taxa, the Carnian of 35 taxa and the Norian of 7 taxa only (Tab. 1, 3, 4). This apparent decrease in taxa could be in part artificial and not reflect a general decrease in diversity throughout the Triassic, because it appears in comparison with the best-preserved, and therefore unusually diverse Anisian plant fossil assemblage from the Kühwiesenkopf/Monte Prà della Vacca and the Recoaro plant assemblage, which needs further taxonomic revision. The Carnian and Norian plant assemblages are also in need of a taxonomic revision and/or study of the available collections. This could noticeably change our understanding of the diversity within the various stages.
On a generic level and excluding the problematic eight genera of the Recoaro and Raibl/Cave del Predil plant assemblages, 45 different taxa can be distinguished in the Eastern Southern Alps (Tab. 5). Only few of them are long-ranging taxa present from the Anisian to the Norian, i.e., *Equisetites* among the horsetails and *Pelourdea* and *Voltzia* among the conifers (Tab. 5). The lycophytes are represented by four different genera (*Isoetites*, *Lycopia*, *Selaginellites* and *Lepacyclotes*), all of which are restricted to the Middle Triassic. With the exception of *Pleuromeia*, the

Group	Genus	Anisian	Ladinian	Carnian	Norian
Lycophytes	*Isoetites*	x			
	Lycopia	x			
	Selaginellites	x			
	Lepacyclotes	x	x		
Horsetails	*Echinostachys*	x			
	Neocalamites	x			
	Equisetites	x	x	x	x
Ferns	*Sphenopteris*	x			
	Anomopteris	x	x		
	Gordonopteris	x	x		
	Scolopendrites	x	x		
	Cladophlebis	x	x	x	
	Neuropteridium	x	x	x	
	Symopteris	?			
	Marattiopsis	?			
	Danaeopsis	?	?	x	
	Phlebopteris		x		
	Thaumatopteris		x		
	Chiropteris		x	x	
	Rhacophyllum			x	
Seed ferns	*Peltaspermum*	x			
	Scytophyllum	x	x		
	Sagenopteris	x		x	
	Ptilozamites	?	x	x	
Cycadophytes	*Bjuvia*	x	x	?	
	Nilssonia	x	x	x	
	Dioonitocarpidium	x	x	x	
	Macrotaeniopteris		x	x	
	Apoldia			?	
Conifers	*Pseudovoltzia*	?			
	Elatocladus	x	x		
	Albertia	x	x		?
	Pelourdea	x	x	x	x
	Voltzia	x	x	x	x
	Brachyphyllum			x	x
	Pagiophyllum				x
Incertae sedis	*Lugardonia*	x			
	Taeniopteris	x	x	x	
	Carpolithes	x	x	x	
	Macropterygium		x	x	
	Phylladelphia			x	

Table 5: Occurrences of plant macrofossil genera in the Anisian to Norian stages within the Eastern Southern Alps.

most characteristic Early Triassic lycophyte genus of Europe, all relevant Triassic lycophyte genera are thereby present in the Eastern Southern Alps. With the exception of *Schizoneura* and *Broomsgrovia*, all relevant European sphenophyte genera are present in the Eastern Southern Alps as well. The fern group is the most diverse plant group in the Triassic of the Eastern Southern Alps (14 genera) and shows an interesting stratigraphic pattern (Tab. 5). The Anisian and Ladinian plant assemblages are mainly dominated (both in abundance and diversity) by Osmundales; Marattiales occur already putatively in the Anisian assemblages (*Marattiopsis*, *Danaeopsis*) but are confirmed only in the Carnian (*Danaeopsis*; Kustatscher et al., 2012b). *Asterotheca*, a typical element of Ladinian and Carnian floras in Europe is conspicuously absent (e.g., Kustatscher & Van Konijnenburg-van Cittert, 2011; Pott et al., 2018). The Dipteridaceae and Matoniaceae appear within the Ladinian and/or Carnian of the Eastern Southern Alps, constituting some of the earliest representatives of these families in the fossil record (Kustatscher et al., 2014).

All seed fern genera in the Eastern Southern Alps are already present in Anisian plant assemblages, although the occurrence of *Ptilozamites* is still putative. These four genera (*Scytophyllum, Peltaspermum, Sagenopteris,* and *Ptilozamites*) are among the most important Triassic genera in Europe. Peculiarly, the first occurrences of all these genera are stratigraphically lower in the South Eastern Alps than in the Central European Basin (cf. Kustatscher & Van Konijnenburg-van Cittert, 2013). A similar pattern can be observed in the cycadophytes. The occurrences of *Bjuvia* and *Dioonitocarpidium* in the Anisian of the Kühwiesenkopf/Monte Prà della Vacca are the earliest occurrences of these two genera in Europe, although megasporophylls assigned to *Dioonitocarpidium* have even been described from the Permian of Texas (DiMichele et al., 2001). The genus *Pterophyllum* is currently considered part of the Ladinian flora, although cuticle analyses would be necessary in order to confirm the early presence of this bennettitalean.

The conifers are the second most abundant and diverse group within individual plant assemblages. With the exception of the long-ranging taxa *Pelourdea* and *Voltzia*, most genera are present in short time slices only. Confirmed findings of *Aethophyllum* and *Albertia* (the last with a putative record in the Norian) are restricted to the Middle Triassic of the Eastern Southern Alps. Both genera are well described from the Buntsandstein of the Germanic Basin, which is slightly older in age (e.g., Schimper & Mougeot, 1844; Fliche, 1910; Grauvogel-Stamm, 1978). Peculiar is the putative presence of *Pseudovoltzia* and conifer shoots with cuticles that resemble walchian-type conifers in the Carnian Dibona locality. Detailed studies will be necessary in order to confirm whether these two genera survived the end-Permian mass extinction. Five genera can so far not be assigned to any major plant group.

