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THE LADINIAN FLORA (MIDDLE TRIASSIC) OF THE DOLOMITES: PALAEOENVIRONMENTAL RECONSTRUCTIONS AND PALAEOCLIMATIC CONSIDERATIONS

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With 7 figures and 5 tables

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Abstract

The study of several plant fossils from the Ladinian of the Dolomites, that either had been described a long time ago or had never been described at all, has led to a revision of this flora. The Ladinian flora now consists of the following taxa: *Annalepis zeilleri* (Lycophyta), *Equisetites arenaceus* (Sphenophyta), *Cladophlebis leuthardtii, C. ruetimeyeri, Neuropteridium elegans, Scolopendrites* sp., *Gordonopteris lorigae* (Pteridophyta), *Ptilozamites heeri* (Pteridospermae), *Bjuvia dolomitica, Dioonitocarpidium moroderi, Pterophyllum jaegeri,* ?*Pterophyllum* sp., *Sphenozamites wengensis*, *Sphenozamites* cf. *bronnii*, *Taeniopteris* sp. (Cycadophyta), *Voltzia dolomitica, V. ladinica, V. pragsensis, V. zoldana, Voltzia* sp., *Pelourdea vogesiaca* und *Elatocladus* sp. (Coniferophyta).

The flora, and especially the large number of specimens housed in the Natural History Museum at Bolzano (I), indicates a dominance of conifers over (in this sequence) seedferns, cycads, ferns and horsetails. Several factors may have caused this: climatic (an arid climate on the mainland), edaphic (immature soil) or taphonomic (caused by selection during transport). Quantitative palynological analyses of three localities (Ritberg near Wengen, and Seewald and Innerkohlbach near Prags, indicate a generally warm and humid climate. The dominance of the conifers and seedferns may, therefore, have been caused by their larger resistance during transport rather than by climatic factors.

Ladinian palaeoclimatic reconstructions and the plant fossils studies indicate that during the late Ladinian the Dolomites consisted of carbonate or volcanic islands of various sizes, which were covered with several biotopes: coastal and ‚hinterland'; the latter divided into a more humid and a more arid zone.

Zusammenfassung

Das Studium verschiedener historischer, ebenso wie bisher unbeschriebener Pflanzenfossilien aus dem Ladin der Dolomiten, die in italienischen und ausländischen Museen aufbewahrt werden, führte zu einigen Erstbeschreibungen und systematischen Revisionen. Die Ladinflora setzt sich nunmehr aus folgenden Arten zusammen: *Annalepis zeilleri* (Lycophyta), *Equisetites arenaceus* (Sphenophyta), *Cladophlebis leuthardtii, C. ruetimeyeri*, *Neuropteridium elegans*, *Scolopendrites* sp., *Gordonopteris lorigae* (Pteridophyta), *Ptilozamites heeri* (Pteridospermae), *Bjuvia dolomitica, Dioonitocarpidium moroderi, Pterophyllum jaegeri,* ?*Pterophyllum* sp., *Sphenozamites wengensis*, *Sphenozamites* cf. *bronnii, Taeniopteris* sp. (Cycadophyta), *Voltzia dolomitica, V. ladinica, V. pragsensis, V. zoldana, Voltzia* sp., *Peloürdea vogesiaca* und *Elatocladus* sp. (Coniferophyta).

Die Flora, insbesondere die, die sich im Naturmuseum Südtirol (BZ) befindet, weist eine Dominanz der Koniferen über Samenfarne, Cycadeen, Farne und Schachtelhalmen auf. Eine derartige Zusammensetzung kann auf verschiedenen Faktoren beruhen: (i) Klimatische (arides Klima auf dem Festland), (ii) edaphische (unreife Böden) oder auch (iii) taphonomische (Selektion während des Transportes). Die quantitativen Analysen der Palynofloren der drei Fundorte Ritberg (Wengen), Seewald und Innerkohlbach (Prags) weisen auf ein generell warmes und feuchtes Klima hin. Aus diesem Grund scheint die Dominanz der Koniferen und Samenfarne eher auf die größere Resistenz dieser Pflanzen gegen Zerstörung während des Transports, als auf klimatische Auslese zurückzuführen zu sein.

Paläoklimatische Rekonstruktionen aus dem Ladin sowie die Analyse der Pflanzenfossilien weisen darauf hin, dass die Dolomiten im oberen Ladin von karbonatischen oder vulkanischen Inseln verschiedener Größe bedeckt waren, wo sich verschiedene Biotope gebildet hatten: das Küstengebiet und das Hinterland, das sich wiederum in feuchtere und trockener Zonen unterteilen lässt.

Riassunto

Recenti studi sistematici della flora ladinica delle Dolomiti, condotti su collezioni sia storiche che inedite di musei italiani e stranieri hanno portato a nuove segnalazioni e ad alcune revisioni sistematiche. La flora ladinica risulta essere composta dai seguenti taxa: *Annalepis zeilleri* (Lycophyta), *Equisetites arenaceus* (Sphenophyta), *Cladophlebis leuthardtii*, *C. ruetimeyeri*, *Neuropteridium elegans*, *Scolopendrites* sp., *Gordonopteris lorigae* (Pteridophyta), *Ptilozamites heeri* (Pteridospermae), *Bjuvia dolomitica*, *Dioonitocarpidium moroderi*, *Pterophyllum jaegeri*, ?*Pterophyllum* sp., *Sphenozamites wengensis*, *Sphenozamites* cf. *bronnii*, *Taeniopteris* sp. (Cycadophyta), *Voltzia dolomitica*, *V. ladinica*, *V. pragsensis*, *V. zoldana*, *Voltzia* sp., *Pelourdea vogesiaca* ed *Elatocladus* sp. (Coniferophyta).

La flora, in particolare quella depositata nel Museo di Scienze Naturali dell'Alto Adige (BZ), presenta una generale dominanza delle conifere e pteridosperme, sulle cicadee, felci e sfenofite. Una simile composizione può essere imputabile a vari fattori: climatici (aridità delle terre emerse), edafici (suoli immaturi) e tafonomici (selezione tassonomica causata da un trasporto prolungato). Le analisi quantitative della palinoflora, effettuate nei tre affioramenti di Ritberg (La Valle), Seewald ed Innerkohlbach (Braies), indicano un clima complessivamente caldo umido. Pertanto, la dominanza delle conifere e pteridosperme sembra essere dovuta ad una maggiore resistenza di queste piante ai processi putrefattivi, che avvengono durante il trasporto, piuttosto che a cause climatiche.

Sulla base delle ricostruzioni paleogeografiche del Ladinico superiore e sui resti macrofloristici determinati, le Dolomiti presentavano una serie di piccole piattaforme carbonatiche emerse e isole vulcaniche, sulle quali si dovevano esistere biotopi differenti: aree costiere, e l'ambiente di entroterra, a sua volta suddivisa in zone più umide e più aride.

1 Introduction

The first Ladinian plant remains from the Dolomites have been figured by Wissmann and Münster (1841). Afterwards several authors mentioned and figured plant fossils from the "Buchensteiner Schichten" and "Wengener Schichten" of various areas in the Dolomites (Mojsisovics, 1879; Arthaber,1903; Ogilvie Gordon, 1927, 1934; Mutschlechner, 1932; P. Leonardi, 1953, 1968; Calligaris, 1983, 1986; Jung *et al.*, 1992) and from Sappada (G. Leonardi, 1964) (for more detailed information see also, Wachtler & van Konijnenburg – van Cittert, 2000a, b; Kustatscher, 1999, 2001, 2004). On this account, a high number of different plant remains have been described from the Dolomites at the end of the last century (Table 1).

However, an extended search and study of local and international plant collections with both already described and unpublished material from the Dolomites provided material for a first report and some taxonomic revisions of the material (Kustatscher, 2004; Kustatscher *et al.*, 2004).

Also several palynological studies have been applied during the last 25 years regarding successions of Ladinian age from the Dolomites (Cros & Doubinger, 1982; van der Eem, 1982; Blendinger, 1988; Roghi, 1995a, 1995b; Broglio Loriga *et al.*, 1999). However, most of the articles use palynological data only on a biostratigraphic point of view (Blendinger, 1988, Roghi, 1995a, 1995b; Broglio Loriga et al., 1999). Only in one of them (van der Eem, 1982) the palynomorphs are considered also as a source for paleoclimatic data.

2 Material and methods

The historical and often unpublished plant fossil collections are stored in several local and international museum and universities. In detail, the plant remains figured by Ogilvie Gordon (1927) are kept in the "Paläontologisches Museum" (Munich, D), Mutschlechner's (1932) material in the "Geologisch-Paläontologisches Institut" of the University of Innsbruck. The plant fossils discussed in Leonardi (1953) are treasured at the "Museum de Gherdëina" (Ortisei, I) and at the "Museo di Geologia e Paleontologia" of the University of Padova (I). Some specimens are kept at the "Museo di Paleontologia e Preistoria P. Leonardi" of the University of Ferrara (I) as also the fossil plants from Sappada figured by G. Leonardi (1964) and the plants figured in Leonardi (1968) and Bosellini (1989, 1996). The neuropteridian leaf fragment, figured by Zardini (1980) is exposed in the "Museo Paleontologico Rinaldo Zardini" (Cortina, I). The material discussed and figured by Calligari (1986) is stored in the Museo di Scienze Naturali (Trieste, I). Finally, the material discussed by Wachtler & van Konijnenburg – van Cittert (2000a, 2000b) and Kustatscher (1999, 2001, 2004 p.p.) is stored in the "Museo di Scienze Naturali Alto Adige / Naturmuseum Südtirol" (Bolzano / Bozen, I), in the Museum de Gherdëina (Ortisei) and in the "Museo Paleontologico Rinaldo Zardini" (Cortina). Unfortunately the material mentioned by Mojsisovics (1879) seems to have been lost. Additionally unpublished material is stored in the Museums discussed above and also at the Museo Ladino Fodom (Livinallongo del Col di Lana, I), the Naturhistorisches Museum, the Geologische Bundesanstalt (Vienna, I) and at the Geologisches Landesamt (Munich, D).

For paleoclimatic considerations palynomorph analyses have been carried out for 6 samples collected at two plant localities near Braies / Prags (Seewald and Innerkohlbach) and one near La Valle (Ritberg), belonging respectively to the upper part of the Fernazza Formation (Ritberg and Seewald) and to the base of the Wengen / La Valle Formation (Innerkohlbach) (see Fig. 1).

The samples have been crushed into small fragments and treated with the standard palynological techniques, including HCl (37%), HF (40%) and saturated $ZnCl_2$ solution (D ≈ 2,3 g/ml). Afterwards, the slides have been mounted in Canadian balsam.

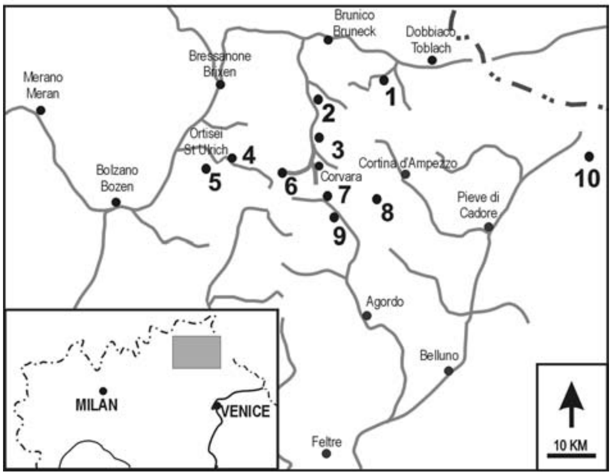

Fig. 1: Geographic distribution of the studied sections and fossil plant localities cited in the article. 1. Prags / Braies, Seewald, Innerkohlbach; 2. Gadertal / Val Badia, Wengen / La Valle, Ritberg; 3 St. Leonhard in Abtei / S. Leonardo in Badia, St. Kassian/ San Cassiano, 4. Grödental / Val Gardena; 5. Pufels / Bulla, Puflatsch / Bullaccia, Schgaguler Alm / Malga Scagul, Seiser Alm / Alpe di Siusi; 6. Grödner Joch / Passo Gardena, Corvara; 7. Monte Sief, Arabba; 8. Forcella Giau, Corvo Alto, Mondeval; 8. Laste (Livinallongo); 9. Cercenà, Spiz Agnelessa; 10. Sappada.

For the quantitative analyses at least 300 palynomorphs have been counted for each sample; the material has been divided into the main groups as pollen, spores, fungal remains, algal cysts, acritarchs and foraminiferous lignins. For the quantitative data the palaeoclimate methods proposed by Visscher & van der Zwan (1981) and Abbink (1998) have been applied. The frequencies of each group has been plotted with the aid of a specialised program, named Graph4win.

All the material (macrofossil and palynological) from the plant localities of Ritberg, Seewald and Innerkohlbach is stored at the Museo di Scienze Naturali dell'Alto Adige / Naturmuseum Südtirol (Bolzano / Bozen).

3 Macrofloral composition

The Ladinian flora from the Dolomites is composed of the following taxa. The synonymy includes only all references from the Ladinian of the Dolomites, not from other areas. The localities from which material has been recovered, are indicated as well.

Division Lycophyta
Order Isoetales
***Annalepis zeilleri* Fliche, 1910**

2004 *Annalepis zeilleri* Fliche – Kustatscher, p. 157, pl. 10, fig. 1.
2004 *Annalepis zeilleri* Fliche – Kustatscher *et al*., p. 58, pl. 1, fig. 1.
Localities: Wengen / La Valle.

Division Sphenophyta
Order Equisetales
Family Equisetaceae
***Equisetites arenaceus* (Jaeger, 1827) Schenk, 1864**

1999 *Equisetites arenaceus* - Avanzini & Wachtler, p. 118.
2000a *Equisetites arenaceus* (Jaeger) Schenk - Wachtler & van Konijnenburg - van Cittert, p. 107, pl. 1, fig. 1, 2.
2000b *Equisetites arenaceus* (Jaeger) Schenk - Wachtler & van Konijnenburg - van Cittert, p. 116, pl. 1, fig. 1, 2.
2004 *Equisetites arenaceus* (Jaeger) Schenk – Kustatscher, p. 158, pl. 10, fig. 2.
Localities: Wengen / La Valle, Sappada.

cf. *Equisetites*

1953 *Equisetites* vel *Calamites*? – Leonardi, pl. 4, figs. 4–5.
1964 impronta riferibile probabilmente ad Equisetale - Leonardi, pl. 5, fig. 10.
1964 frammento di fusto di Equisetale, forse *Neocalamites* sp. - Leonardi, pl. 5, fig. 11.
2004 cf. *Equisetites* – Kustatscher, p. 159, pl. 10, fig. 3.
Localities: Pufels / Bulla, Wengen / La Valle, Seiser Alm / Alpe di Siusi, Arabba, Cercenà, Sappada.