Only very few taxa are distributed throughout the entire Eastern Southern Alps, from the westernmost part (i.e., Val di Non, Monte Agnello), to the northernmost Dolomites (Kühwiesenkopf/Monte Prà della Vacca, Piz da Peres, Prags/Braies and Wengen/La Valle), to the Julian/Carnic Alps in the East (e.g., Dogna, Rio Serai, Raibl/Cave del Predil) and to the Venetian Alps in the South (Recoaro). In fact, only two genera are represented in all areas of the Eastern Southern Alps, i.e., the sphenophyte genus *Equisetites* and the conifer genus *Voltzia*, although *Equisetites* is missing in Monte Agnello. The conifer *Pelourdea*, on the other hand, is stratigraphically present through all stages in the Eastern Southern Alps, but is not present in the westernmost localities, in the Non Valley and at Recoaro (Tab. 1, 3, 4). Whether this is a collecting artefact or has a biogeographical reason, can so far not be determined.

The lycophytes in general do not only have stratigraphical constraints in the Dolomites but are also restricted to the Northern Dolomites and Sappada. Among the ferns, the geographically most widely distributed ones are the genera *Cladophlebis*, *Neuropteridium* and *Gordonopteris*. Among the seed ferns, *Scytophyllum* is restricted to the Dolomites, whereas *Ptilozamites* is present both in the Dolomites and in the Julian Alps. Cycadophytes are generally rare in specific plant assemblages but have a geographically wide distribution in the Dolomites and Julian Alps. Within the conifers, *Albertia* is also a widely distributed genus, missing only in the Non Valley and in the Julian Alps.

11. CONCLUSIONS

The presented overview of all the Triassic macro- and microplant assemblages from the Eastern Southern Alps, includes 62 main outcrop areas (Figs. 1, 9, 12). Some of these floras have been known for centuries (e.g., Raibl, Recoaro), but the majority has been discovered in the 20th and 21st century. Both historically famous plant fossil assemblages are in need of taxonomic revision, as they have not been studied in detail since the end of the 19th century. Consequently, some of the species and genera known from the historical papers have not been considered in the context of palaeogeography and stratigraphy.

The more recently collected floras (e.g., Kühwiesenkopf/Monte Prà della Vacca, Agordo, Piz da Peres, Monte Agnello) and/or revised museum collections (e.g., Val di Non) are well-documented and add a considerable amount of interesting data to our knowledge of the flora in the Eastern Southern Alps during the Triassic. Some of the newly discovered plant fossil assemblages are quite rich in specimens and diverse in taxonomic composition (e.g., the Anisian flora of Kühwiesenkopf/Monte Prà della Vacca and the Ladinian flora of Monte Agnello). These new collections allow new insights into the vegetation composition of the Western Tethys Realm during the Triassic. What previously seemed to be a mainly conifer-dominated flora is now recognized as more diverse, with a large number of fern and cycadophyte taxa.

In general, the Triassic flora of the Eastern Southern Alps is diverse, with at least 95 taxa (belonging to at least 45 genera) occurring within the Triassic System. However, the comprehensive compilation of data shows clearly that most of these taxa are described only from one or few localities, in general from the most abundant and diverse plant fossils assemblages indicated above. The only exceptions are the horsetail *Equisetites* and the conifer *Voltzia*, which are both diverse and very abundant through time and occur geographically over the entire Eastern Southern Alps. A general decrease in taxonomic diversity trough time can be observed. This is an artifact related to the increasing scarcity of diverse and abundant plant assemblages and the need for revision of some of the Late Triassic floras. Moreover, the fact that several genera seem to be restricted to certain areas of the Eastern Southern Alps may be related to the patchy record. We cannot exclude the possibility that a severe collecting bias is still influencing our understanding of the geographic and

stratigraphic distribution of the various taxa.

Palynological studies on the Triassic sequences of the Eastern Southern Alps have been in full swing since the 1980s and provided us with a large amount of data not only on specific assemblages, but also on palaeoecological and palaeoclimatological changes in the Eastern Southern Alps during the Triassic. These led to (chrono-)stratigraphic revisions of several plant fossil localities, permitting us to obtain a better correlation between the different plant assemblages. The biostratigraphic phases, zones or assemblages are calibrated with the aid of ammonoid, and rarely conodont, biozones, thus, enabling an exceptional temporal resolution. A detailed, high-resolution sampling of the Late Triassic and earliest Triassic will permit to extend and improve the biostratigraphic scale (Fig. 4), filling up some of the existing gaps in the Southern Eastern Alps.

Quantitative palynological analyses have evidenced several shifts (i.e., in the late Anisian, in the late Ladinian and in the middle Carnian), that are partly overlapping with regional and/or global shifts from xerophytic to hygrophytic plant communities, showing that the climate during the Triassic was not as uniform as sometimes presumed. These shifts in the climatic signal are coeval with amber findings in the Eastern Southern Alps. This includes the late Pelsonian shift with amber droplets on *Voltzia recubariensis* from Recoaro, the late Ladinian shift with amber from the Wengen Formation of Wengen/La Valle and the famous Carnian Pluvial Episode with abundant amber findings throughout the Dolomites, including major occurrences near Heiligkreuz, Rifugio Dibona and Dogna. At a first glance it may appear that the shifts correspond to the major occurrences in plant fossil assemblages, such as for example with Kühwiesenkopf/Monte Prà della Vacca and Recoaro. On the other hand, other important plant fossil outcrops, such as Monte Agnello or Raibl/Cave del Predil, do not correspond with the humid shifts but are slightly older. At Dogna and Rifugio Dibona, plant remains were found in great numbers, but the collected plant assemblages are not very diverse.