Division Pteridophyta
Order Filicales
Family Osmundaceae or indet.
***Cladophlebis leuthardtii* Leonardi, 1953**

1841 Fahrenwedel – Wissmann & Münster, p. 22, pl. 16, fig. 10.
1953 *Cladophlebis leuthardti* Leonardi, p. 11, pl. 2, figs. 1-5.
1953 *Cladophlebis rütimeyeri* Heer n.var. *heeri* – Leonardi, p. 11, pl. 1, fig. 1.
1964 *Cladophlebis* sp. - Leonardi, p. 201 pl. 5, fig. 7.
1968 *Cladophlebis* cfr. *denticulata* Brongniart – Leonardi p. 179, pl. 28, fig. 7.
1986 *Cladophlebis leuthardti* – Calligaris, p. 9, fig. B29.
1993 *Cladophlebis leuthardti* – Pozzi, p. 82, fig. 103.
1998 cf. *Pecopteris reticulata* (Leuthardt) - Stingl & Wachtler, p. 82.
1999 ?*Anomopteris mougeotii* Brongniart, 1828 - Kustatscher, p. 43, pl. 1, fig. B; pl. 2, fig. A.
2000a *Cladophlebis leuthardtii* Leonardi - Wachtler & van Konijnenburg – van Cittert, p. 109, pl. 1, fig. 3.
2000b *Cladophlebis leuthardtii* Leonardi - Wachtler & van Konijnenburg - van Cittert, p. 117-8, pl. 1, fig. 3.
2004 *Cladophlebis leuthardtii* Leonardi – Kustatscher, p. 160, pl. 10, fig. 5; pl. 11, fig. 1.
Localities: Prags / Braies, Wengen / La Valle, Seiser Alm / Alpe di Siusi, Pufels / Bulla, Grödner Joch / Passo Gardena, Corvo Alto, Corvara, Monte Sief, Laste (Livinallongo), Cercenà, Sappada.

***Cladophlebis ruetimeyeri* (Heer, 1877) Leonardi, 1953**

1953 *Cladophlebis rütimeyeri* Heer - Leonardi, p. 10, pl. 1, fig. 15, pl. 3 figs. 6.
1953 *Cladophlebis* sp. - Leonardi, pl. 1 figs. 3-4.
1994 Pecopteris – Costamoling & Costamoling, p. 47, fig. 19.
2004 *Cladophlebis ruetimeyeri* (Heer) Leonardi – Kustatscher, p. 161, pl. 11, fig. 2.
Localities: Seiser Alm / Alpe di Siusi, Col Alto, Cercenà.

***Neuropteridium elegans* (Brongniart, 1828) Schimper, 1869**

1993 *Cladophlebis* sp. – Pozzi, p. 85, fig. 107.
1998 *Neuropteridium* sp. - Stingl & Wachtler, p. 82.
1999 *Neuropteridium grandifolium* (Schimper et Mougeot) Schimper - Kustatscher, p. 44, pl. 2, fig. B.

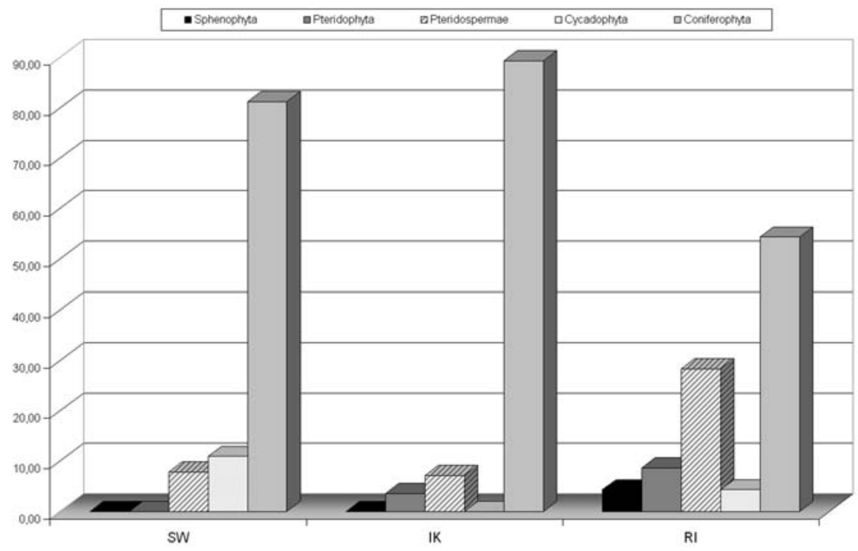

Fig. 2: Relative abundance of the main plant groups present in the three main macrofloral localities (Seewald, Innerkohlbach, Ritberg).

2000a *Neuropteridium grandifolium* (Schimper et Mougeot) Schimper - Wachtler & van Konijnenburg - van Cittert, p. 108, pl. 2, fig. 1.
2000b *Neuropteridium grandifolium* (Schimper et Mougeot) Schimper - Wachtler & van Konijnenburg - van Cittert, p. 117, pl. 2, fig. 1.
2004 *Neuropteridium elegans* (Brongniart) Schimper – Kustatscher, p. 161, pl. 11, fig. 3.
2004 *Neuropteridium elegans* (Brongniart) Schimper – Kustatscher *et al*., p. 59, pl. 1, fig. 2.
Localities: Forcella Giau.

***Scolopendrites* sp.**

2004 *Scolopendrites* sp. – Kustatscher, p. 162, pl. 11, fig. 4.
2004 *Scolopendrites* sp. – Kustatscher *et al*., p. 60, pl. 1, fig. 3.
Localities: St. Kassian / San Cassiano.

***Gordonopteris lorigae* van Konijnenburg – van Cittert *et al.* (name in submitted manuscript)**

1953 felce indeterminata - Leonardi, p.13, pl. 1, figs. 9.
1953 *Pecopteris* cf. (*Lonchopteris*) *reticulata* Leuthardt - Leonardi, p. 10, pl. 1, fig. 10.
1953 cf. *Pecopteris sulzensis* Schimper - Leonardi, p. 10, pl. 1, fig. 14.
?1986 *Pecopteris* sp. - Calligaris, p. 9, fig. A48.
1998 *Anomopteris mougeotii* - Stingl & Wachtler, p. 81.
1999 *Anomopteris mougeotii* – Avanzini & Wachtler, p. 117.
2000a *Anomopteris mougeotii* Brongniart - Wachtler & van Konijnenburg - van Cittert, p. 108, pl. 1, figs. 4-5.
2000b *Anomopteris mougeotii* Brongniart - Wachtler & van Konijnenburg - van Cittert, p. 116, pl. 1, figs. 4-5.
2001 *Anomopteris mougeotii* - Kustatscher, p. 3.
2004 ?Filicales indet. – Kustatscher, p. 162-3, pl. 10, fig. 4.
2004 Fern *incertae sedis* – Kustatscher *et al*., p. 60-1, pl. 1, fig. 4.
Localities: Wengen / La Valle, Mondeval, Corvo Alto, Cercenà, Sappada.

Division Pteridospermatophyta
Order indet.
***Ptilozamites heeri* Nathorst, 1878**

1927 *Pterophyllum brevipenne* Kurr - Ogilvie-Gordon, pl. 8, fig. 1.
1980 cfr. *Pterophyllum venetum* - Zardini, pl.1, fig. 8.

1985 *Cladophlebis* cf. *denticulata* Brongniart - Moroder, p. 27, fig. 21.
1993 *Cladophlebis* cfr. *denticulata* – Pozzi, p. 83, fig. 105.
1999 *Ptilozamites heeri* - Avanzini & Wachtler, p. 118.
2000a *Ptilozamites heeri* Nathorst - Wachtler & van Konijnenburg - van Cittert, p. 108, pl. 2, figs. 2-9.
2000b *Ptilozamites heeri* Nathorst - Wachtler & van Konijnenburg - van Cittert, p. 118, pl. 2, figs. 2-9.
2004 *Ptilozamites heeri* Nathorst – Kustatscher, p. 163, pl. 11, fig. 5; pl. 12, fig. 1.
Localities: Prags / Braies, Wengen / La Valle, Gadertal / Val Badia, Grödental / Val Gardena, Corvo Alto.

Division Cycadophyta
Order Cycadales
***Bjuvia* Florin, 1933**
***Bjuvia dolomitica* Wachtler et van Konijnenburg - van Cittert, 2000**

1927 *Zamites* sp. - Ogilvie-Gordon, p. 68, pl. 8, fig. 4.
1953 *Pterophyllum* sp. - Leonardi, p. 13, pl. 3, fig. 2.
1999 *Bjuvia dolomitica* Wachtler et van Konijnenburg - van Cittert (in stampa) - Kustatscher, p. 45, pl. 1, fig. C; p. 49, pl. 4, fig. A.
1999 *Bjuvia dolomitica* - Avanzini & Wachtler, p. 113.
2000a *Bjuvia dolomitica* Wachtler et van Konijnenburg - van Cittert, p. 110-111, pl. 4, fig. 1-3; pl. 5, fig. 1-5.
2000b *Bjuvia dolomitica* Wachtler et van Konijnenburg - van Cittert, p. 120-1, pl. 4, fig. 1-3; pl. 5, fig. 1-5.
2004 *Bjuvia dolomitica* Wachtler et van Konijnenburg - van Cittert – Kustatscher, p. 165, pl. 12, fig. 3.
Localities: Wengen / La Valle, Grödental / Val Gardena, Schgaguler Alm / Malga Scagul, Mondeval.

cf. *Bjuvia*

1927 "*Zamites* sp." - Ogilvie-Gordon, p. 68, pl. 8, fig. 4.
1927 *Nilssonia* sp. - Ogilvie-Gordon, p. 68, pl. 8, fig. 6.
2004 cf. *Bjuvia* – Kustatscher, p. 165.
Localities: Schgaguler Alm / Malga Scagul, Grödner Joch / Passo Gardena, Corvara, Sappada.

***Sphenozamites wengensis* Wachtler et van Konijnenburg - van Cittert, 2000**

1999 *Sphenozamites* - Avanzini & Wachtler, p. 118.
2000a *Sphenozamites wengensis* Wachtler et van Konijnenburg - van Cittert, p. 109, pl. 3, figs. 1-2.
2000b *Sphenozamites wengensis* Wachtler et van Konijnenburg - van Cittert - Wachtler & van Konijnenburg - van Cittert, p. 119, pl. 3, figs. 1-2.
2004 *Sphenozamites wengensis* Wachtler et van Konijnenburg - van Cittert – Kustatscher, p. 166, pl. 12, fig. 4.
Localities: Prags / Braies, Wengen / La Valle.

***Sphenozamites* sp. cf. *S. bronnii* (Schenk) Passoni & van Konijnenburg - van Cittert, 2003**

2004 *Sphenozamites* cf. *bronnii* (Schenk) Passoni & van Konijnenburg - van Cittert – Kustatscher, p. 166, pl. 13, fig. 2.
2004 *Sphenozamites* sp. cf. S. *bronnii* (Schenk) Passoni & van Konijnenburg - van Cittert – Kustatscher *et al.*, p. 62, pl. 2, fig. 2-6.
Localities: St. Leonhard in Abtei / S. Leonardo in Badia, Laste (Livinallongo).

***Dioonitocarpidium moroderi* (Leonardi) Kustatscher *et al.*, 2004**

1953 *Cycadeoidea* (?) *moroderi* Leonardi - Leonardi, p. 14, pl. 2, figs. 6-8.
1968 *Cycadeoidea* (?) *moroderi* Leonardi - Leonardi, p. 176, pl. 28, fig. 5.
1999 *Dioonitocarpidium* sp. - Kustatscher, p. 49, 58, pl. 3, fig. A-B.
2000a *Dioonitocarpidium* sp. - Wachtler & van Konijnenburg - van Cittert, p. 112, pl. 6, fig. 2.
2000b *Dioonitocarpidium* sp. - Wachtler & van Konijnenburg - van Cittert, p. 123, pl. 6, fig. 2.

2004 *Dioonitocarpidium moroderi* (Leonardi) nov comb. – Kustatscher, p. 168, pl. 13, fig. 5.
2004 *Dioonitocarpidium moroderi* (Leonardi) nov comb. – Kustatscher *et al.*, p. 61-2, pl. 2, fig. 1.
Localities: Schgaguler Alm / Malga Scagul.

Order Bennettitales
***Pterophyllum jaegeri* Brongniart, 1828**

1953 *Pterophyllum jaegeri* Brongniart - Leonardi, p. 13, pl. 2, fig. 12.
1968 *Pterophyllum jaegeri* Brongniart - Leonardi, p. 176, pl. 28, fig. 4.
1989 *Pterophyllum* – Bosellini, p. 19, fig. 2.1.
1999 *Pterophyllum jaegeri* - Kustatscher, p. 57, pl. 4, fig. B.
1999 *Pterophylliium jaegeri* - Avanzini & Wachtler, p. 118.
2000a *Pterophyllum jaegeri* Brongniart - Wachtler & van Konijnenburg - van Cittert, p. 112, pl. 3, figs. 3-4.
2000b *Pterophyllum jaegeri* Brongniart - Wachtler & van Konijnenburg - van Cittert, p. 122-3, pl. 3, figs. 3-4.
2001 *Pterophyllum jaegeri* - Kustatscher, p. 6.
2004 *Pterophyllum jaegeri* Brongniart – Kustatscher, p. 168, pl. 12, fig. 2.
2004 *Pterophyllum* sp. – Kustatscher, p. 169.
Localities: Prags / Braies, Wengen / La Valle, St. Kassian / San Cassiano, Corvara, Cercenà.

***?Pterophyllum* sp.**

2004 *?Pterophyllum* sp. – Kustatscher, p. 170, pl. 13, fig. 3.
Localities: Laste (Livinallongo).