Almost 180 years after the first figure of a plant remain (small fern frond fragment) from the Eastern Southern Alps, the vegetation record has become well-stocked with a wide range of plant groups and taxa. The different taxa necessitated different habitats, nutrients, soil and water availability, occupying, thus, different types of environments. The Southern Alps were, during the Triassic, a dynamic and changing landscape due to tectonic movements, volcanic activities and sea-level changes. These provided a wide range of environmental settings that changed through time. The dynamic landscape is reflected in the different plant fossil assemblages that can be observed in the different plant fossil localities. Although the micro-and macroplant assemblages are distributed unevenly across the geographic area and the stratigraphic succession, they show a high potential for the reconstruction of these different environments due to the excellent biostratigraphic time constraints (combination of palynological and ammonoid zones). Moreover, the exceptional preservation and the possibility to study macro-plant remains, microfloral assemblages and *in situ* spores and pollen, permit to combine and improve both proxies.

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APPENDIX 1:

List of all macrofossil taxa discussed in this paper, their stratigraphic attribution, age constraints and collocation in the various national and international collections, or – in cases where the present location is unknown – references to the publications in which they have been described/figured. Taxa with names between quotation marks (" ") require revision.

LYCOPHYTES

***Isoetites brandneri* Kustatscher et al., 2010**
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL)

***Lepacyclotes bechstaedtii* Kustatscher et al., 2010**
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL)

***Lepacyclotes zeilleri* (Fliche) Retallack, 1997**
Ladinian: upper part of the Fernazza Formation (Longobardian) of Ritjoch/Forcela da Cians (Wengen/La Valle; NMS PAL), Wengen Formation (Longobardian) of Wengen/La Valle (NHMW)

***Lepacyclotes* sp.**
Anisian: undifferentiated Anisian of Culzei (Prato Carnico, MFSNgp)

***Lycopia dezanchei* Kustatscher et al., 2010**
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL)

***Selaginellites leonardii* Kustatscher et al., 2010**
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL)

HORSETAILS

***Echinostachys* sp.**
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL), Agordo Formation, Richthofen Conglomerate or Morbiac Limestone (Bithynian–Pelsonian) of Valle San Lucano, Agordo (NMS PAL)

***Equisetites arenaceus* (Jaeger) Schenk, 1864**
Anisian: "Strati a Voltzia" (part of the Voltago Conglomerate, early Pelsonian) of Recoaro (MPP), "Torbiditi d'Aupa" (Illyrian) of Val Aupa (Moggio Udinese; MFSNgp)
Ladinian; upper part of the Fernazza Formation (Longobardian) of Ritjoch/Forcela da Cians (Wengen/La Valle; NMS PAL), Wengen Formation (Longobardian) of Sappada (MPL)
Carnian: Heiligkreuz Formation (late Julian-early Tuvalian) of Heiligkreuz (Bosellini & Largaiolli, 1965), undifferentiated Carnian of Seiser Alm/Alpe di Siusi (GII)

***Equisetites conicus* Sternberg, 1833**
Anisian: Voltago Limestone or Giovo Formation (Pelsonian) of Monte Avert (Val di Non; GZG)

***Equisetites mougeotii* (Brongniart) Wills, 1910**
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL)

***?Equisetites mougeotii* (Brongniart) Wills, 1910**
Anisian: Richthofen Conglomerate (Illyrian) of Piz da Peres (NMS PAL)

***Equisetites* sp.**
Anisian: "Strati a Voltzia" (part of the Voltago Conglomerate, early Pelsonian) of Recoaro (MB.Pb, MPP) and "Torbiditi d'Aupa" (Illyrian) of Val Aupa (Moggio Udinese; MFSNgp)
Ladinian: undifferentiated Ladinian of Monte Nebria (Malborghetto Valbruna; MFSNgp)
Carnian: Rio del Lago Formation (Julian) of Dogna (MPP), Predil Limestone (Julian) of Raibl/Cave del Predil (MB.Pb, GBA, BII), Heiligkreuz Formation (Tuvalian) of Rifugio Dibona (MPP)
Norian: Dolomia di Forni (Alaunian–Sevatian) of Rio Seazza (MFSNgp)

***?Equisetites* sp.**
Anisian: Agordo Formation, Richthofen Conglomerate or Morbiac Limestone (Bithynian–Pelsonian) of Valle San Lucano, Agordo (NMS PAL), undifferentiated Anisian of Culzei (Prato Carnico; MFSNgp) and unspecified Prato Carnico (MFSNgp)
Ladinian: upper part of the Fernazza Formation (Longobardian) of Ritjoch/Forcela da Cians (Wengen/La Valle; NMS PAL), Wengen Formation (Longobardian) of Wengen/La Valle (NHMW), St. Kassian/San Cassiano (Hochabteiltal/alta Val Badia; NMP), Cercenà (Val Zoldana, MPP), Sappada (MPL), undifferentiated Ladinian of Monte Sief (Livinallongo, GII), Bevorchians (Moggio Udinese; MFSNgp)
Carnian: San Cassian Formation (Julian) of Stuores Wiesen/ Pralongià (Hochabteiltal/alta Val Badia; ItTr; Bizzarini et al., 2001), Predil Limestone (Julian) of Raibl/Cave del Predil (NHMW)

***Neocalamites* sp.**
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL), Voltago Limestone or Giovo Formation (Pelsonian) of Monte Avert (Val di Non; GZG)