Order indet.
***Taeniopteris* sp.**

1927 *Taeniopteris angustifolia* Schenk - Ogilvie-Gordon, p.67, pl. 8, fig. 2.
1953 cfr. *Taeniopteris* sp. - Leonardi, p. 12, pl. I, fig. 18.
1964 *Taeniopteris* (*Nilssonia* ?) - Leonardi, pl. 4, fig. 3.
1999 *Taeniopteris* sp. - Kustatscher, p. 57, pl. 2, fig. C; pl. 3, fig. C.
2000a *Taeniopteris* sp. - Wachtler & van Konijnenburg - van Cittert, p. 112, pl. 6, fig. 1.
2000b *Taeniopteris* sp. - Wachtler & van Konijnenburg - van Cittert, p. 122, pl. 6, fig. 1.
2004 *Taeniopteris* sp. – Kustatscher, p. 171, pl. 13, fig. 1.
Localities: Prags / Braies, Grödental / Val Gardena, Gadertal / Val Badia, Corvara, Cercená, Sappada.

Division Coniferophyta
Order Coniferales
***Elatocladus* sp.**

1968 *Pterophyllum* sp. - Leonardi, p. 176, pl. 28, fig. 2.
1985 *Pterophyllum* - Moroder, p. 31, fig. 26.
1989 *Pterophyllum* sp. - Bosellini, p. 89, fig. 12.9.
1993 *Pterophyllum* sp. – Pozzi, p. 85, fig. 108.
1996 *Pterophyllum* - Bosellini, p. 121, fig. 13.8.
1999 *Elatocladus* sp. - Avanzini & Wachtler, p. 119.
1999 *Elatocladus* sp. - Kustatscher, p. 51, pl. 5, fig. A.
2000a *Elatocladus* sp. - Wachtler & van Konijnenburg - van Cittert, p. 113, pl. 6, fig. 3.
2000b *Elatocladus* sp. - Wachtler & van Konijnenburg - van Cittert, p. 121, pl. 6, fig. 3.
2004 *Elatocladus* sp. – Kustatscher, p. 172, pl. 14, fig. 2.
Localities: Puflatsch / Bullaccia.

***Pelourdea vogesiaca* (Schimper et Mougeot, 1844) Seward 1917**

1953 *Yuccites vogesiacus* Schimper et Mougeot - Leonardi, p.15, pl. 2, fig. 9, 11; pl. 3, figs. 3-4.
1986 *Yuccites* sp. - Calligaris, p. 15, figs. B21, 42.
1999 *Yuccites vogesiacus* - Avanzini & Wachtler, p. 119.
2000a *Yuccites vogesiacus* Schimper et Mougeot - Wachtler & van Konijnenburg – van Cittert, p. 113, pl. 6, figs. 4, 5.
2000b *Yuccites vogesiacus* Schimper et Mougeot - Wachtler & van Konijnenburg – van Cittert, p. 121-2, pl. 6, figs. 4, 5.
2004 *Pelourdea vogesiaca* (Schimper et Mougeot) Seward – Kustatscher, p. 172-4, pl. 13, fig. 4.
2004 *Pelourdea vogesiaca* (Schimper et Mougeot) Seward – Kustatscher *et al.*, p. 63, pl. 1, fig. 5.

Localities: Prags / Braies, Wengen / La Valle, Schgaguler Alm / Malga Scagul.

?*Pelourdea* sp.

1953 *Yuccites* sp. – Leonardi, pl. 3, fig. 5.
2004 ?*Pelourdea* sp. – Kustatscher, p. 174.
Localities: Seiser Alm / Alpe di Siusi, Cercenà.

Order Voltziales
Family Voltziaceae
***Voltzia dolomitica* Wachtler et van Konijnenburg - van Cittert, 2000**

1927 *Voltzia recubariensis* Schenk - Ogilvie-Gordon, p. 67, pl. 8, fig. 7.
1932 *Voltzia* sp. - Mutschlechner, p. 31.
1953 *Pagiophyllum* (?) *massalongi* Zigno - Leonardi, p. 18, pl. 3, figs. 8, 10; pl. 4, fig. 2.
1968 *Brachyphyllum* sp. - Leonardi, p. 176, pl. 28, fig. 1.
1986 *Pagiophyllum* cf. *massalongi* Zigno - Calligaris, p. 16, figs. A64, B6, B7, B11, B19, B27, B31.
1995 *Voltzia recubariensis* Schenk - Jung *et al.*, p. 171, fig. 8.3.
1999 *Voltzia dolomitica* - Avanzini & Wachtler, p. 117, 119.
2000a *Voltzia dolomitica* Wachtler et van Konijnenburg - van Cittert 2000, p. 113-14, pl. 7, fig. 1-4; pl. 5, fig.1-6.
2000b *Voltzia dolomitica* Wachtler et van Konijnenburg - van Cittert - Wachtler & van Konijnenburg - van Cittert, p. 123-4, pl. 7, fig. 1-4; pl. 5, fig.1-6.
2001 *Voltzia dolomitica* - Kustatscher, p. 4.
2004 *Voltzia dolomitica* Wachtler et van Konijnenburg - van Cittert – Kustatscher, p. 175, pl. 14, fig. 1.
Localities: Prags / Braies, Wengen / La Valle, Schgaguler Alm / Malga Scagul, Puflatsch / Bullaccia, Sappada.

***Voltzia ladinica* Wachtler et van Konijnenburg - van Cittert, 2000**

1999 *Voltzia ladinica* Wachtler et van Konijnenburg - van Cittert (in stampa)- Kustatscher, p. 52, pl. 4, fig. C.
2000a *Voltzia ladinica* Wachtler et van Konijnenburg - van Cittert, p. 115, pl. 10, figs. 1-5; pl. 11, figs. 1-4
2000b *Voltzia ladinica* Wachtler et van Konijnenburg - van Cittert - Wachtler & van Konijnenburg - van Cittert, p. 125-6, pl. 10, figs. 1-5; pl. 11, figs. 1-4
2004 *Voltzia ladinica* Wachtler et van Konijnenburg - van Cittert – Kustatscher, p. 176-7, pl. 14, fig. 3.
Localities: Prags / Braies, Wengen / La Valle, Grödental / Val Gardena.

***Voltzia pragsensis* Wachtler et van Konijnenburg - van Cittert, 2000**

1953 *Pagiophyllum* cfr. *foetterlei* Stur - Leonardi, p.19, pl. 4, fig. 6, 7, 9.
1986 *Pagiophyllum* cf. *foetterlei* Stur - Calligaris, p. 17, figs. A58.
1998 *Voltzia* sp. - Stingl & Wachtler, p. 79.
1999 *Voltzia* - Avanzini & Wachtler, p. 119.
2000a *Voltzia pragsensis* Wachtler et van Konijnenburg - van Cittert, p. 115, pl. 9, fig. 1-2.
2000b *Voltzia pragsensis* Wachtler et van Konijnenburg - van Cittert - Wachtler & van Konijnenburg - van Cittert, p. 125, pl. 9, fig. 1-2.
2004 *Voltzia pragsensis* Wachtler et van Konijnenburg - van Cittert – Kustatscher, p. 177-8, pl. 14, fig. 4.
Localities: Prags / Braies, Wengen / La Valle, Schgaguler Alm / Malga Scagul.