FERNS

***Anomopteris mougeotii* Brongniart, 1828**
Anisian: Agordo Formation, Richthofen Conglomerate or Morbiac Limestone (Bithynian–Pelsonian) of Valle San Lucano, Agordo (NMS PAL), middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL), Richthofen Conglomerate (Illyrian) of Piz da Peres (NMS PAL), "Torbiditi d'Aupa" (Illyrian) of Val Aupa (Moggio Udinese; MFSNgp)

Ladinian: Wengen Formation (Longobardian) of Corvara (Hochabteiltal/alta Val Badia; GPIT), undifferentiated Ladinian of Bevorchians (Moggio Udinese; MFSNgp)

"*Asterotheca*" spp.
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (Stur, 1885)

"*Camptopteris*" sp.
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (Stur, 1885)

***Chiropteris monteagnellii* Kustatscher et al., 2014**
Ladinian: Pyroclastic layers (part of the Caotico Eterogeneo) of early Longobardian age of Monte Agnello (MGP)

***Chiropteris lacerata* (Quenstedt) Rühle von Lilienstern, 1931**
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (Bronn, 1858)

***Cladophlebis ladinica* Kustatscher et al., 2014**
Ladinian: Pyroclastic layers (part of the Caotico Eterogeneo) of early Longobardian age of Monte Agnello (MGP)

***Cladophlebis leuthardtii* Leonardi, 1953**
Anisian: Richthofen Conglomerate (Illyrian) of Piz da Peres (NMS PAL)
Ladinian: upper part of the Fernazza Formation (Longobardian) of Ritjoch/Forcela da Cians (Wengen/La Valle; NMS PAL) and Innerkohlbach (Prags/Braies; NMS PAL), Wengen Formation (Longobardian) of Corvara (Hochabteiltal/alta Val Badia; NHMW), Cercenà (Val Zoldana; MPL, MPP), Schgaguler Schwaige/Malga Schgaguler (Seiser Alm/Alpe di Siusi; BSGP), Pufels/Bulla (Gröden/Val Gardena; MPL), Grödner Joch/Passo Gardena (Hochabteiltal/alta Val Badia; GLA), Corvo Alto (Croda da Lago Group; MDR) and Sappada (MPL)
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (NHMW)

***Cladophlebis remota* (Presl) Van Konijnenburg-van Cittert et al., 2006**
Anisian: Agordo Formation, Richthofen Conglomerate or Morbiac Limestone (Bithynian–Pelsonian) of Valle San Lucano, Agordo (NMS PAL), middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL)

***Cladophlebis ruetimeyeri* (Heer) Leonardi, 1953**
Ladinian: Wengen Formation (Longobardian) of Cercenà (Val Zoldana; MPP, MPL), Schgaguler Schwaige/Malga Schgaguler (Seiser Alm/Alpe di Siusi; MPL) and Col Alto (Hochabteiltal/alta Val Badia; MDR)
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (GBA)

***Cladophlebis* sp.**
Anisian: Middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL)
Ladinian: Pyroclastic layers (part of the Caotico Eterogeneo) of early Longobardian age of Monte Agnello (MGP), Wengen Formation (Longobardian) of Corvo Alto (MDR)

"*Clathropteris*" spp.
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (Stur, 1885)

?*Danaeopsis angustifolia* (Schenk) Kustatscher et al. 2012
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL), Richthofen Conglomerate (Illyrian) of Piz da Peres (NMS PAL)
Ladinian: upper part of the Fernazza Formation (Longobardian) of Innerkohlbach (Prags/Braies; NMS PAL)
Carnian: Rio del Lago Formation (Julian) of Dogna (MPP)

?*Danaeopsis marantacea* (Presl) Schimper, 1869
Ladinian: Wengen Formation (Longobardian) of Corvara (Hochabteiltal/alta Val Badia; Mojsisovics, 1879)
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (Schenk, 1866–7)

***Danaeopsis* sp.**
Carnian: Rio del Lago Formation (Julian) of Dogna (MPP)

***Gordonopteris lorigae* Van Konijnenburg-van Cittert et al., 2006**
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL, GII), Richthofen Conglomerate (Illyrian) of Piz da Peres (NMS PAL), Voltago Limestone or Giovo Formation (Pelsonian) of Monte Avert (Val di Non; GZG)
Ladinian: upper part of the Fernazza Formation (Longobardian) of Ritjoch/Forcela da Cians (Wengen/La Valle; NMS PAL), Wengen Formation (Longobardian) of Cercenà (Val Zoldana, MPP) and Sappada (MPL)

?*Gordonopteris lorigae* Van Konijnenburg-van Cittert et al., 2006
Ladinian: Wengen Formation (Longobardian) of Corvo Alto (MDR)

"*Laccopteris lunzensis* Stur, 1885"
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (Stur, 1885)

?*Marattiopsis* sp.
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL)

***Neuropteridium elegans* (Brogniart) Schimper, 1879**
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL, GII), Voltago Limestone or Giovo Formation (Pelsonian) of Monte Avert (Val di Non; GZG), Richthofen Conglomerate (Illyrian) of Piz da Peres (NMS PAL)
Ladinian: Pyroclastic layers (part of the Caotico Eterogeneo) of early Longobardian age of Monte Agnello (MGP), upper part of the Fernazza Formation (Longobardian) of Ritjoch/Forcela da Cians (Wengen/La Valle; NMS PAL), Wengen Formation (Longobardian) of Forcella Giau (MDR), Monte Sief (Livinallongo; BSPG) and Sappada (MPL)
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (GBA)

***Neuropteridium grandifolium* (Schimper et Mougeot) Compter, 1883**
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL)
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (GBA)