***Voltzia zoldana* Leonardi 1953**

1953 *Voltzia zoldana* - Leonardi, p. 19, pl. 4, fig. 1
1968 *Voltzia zoldana* Leonardi - Leonardi, p. 176, pl. 28, fig. 3.
2004 *Voltzia zoldana* Leonardi – Kustatscher, p. 178, pl. 14, fig. 5.
Localities: Spiz Agnelessa.

***Voltzia* sp.**

1927 *Voltzia* sp. - Ogilvie Gordon, p. 69, pl. 8, fig. 8.
1953 *Voltzia* sp. - Leonardi, pl. 4, figs. 3, 8.

1953 *Pagiophyllum* (?) *massalongi* Zigno - Leonardi, p. 18, pl. 4, fig. 2.
1964 Ramoscello di *Brachyphyllum* o *Pagiophyllum* sp. - Leonardi, pl. 4, fig. 4.
1994 *Ullmannia Broni* – Costamoling & Costamoling, p. 47, fig. 20.
2004 *Voltzia* sp. – Kustatscher, p. 178.

Localities: Prags / Braies, Wengen / La Valle, Seiser Alm / Alpe di Siusi, Pufels / Bulla, Cercenà, Sappada.

4 Palaeoclimatic considerations

Macroflora

Most of the studied plant fossil collections are composed of a few specimens only, collected in various and often not well-defined localities. However, the main composition shows a dominance of conifers, whereas cycads, pteridosperms, ferns and horsetails occur only occasionally. Only one collection (in Bolzano) is composed of a higher number of specimens (more than 150 specimens). Those plant remains have been collected at two plant localities near Braies / Prags (Seewald and Innerkohlbach) and one near La Valle (Ritberg), belonging respectively to the upper part of the Fernazza Formation (Ritberg and Seewald) and to the base of the Wengen / La Valle Formation (Innerkohlbach).

The pollen samples collected at those fossil-bearing horizons, attribute them to the *secatus* – *vigens* phase *sensu* Van der Eem (1982), or to the *pseudoalatus-baculatus* phase *sensu* Roghi (1995a, b). Moreover, the plant deposits of Ritberg and Innerkohlbach (Fig. 1) belong to the *Conbaculatisporites mesozoicus* zone *sensu* Roghi (1995), referred to the upper part of *Neumayri* Subzone and to the base of *Regoledanus* Subzone (Protrachyceras Zone, uppermost Longobardian). The ammonoids (*Lecanites glaucus*, *Protrachyceras* cf. *ladinum*, cf. *Protrachyceras*, "*Eoprotrachyceras*" *neumayri*, cf. *Joannites*, cf. *Mepinoceras* and *Megaphyllites* sp., det. P. Mietto) collocate the localities to the *Neumayri* Subzone of the *Protrachyceras* Zone (*sensu* Mietto & Manfrin, 1995). On the other hand, at Seewald no palynomorph zonal marker of Roghi's scale has been found. Also the collected ammonoid (*Macleanoceras* sp., det. P. Mietto) permits to refer the locality only to the *Protrachyceras* Zone (Longobardian). However, the lithostratigraphic attribution of the deposit to the Fernazza Formation, narrows its age down to the upper Longobardian (De Zanche *et al.*, 1993) (for more information see also Kustatscher, 2004).

The macrofossil collections, discussed already partly in Kustatscher (1999, 2001, 2004), Wachtler & van Konijnenburg – van Cittert (2002a, 2002b) and Kustatscher *et al.* (2004), permit us to take a closer look at the quantitative composition of the Upper Ladinian macroflora (Fig. 2). All three plant localities show a distinct dominance of the conifers (*Voltzia*, *Pelourdea*). Also the pteridosperms (*Ptilozamites*) are well represented in all three floras, whereas horsetails (*Equisetites*), ferns (*Cladophlebis*, Gordonopteris) and cycadophytes (*Pterophyllum*, *Sphenozamites* and *Taeniopteris*) are rare and occur often only in one or two of the plant deposits.

This composition may be due to various factors such as climate (aridity), edaphic (immature soils) and taphonomy (i.e. selection due to transport).

Conifers are generally referred to arid environments due to their reduced leaf-surface, the thickness of their cuticles and the protection of their stomata by papillae. On the base of these considerations, the composition of the Ladinian Flora from the Dolomites might be referred to an arid climate which the slightly imbricate pinnules of *Cladophlebis* might indicate as well.

On the other hand, the fossil material is preserved within basinal sediments, and therefore, has been subject to selection due to transport previously to its deposition. The high abundance of conifers compared with the other groups (Innerkohlbach and Seewald above 80%, Ritberg ca. 50%) could be referred to selection caused by transport, as only the more woody and resistant plants preserved after the biostratinomic processes. However, the floral composition cannot be explained exclusively by means of taphonomy. The thickness of the cuticles suggests also a certain degree of environmental stress, related to adverse palaeoenvironment. This could correspond to climatic or edaphic conditions. The latter would suggest immature soils and shallow water level. In this case the papillae on the stomata might protect the stomata from salted sprays. On the other hand, the presence of rare specimens of ferns (*Cladophlebis*, *Gordonopteris*) and horsetails (*Equisetites*), suggests the presence of restricted humid microenvironments in the terrestrial habitats as understorey and small ponds.

Microflora

The hypothesis of an arid climate during the upper Ladinian is also in conflict with palynological data available from literature. Van der Eem (1982) suggests a progressive increase in humidity during the Ladinian, opposed to the arid environmental conditions at the end of the Anisian. These environments are however considered to be local, due to the considerable amount of elements derived from xerophytic plant-communities often present as well (van der Eem, 1982, p. 72).

Additionally palynological data are known also from the plant deposits (Kustatscher, 2004); in the small outcrops of Seewald (SW) and Innerkohlbach (IK) one pollen sample each has been studied, while from the more extensive outcrop of Ritberg (RI) four samples have been analysed.

Observing the main groups (spores, pollen grains, algal cysts, acritarchs), Seewald is clearly dominated by pollen grains, Innerkohlbach by spores whereas in the Ritberg section an upwards increase of the pollen fraction is observed (Table 2). These quantitative palynomorph fluctuations could be interpreted both as climatic oscillations, and as variations in the distance between the coast and the marine sedimentary environment, caused by sea level changes.

Applying the proposal of Visscher & Van der Zwan (1981) for palaeoclimatic analysis, the palynomorphs have been divided into 15 groups (Table 3). Some of the groups such as A - monolete acavate spores, F – *Porcellispora* complex and J – *Samaropollenites* complex are absent. Taxa, such as *Vallasporites ignacii* and *Enzonalasporites vigens*, referred by Visscher & Van der Zwan (1981) and van der Eem (1982) to the vesicate pollen grains (M) are now attributed to the (proto)monosaccate pollen grains (N).

The pollen sample from Seewald (SW) is dominated by the *Triadispora* complex (L), trilete acavate laevigate or apiculate spores (B) and alete (proto)bisaccate pollen grains (I). Trilete laevigate or apiculate spores (B), on the other hand, dominate the Innerkohlbach (IK) sample. This would suggest a more arid climate during deposition of the sediments corresponding with the Seewald plant deposit, and a more humid climate when the Innerkohlbach flora has been deposited.