***Neuropteridium voltzii* (Brogniart) Schimper, 1879**
Anisian: Agordo Formation, Richthofen Conglomerate or Morbiac Limestone (Bithynian–Pelsonian) of Valle San Lucano, Agordo (NMS PAL), middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL), Richthofen Conglomerate (Illyrian) of Piz da Peres (NMS PAL), undifferentiated Anisian of the Ponte di Rio Freddo/Kaltwasser (MFSNgp)

"*Oligocarpia*" sp.
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (Stur, 1885)

***Phlebopteris fiemmensis* Kustatscher et al., 2014**
Ladinian: Pyroclastic layers (part of the Caotico Eterogeneo) of early Longobardian age of Monte Agnello (MGP)

"*Rhacopteris*" sp.
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (Stur, 1885)

"*Rhacopteris raiblensis* Stur, 1885"
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (Stur, 1885)

***Rhacophyllum crispatum* (Münster in Sternberg) Kustatscher et Van Konijnenburg-van Cittert, 2011**
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (Stur, 1885)

***Scolopendrites grauvogelii* Van Konijnenburg-van Cittert et al., 2006**
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL)

***Scolopendrites scolopendrioides* (Brogniart) Van Konijnenburg-van Cittert et al., 2006**
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL)

***Scolopendrites* sp.**
Anisian: Agordo Formation, Richthofen Conglomerate or Morbiac Limestone (Bithynian–Pelsonian) of Valle San Lucano, Agordo; NMS PAL), Richthofen Conglomerate (Illyrian) of Piz da Peres (NMS PAL)
Ladinian: Wengen Formation (Longobardian) of St. Kassian/San Cassiano (Hochabteiltal/alta Val Badia; GII)

"*Speirocarpus*" sp.
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (Stur, 1885)

***Sphenopteris schoenleiniana* (Brongniart) Presl, 1838**
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL)

***Symopteris* sp.**
Anisian: undifferentiated Anisian of Rio Tschofen (Tarvisio, MFSNgp)

***Thaumatopteris* sp.**
Ladinian: Pyroclastic layers (part of the Caotico Eterogeneo) of early Longobardian age of Monte Agnello (MGP)

Dipteridaceae indet.
Ladinian: Pyroclastic layers (part of the Caotico Eterogeneo) of early Longobardian age of Monte Agnello (MGP)

Pteridophyta incertis sedis
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL)

SEED FERNS

***Peltaspermum bornemannii* Kustatscher et al. 2007**
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL), Richthofen Conglomerate (Illyrian) of Piz da Peres (NMS PAL)

***Peltaspermum* sp.**
Anisian: Agordo Formation, Richthofen Conglomerate or Morbiac Limestone (Bithynian–Pelsonian) of Valle San Lucano, Agordo (NMS PAL), undifferentiated Anisian of Culzei (Prato Carnico, MFSNgp)

***Ptilozamites sandbergeri* (Schenk) Kustatscher et Van Konijnenburg-van Cittert, 2007**
Ladinian: upper part of the Fernazza Formation (Longobardian) of Ritjoch/Forcela da Cians (Wengen/La Valle; NMS PAL) and Innerkohlbach (Prags/Braies; NMS PAL), Wengen Formation (Longobardian) of Seewald (Prags/Braies; NMS PAL), St. Leonhard im Abteital/S. Leonardo in Badia (Hochabteiltal/alta Val Badia; NHMW), Seiser Alm/Alpe di Siusi (MDG), Wengen/La Valle (BSPG), Pufels/Bulla (Gröden/Val Gardena; BSPG) and Corvo Alto (Forcella Giau; MDR)
Carnian: Rio del Lago Formation (Julian) of Dogna (MPP), Predil Limestone (Julian) of Raibl/Cave del Predil (NHMW, GBA, GII), undifferentiated Carnian of Canale Prasnig (Raibl/Cave del Predil; MFSNgp)

?*Ptilozamites* sp.
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL)

***Sagenopteris* sp.**
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL)
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (GBA)

***Scytophyllum bergeri* Bornemann, 1856**
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL), Richthofen Conglomerate (Illyrian) of Piz da Peres (NMS PAL)
Ladinian: Pyroclastic layers (part of the Caotico Eterogeneo) of early Longobardian age of Monte Agnello (MGP), Wengen Formation (Longobardian) of Corvara (BGA)

CYCADOPHYTES

?*Apoldia tenera* (Compter) Wesley, 1958
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (NHMW)

***Bjuvia dolomitica* Wachtler et Van Konijnenburg-van Cittert, 2000**
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL), Richthofen Conglomerate (Illyrian) of Piz da Peres (NMS PAL),
Ladinian: upper part of the Fernazza Formation (Longobardian) of Ritjoch/Forcela da Cians (Wengen/La Valle; NMS PAL), Wengen Formation (Longobardian) of Schgaguler Schwaige/Malga Schgaguler (Seiser Alm/Alpe di Siusi; BSPG), undefined Seiser Alm/Alpe di Siusi (MDG), Wengen/La Valle (NHMW), Corvara (Hochabteiltal/alta Val Badia; BSPG), Corvo Alto (Croda da Lago Group; MDR), Mondeval (Croda da Lago Group; MDR) and Gröden/Val Gardena (MDG)

?*Bjuvia* sp.
Ladinian: Pyroclastic layers (part of the Caotico Eterogeneo) of early Longobardian age of Monte Agnello (MGP), Wengen Formation (Longobardian) of Livinallongo (PL), Grödner Joch/Passo Gardena (Hochabteiltal/alta Val Badia; GLA), Schgaguler Schwaige/Malga Schgaguler (Seiser Alm/Alpe di Siusi; BSPG), Corvara (Hochabteiltal/alta Val Badia; NMS PAL), Sappada (MPL)

***Cycadites suessi* Stur, 1885**
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (Stur, 1885)

***Dioonites pachyrrhachis* (Schenk) Stur, 1885**
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (NHMW, GBA)

***Dioonitocarpidium moroderi* (Leonardi) Kustatscher et al., 2004**
Ladinian: Wengen Formation (Longobardian) of Schgaguler Schwaige/Malga Schgaguler (Seiser Alm/Alpe di Siusi; MDG)

?*Dioonitocarpidium pennaeformis* (Schenk) Rühle von Lilienstern, 1928
Anisian: Voltago Limestone or Giovo Formation (Pelsonian) of Monte Avert (Val di Non; GZG)

***Dioonitocarpidium* sp.**
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL), Richthofen Conglomerate (Illyrian) of Piz da Peres (NMS PAL)
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (GBA)

***Macrotaeniopteris* sp.**
Ladinian: Pyroclastic layers (part of the Caotico Eterogeneo) of early Longobardian age of Monte Agnello (MGP)
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (GBA, NHMW)

***Nilssonia* sp.**
Ladinian: Pyroclastic layers (part of the Caotico Eterogeneo) of early Longobardian age of Monte Agnello (MGP)
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (GBA)

"*Pterophyllum filicoides* (Schlotheim) Zeiller, 1906"
Ladinian: Wengen Formation (Longobardian) of Livinallongo (PL), Corvara (Hochabteiltal/alta Val Badia; GII), Cercenà (Val Zoldana, MPP, MPL) and St. Kassian/San Cassiano (Hochabteiltal/alta Val Badia; MPL)
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (NHMW, GBA)

"*Pterophyllum giganteum* Schenk, 1865"
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (UU)

"*Pterophyllum*" sp.
Ladinian: Wengen Formation (Longobardian) of Corvara (Hochabteiltal/alta Val Badia, SMNS), Seiser Alm/Alpe di Siusi (MDG), ?Laste/Monte Sief (Livinallongo; PL)
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (NHMW, GBA)

"*Zamites* sp."
Ladinian: Wengen Formation (Longobardian) of St. Kassian/San Cassiano (GPIT)

CONIFERS

"*Aethophyllum foetterlianum* Massalongo ex De Zigno, 1862"
Anisian: "Strati a Voltzia" (part of the Voltago Conglomerate, early Pelsonian) of Recoaro (MSNV)

***Albertia* sp.**
Anisian: Agordo Formation, Richthofen Conglomerate or Morbiac Limestone (Bithynian–Pelsonian) of Valle San Lucano, Agordo (NMS PAL), "Strati a Voltzia" (part of the Voltago Conglomerate, early Pelsonian) of Recoaro (MSNV, MPP), middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL), undifferentiated Anisian of Culzei (Prato Carnico; MFSNgp) and undefined Prato Carnico (MFSNgp)
Ladinian: undifferentiated Ladinian of Dierico (MFSNgp)
Norian: Dolomia di Forni (Alaunian–Sevatian) of Rio Seazza (MFSNgp)

?*Albertia* sp.
Norian: Dolomia di Forni (Alaunian–Sevatian) of Rio Seazza (MFSNgp)

"*Araucarites agordicus* Anger, in schedis"
Anisian: "Strati a Voltzia" (part of the Voltago Conglomerate, early Pelsonian) of Recoaro (MSNV)

"*Araucarites albuctenoides* Mass., in schedis"
Anisian: "Strati a Voltzia" (part of the Voltago Conglomerate, early Pelsonian) of Recoaro (MCSNV)

"*Araucarites massalongii* De Zigno, 1862"
Anisian: "Strati a Voltzia" (part of the Voltago Conglomerate, early Pelsonian) of Recoaro (MCSNV)

"*Araucarites pachyphyllus* De Zigno, 1862"
Anisian: "Strati a Voltzia" (part of the Voltago Conglomerate, early Pelsonian) of Recoaro (MPP)

***Brachyphyllum* sp.**
Carnian: Rio del Lago Formation (early Carnian) of Dogna (MPP)
Norian: Dolomia di Forni (Alaunian–Sevatian) of Rio Seazza (MFSNgp), Rio Forchiar (MFSNgp) and Rio Secco (MFSNgp)

"*Cephalotaxites raiblensis* Stur, 1885"
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (GBA)

***Elatocladus* sp.**
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL)
Ladinian: Wengen Formation (Longobardian) of Puflatsch / Bullaccia (MDG)

***Pagiophyllum* sp.**
Anisian: "Strati a Voltzia" (part of the Voltago Conglomerate, early Pelsonian) of Recoaro (MCSNV)
Norian: Dolomia di Forni (Alaunian–Sevatian) of Rio Seazza (MFSNgp) and Rio Forchiar (MFSNgp)

***Pelourdea vogesiaca* (Schimper et Mougeot) Seward, 1917**
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL), undifferentiated Anisian of Culzei (Prato Carnico; MFSNgp) and unspecified Prato Carnico (MFSNgp)
Ladinian: upper part of the Fernazza Formation (Longobardian) of Ritjoch/Forcela da Cians (Wengen/La Valle; NMS PAL) and Innerkohlbach (Prags/Braies; NMS PAL), Wengen Formation (Longobardian) of Seewald (Prags/Braies; NMS PAL) and Schgaguler Schwaige/Malga Schgaguler (Seiser Alm/Alpe di Siusi; MDG)
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (MB. Pb, NMHW)
Norian: Dolomia di Forni (Alaunian–Sevatian) of Rio Seazza (MFSNgp)