Trilete laevigate or apiculate spores (B) dominate also in the Ritberg outcrop. Furthermore, from the bottom to the top of this section, the B group, while still dominating, decreases in abundance. A concomitant increase of the *Ovalipollis* complex (H, especially in RI 3), the *Triadispora* complex (L) and alete (proto)bisaccate pollen grains (I) can be observed. This would suggest an increase of the aridity from the bottom to the top of the section.

Also Abbink' s palynomorph quantitative analysis (1998) has been applied to the plant fossil deposits (Table 5). Seewald shows a dominance of the Coastal SEG, whereas Upland, Lowland, River and Tidal SEGs are less abundant. At Innerkohlbach, on the other hand, the more hygrophytic SEGs, such as River and Lowland, dominate. However, as there is only one sample per outcrop, no extended considerations can be deduced.

More information can be obtained from the Ritberg section. This outcrop shows an upwards increase of the Coastal and Tidal SEGs, while the Lowland and Upland SEGs decrease. This trend can be interpreted as an increase of the distance between the coastal line and the area of plant deposition (a transgression event) and thus it seems to support that the palynomorph fluctuations may be mostly due to sea level changes.

Observing in detail the Lowland SEG, the most sensible one to climatic changes (Abbink 1998), almost only taxa considered to be "more humid" can be distinguished (Table 5). This suggests a prevailing humid climate during the late Ladinian.

The hypothesis of sea level changes seems to be confirmed also by the marine palynomorphs. Although acritarchs and algal cysts are only additional elements (less than 20%), the acritarchs, considered as elements of open marine environments, increase from the bottom to the top of the Ritberg section, while algal cysts decrease (Table 2).

The hypothesis of taphonomic selection interacting with the Ladinian macrofloral deposition is supported also by the comparison between the abundance of the main groups (divisions) on macrofloristic and microfloristic levels (Table 4). The conifers, represented by 50 to more than 80% in the macroflora, never exceed 45% in the microflora (max. 42,3 % at Seewald). Also pollen attributed to the pteridosperms (2,6-17,9%) and cycads (microflora 0-1,3%) are less abundant than the macrofloral remains of these groups (respectively 7,8-28,3% and 0-10,9%).

On the other hand, ferns are much more important in the microflora (20,9 – 50,8%) than in the macroflora (0-8,7%), becoming the most important sporomorph group. This may be due to the high fragility of the pinnate fern leaves, which are easily destroyed during transport. Considering on the other hand, that spores are generally underestimated in basinal sediments (Neves effect, Chaloner & Muir, 1968) this dominance is even more important.

Additionally, the lycophytes are quite abundant in the microflora with 3,3 to 17,2 %, while only one macrofloral species attributed to the lycophytes (*Annalepis zeilleri*) is known from the Ladinian of the Dolomites. Spores (especially *Uvaesporites*), however, are often preserved in tetrads probably due to environmental stress of the mother-plants (Looy *et al.*, 2001). In any case, this abundance suggests that the lycophytes were better represented in the Ladinian of the Dolomites than suggested by the macrofloral remains alone.

Very abundant is also the genus *Ovalipollis*, which botanical attribution is still unknown, as it has been never found *in situ*.

Observing the separate plant localities in detail (Table 4), Seewald is dominated by conifers (42,3%), followed closely by ferns (20,9%) and pteridosperms (17,9%). At Innerkohlbach, on the other hand, ferns (50,8%) dominate among the lycophytes (17,1%) and conifers (13,8%). At Ritberg, from bottom to top lycophytes and ferns decrease in number (respectively12,2 - 7,1% and 35,5 – 21,7%), whereas pteridosperms (5 – 13,2%) and conifers increase (19,7 – 31,%).

Concluding, it can be suggested that the plants grew in a general warm and humid local climate. The high abundance of conifers and pteridosperms and respectively low abundance of horsetails, ferns and lycophytes in the macroflora seem to be more due to local edaphic conditions and taphonomic selection than to climate.

5 Palaeoenvironmental reconstructions

During the late Ladinian, the Southern Alps were characterized by wide carbonate platforms bounded by more or less extended basins and were located north of an emerged land now buried under the Po Plain („Southern Mobile Belt" of Brusca *et al.* 1981).

Following the palaeogeographic reconstructions of the uppermost Ladinian known from the literature (Assereto *et al.,* 1977; Brusca *et al.,* 1981; Gianolla, 1993; Bosellini, 1996), Ritberg is situated in a basin surrounded to the west by the carbonate platforms of Putia / Peitler and Odle / Geißler and to the northeast by the carbonate platform which forms today the Piz da Peres. Southwards this basin was bounded by the carbonate platforms of Sassolungo / Langkofel, Sella, Tofane and Marmolada. Additionally the volcanic complex of Monzoni and Predazzo were exposed southwards as well (Fig. 3). Some of these carbonate platforms and the volcanic complex were subaerically exposed during the time of deposition of the Fernazza Formation and, therefore, subject to erosion (i.e. Gianolla, 1993). The plant remains could have been transported from the carbonate islands in the northeast or west, or together with the volcanoclastic turbidites from the south.

Seewald and Innerkohlbach, on the other hand, are positioned in a basinal environment west of the Tre Cime di Lavaredo / Drei Zinnen and east of the Piz da Peres platform. These platforms produced carbonate sediments, whereas the terrigenous material came from the south, from the volcanic complex of Predazzo/Monzoni and perhaps also from source areas more southwards than the Valsugana line.

Considering the palaeogeographic reconstructions known from the literature and the paleoclimate discussed also in this article, the Ladinian plants grew probably on more or less expanded carbonate or volcanic islands. On these islands various environments developed: the coastal belt and the so-called 'hinterland'. The latter can be distinguished in more humid and more arid areas (Fig. 4).

The coastal environment (Fig. 5) was occupied mainly by lycophytes (*Annalepis*) and pteridosperms with thick cuticles (*Ptilozamites*). The *Annalepis* scales were probably inserted on the top of some centimetres high and thick stems with robust roots (Grauvogel-Stamm & Lugardon, 2001), whereas *Ptilozamites* was likely a shrubby plant, although no reconstruction is so far known for this genus.