***Pelourdea* sp.**
Ladinian: Pyroclastic layers (part of the Caotico Eterogeneo) of early Longobardian age of Monte Agnello (MGP)
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (GBA), undifferentiated Carnian of Balador (Rio Lavaz, Dogna area; MFSNgp)
Norian: Dolomia di Forni (Alaunian–Sevatian) of Rio Seazza (MFSNgp), Rio Forchiar (MFSNgp), Rio Spisulò (MFSNgp)

***?Pelourdea* sp.**
Ladinian: Wengen Formation (Longobardian) of Cercenà (Val Zoldana; MPP) and Seiser Alm/Alpe di Siusi (MPL)

***"Podozamites* sp."**
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (GBA, NHMW)

***?Pseudovoltzia* sp.**
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL)

"*Taxites massalongii* De Zigno, 1862"
Anisian: "Strati a Voltzia" (part of the Voltago Conglomerate, early Pelsonian) of Recoaro (MPP)

"*Taxites vincentinus* Massalongo ex De Zigno, 1862"
Anisian: "Strati a Voltzia" (part of the Voltago Conglomerate, early Pelsonian) of Recoaro (MCSNV, MPP)

"*Taxodites saxolimpiae* Massalongo ex De Zigno, 1862"
Anisian: "Strati a Voltzia" (part of the Voltago Conglomerate, early Pelsonian) of Recoaro (MCSNV)

"*Thuites* sp."
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (NHMW)

***Voltzia dolomitica* Wachtler et Van Konijnenburg-van Cittert, 2000**
Ladinian: upper part of the Fernazza Formation (Longobardian) of Ritjoch/Forcela da Cians (Wengen/La Valle; NMS PAL) and Innerkohlbach (Prags/Braies; NMS PAL), Wengen Formation (Longobardian) of Seewald (Prags/Braies; NMS PAL), Wengen/La Valle (NHMW, GII), Schgaguler Schwaige/Malga Schgaguler (Seiser Alm/Alpe di Siusi; MDG) and Sappada (MPL)

?*Voltzia dolomitica* Wachtler et Van Konijnenburg-van Cittert, 2000
Ladinian: Wengen Formation (Longobardian) of Wengen/La Valle (NHMW), undifferentiated Ladinian of Bevorchians (Moggio Udinese; MFSNgp)

***"Voltzia foetterlei* Stur, 1885"**
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (MB. Pb, NHMW, GBA, SMNS, NMP)

***"Voltzia haueri* Stur, 1885"**
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (NHMW, GBA, NMP, BII?), Rio del Lago Formation (Julian) of Dogna (MPP)

"*Voltzia heterophylla* (Brongniart) Schimper et Mougeot, 1844"
Anisian: "Strati a Voltzia" (part of the Voltago Conglomerate, early Pelsonian) of Recoaro (MSNV), middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL), undifferentiated Anisian of Prato Carnico (MFSNgp)
Ladinian: undifferentiated Ladinian of Dierico (MFSNgp)
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (NHMW, ItTr)

***Voltzia ladinica* Wachtler et Van Konijnenburg-van Cittert, 2000**
Ladinian: upper part of the Fernazza Formation (Longobardian) of Ritjoch/Forcela da Cians (Wengen/La Valle; NMS PAL) and Innerkohlbach (Prags/Braies; NMS PAL), Wengen Formation (Longobardian) of Seewald (Prags/Braies; NMS PAL), Wengen/La Valle (NHMW), Seiser Alm/Alpe di Siusi (MDG), Gröden/Val Gardena (WDG), undifferentiated Ladinian of Bevorchians (Moggio Udinese; MFSNgp)

***"Voltzia pachyphylla* Schimper, 1869"**
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (GBA)

***Voltzia pragsensis* Wachtler et Van Konijnenburg-van Cittert, 2000**
Ladinian: upper part of the Fernazza Formation (Longobardian) of Ritjoch/Forcela da Cians (Wengen/La Valle; NMS PAL) and Innerkohlbach (Prags/Braies; NMS PAL), Wengen Formation (Longobardian) of Seewald (Prags/Braies; NMS PAL) and Schgaguler Schwaige/Malga Schgaguler (Seiser Alm/Alpe di Siusi; MDG)

***Voltzia raiblensis* Stur, 1885**
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (NHMW, UU, SMNS, NMP)

***Voltzia recubariensis* (De Zigno) Schenk, 1868**
Anisian: Agordo Formation, Richthofen Conglomerate or Morbiac Limestone (Bithynian–Pelsonian) of Valle San Lucano, Agordo (NMS PAL), "Strati a Voltzia" (part of the Voltago Conglomerate, early Pelsonian) of Recoaro (MB.Pb, MPL, MCSNV, MPP, GZG), middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL, GII), Voltago Limestone or Giovo Formation (Pelsonian) of Monte Avert (Val di Non; GZG), Richthofen Conglomerate (Illyrian) of Piz da Peres (NMS PAL), undifferentiated Anisian of Culzei (Prato Carnico; MFSNgp)

***Voltzia walchiaeformis* Fliche, 1910**
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL)

?*Voltzia walchiaeformis* Fliche, 1910
Anisian: Voltago Limestone or Giovo Formation (Pelsonian) of Monte Avert (Val di Non; GZG)

***Voltzia zoldana* Leonardi, 1953**
Ladinian: Wengen Formation (Longobardian) of Cercenà (Val Zoldana, MPP)

***Voltzia* sp.**
Anisian: Agordo Formation, Richthofen Conglomerate or Morbiac Limestone (Bithynian–Pelsonian) of Valle San Lucano, Agordo; "Strati a Voltzia" (part of the Voltago Conglomerate, early Pelsonian) of Recoaro (MPL), middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL), undifferentiated Anisian of the "Pragser Dolomiten" (BSPG), NMS PAL, MPP), Culzei (Prato Carnico; MFSNgp), unspecified Prato Carnico (MFSNgp) and Monte Bivera (MFSNgp)
Ladinian: Pyroclastic layers (part of the Caotico Eterogeneo) of early Longobardian age of Monte Agnello (MGP), upper part of the Fernazza Formation (Longobardian) of Ritjoch/Forcela da Cians (Wengen/La Valle; NMS PAL) and Innerkohlbach (Prags/Braies; NMS PAL), Wengen Formation (Longobardian) of Seewald (Prags/Braies; NMS PAL), Wengen/La Valle (NHMW, GII), Aschkler Alpe/Malga Mastlè (Seceda, Gröden/Val Gardena; BSPG), Schgaguler Schwaige/Malga Schgaguler (Seiser Alm/Alpe di Siusi; BSGP), Cercenà (Val Zoldana, MPP), and Sappada (MPL), undifferentiated Ladinian of Seiser Alm/Alpe di Siusi (SMNS), Pufels/Bulla (Gröden/Val Gardena; MPL), Bevorchians (Moggio Udinese; MFSNgp), Monte Nebria (Malborghetto Valbruna, MFSNgp) and Dierico (MFSNgp)
Carnian: Rio del Lago Formation (Julian) of Dogna (MPP), San Cassian Formation (Julian) of Stuores Wiesen/Pralongià (Hochabteiltal/alta Val Badia; Bizzarini et al., 2001), Misurina (NMS PAL) and Seelandalpe (Plätzwiese/Prato Piazza; BSPG), Predil Limestone (Julian) of Raibl/Cave del Predil (GPIT, STIPB-PB MPL, MFSNgp, GPIT/PL, NMP, GII, ItTr), Heiligkreuz Formation (Tuvalian) of Rifugio Dibona (MPP), undifferentiated Carnian of Balador (Rio Lavaz, Dogna area; MFSNgp), Canale Klinken (Malborghetto Valbruna; MFSNgp), Canale Placcia (Malborghetto Valbruna; MFSNgp), Canale Prasnig (Raibl/Cave del Predil; MFSNgp), Fusea (MFSNgp), Rio dei Combattenti (Raibl/Cave del Predil; MFSNgp), Rio Freddo/Kaltwasser (Raibl/Cave del Predil; MFSNgp) and Rio Serai (MFSNgp)
Norian: Dolomia di Forni (Alaunian–Sevatian) of Rio Seazza (MFSNgp), Rio Forchiar (MFSNgp) and Rio Secco (MFSNgp)

?"walchian-like" conifer
Carnian: Rio del Lago Formation (early Carnian) of Dogna (MPP)

INCERTAE SEDIS

***Carpolithes* sp.**
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL), undifferentiated Anisian of Culzei (Prato Carnico; MFSNgp)
Ladinian: Wengen Formation (Longobardian) of Seewald (Prags/Braies; NMS PAL), undifferentiated Ladinian of Bevorchians (Moggio Udinese; MFSNgp), Wengen Formation (Longobardian) of Wengen/La Valle (NHMW) and Sappada (MPL)
Carnian: San Cassian Formation (Julian) of Stuores Wiesen/Pralongià (Hochabteiltal/alta Val Badia; Bizzarini et al., 2001)

***Lugardonia paradoxa* Kustatscher et al., 2009**
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL)

***Macropteridium bronnii* (Schenk) Schimper, 1870**
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (NHMW, GBA, BSPG)

?*Macropteridium bronnii* (Schenk) Schimper, 1870
Ladinian: Wengen Formation (Longobardian) of St. Leonhard im Abteital/S. Leonardo in Badia (Hochabteiltal/alta Val Badia; NHMW), and Livinallongo (PL)
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (GBA, BSPG)

***Macropteridium wengensis* (Wachtler et Van Konijnenburg-van Cittert, 2000) Kustatscher et Van Konijnenburg-van Cittert comb. nov.**
Ladinian: upper part of the Fernazza Formation (Longobardian) of Ritjoch/Forcela da Cians (Wengen/La Valle; NMS PAL) and Wengen Formation (Longobardian) of Seewald (Prags/Braies; NMS PAL)

***Macropteridium* sp.**
Ladinian: Pyroclastic layers (part of the Caotico Eterogeneo) of early Longobardian age of Monte Agnello (MGP)

***Phylladelphia strigata* Bronn, 1858**
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (NHMW, GBA)

***Taeniopteris* sp.**
Anisian: middle part of the Dont Formation (middle–late Pelsonian) of Kühwiesenkopf/Monte Prà della Vacca (NMS PAL, GII), Richthofen Conglomerate (Illyrian) of Piz da Peres (NMS PAL), Agordo Formation, Richthofen Conglomerate or Morbiac Limestone (Bithynian–Pelsonian) of Valle San Lucano, Agordo (NMS PAL)
Ladinian: Wengen Formation (Longobardian) of Seewald (Prags/Braies; NMS PAL), Pyroclastic layers (part of the Caotico

Eterogeneo) of early Longobardian age of Monte Agnello (MGP), Wengen Formation (Longobardian) of Cercenà (Val Zoldana, MPP), Corvara (Hochabteiltal/alta Val Badia; BSPG), Sappada (MPL), Gröden/Val Gardena (MPL), unspecified Gadertal/Val Badia (MPL)
Carnian: Predil Limestone (Julian) of Raibl/Cave del Predil (NHMW)

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Artikel/Article: Triassic macro - and microfloras of the Eastern Southern Alps 5-44