The hinterland, on the other hand, might have been composed of ferns (*Neuropteridium*, *Gordonopteris*, *Cladophlebis*), cycads (*Bjuvia*, *Spheno-*

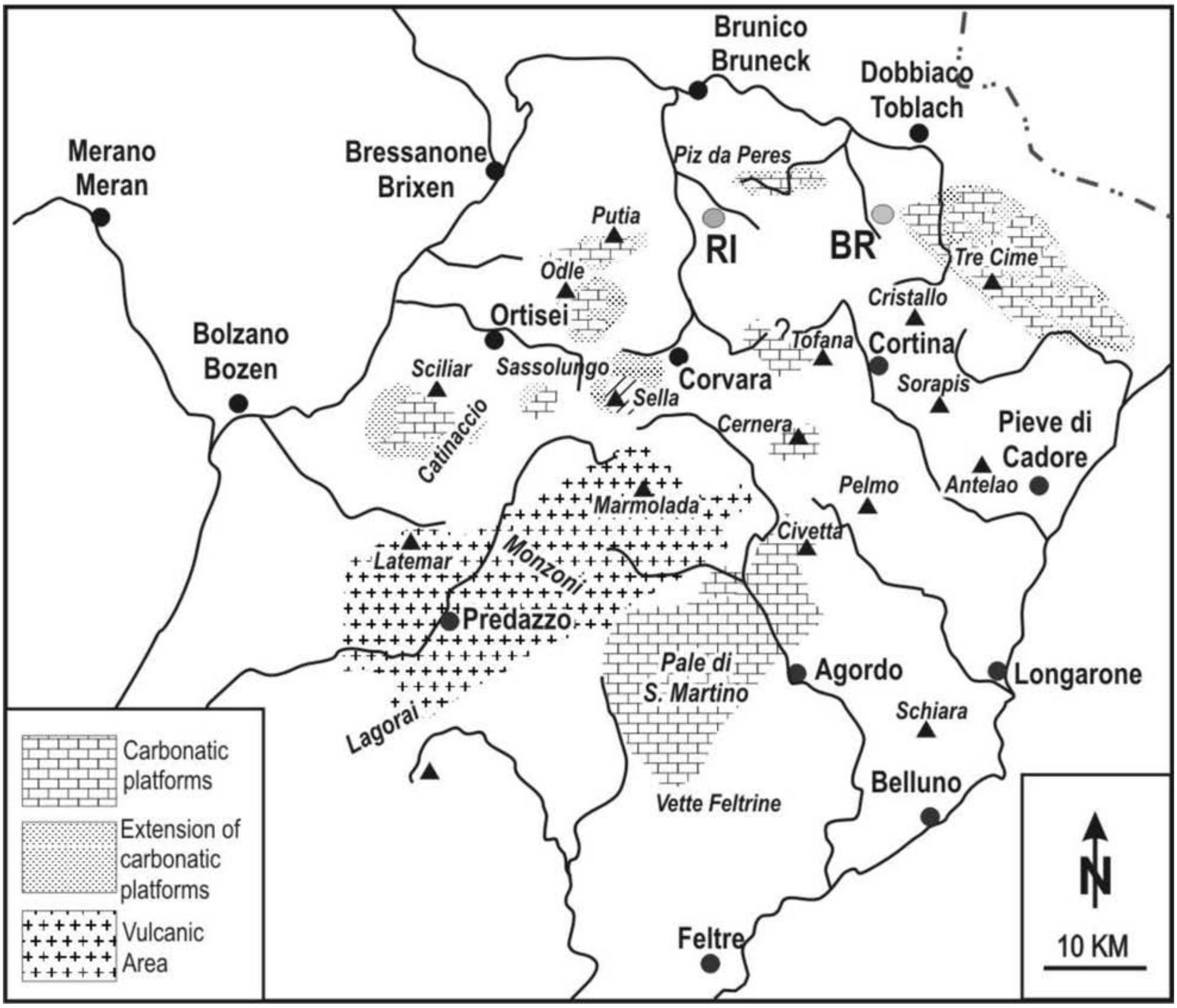

Fig. 3: Palaeogeographic reconstruction of the Dolomites during the late Ladinian (after Gianolla, 1993; Bosellini, 1996, mod.). RI- position of Ritberg, BR- position of the outcrops of Seewald and Innerkohlbach near Braies/Prags.

zamites), Bennettitales (*Pterophyllum*) and conifers (*Voltzia, Pelourdea*).

Bjuvia is probably an arborescent form as discussed in the literature (Florin, 1933; Taylor & Taylor, 1993), just as *Pterophyllum* (Mägdefrau, 1948; Kräusel & Schaarschmidt, 1966). Therefore, these two taxa might have formed the canopy (Fig. 6) of the more arid hinterland flora together with the arborescent *Voltzia*, which, following Gall & Grauvogel-Stamm (2000) could reach a height of several meters. The shaded and more humid micro-environment of the understorey might have been occupied by ferns of small to medium dimensions such as *Neuropteridium*, but also some herbaceous cycads such as *Sphenozamites* (Mägdefrau, 1948). Additionally, also some shrubby conifers such as *Pelourdea* might have grown in the understorey (Mägdefrau, 1948; Seward, 1917, 1959).

In the more humid local environments (Fig. 7), surrounding temporary ponds and swamps or along a small river, larger ferns (*Gordonopteris*) with up to 50 cm long leaves could have grown together with the above mentioned ferns of small to medium size (*Neuropteridium, Cladophlebis*). Shrubby cycads (*Sphenozamites*) and Bennettitales with higher stems might also have inhabited the more humid areas. Exclusively in this environments horsetails (*Equisetites*), with heights of up to 6-8 m, might

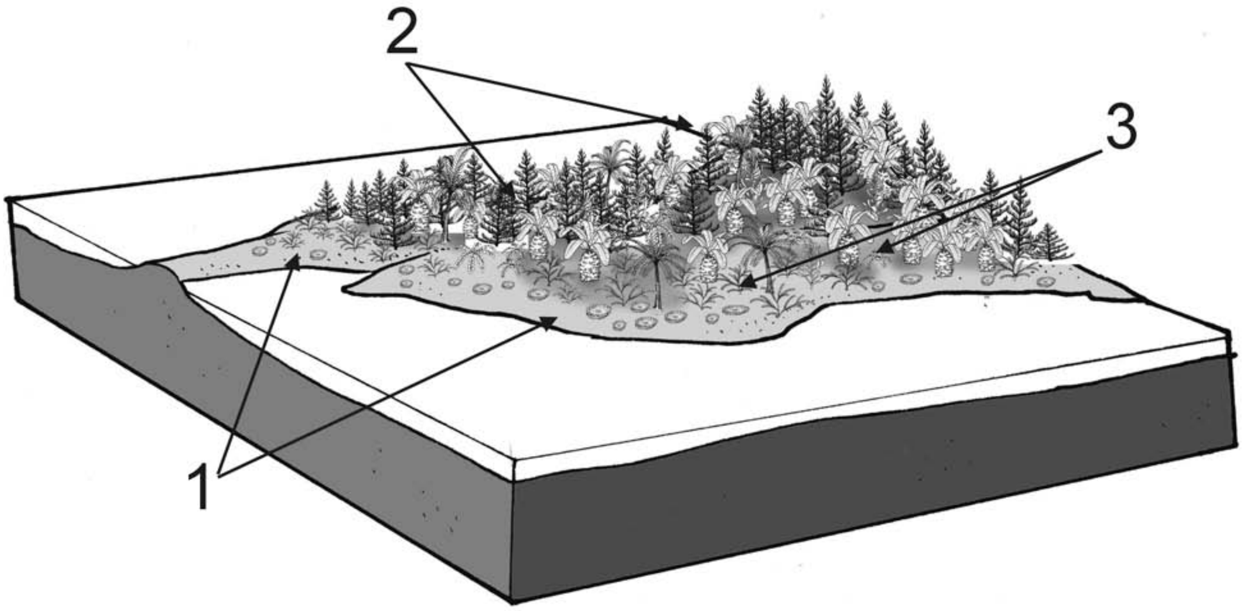

Fig. 4: Reconstruction of a hypothetical environment of the Ladinian plants from the Dolomites. 1 – coastal belt, 2 – 'hinterland', 3 – more humid environments.

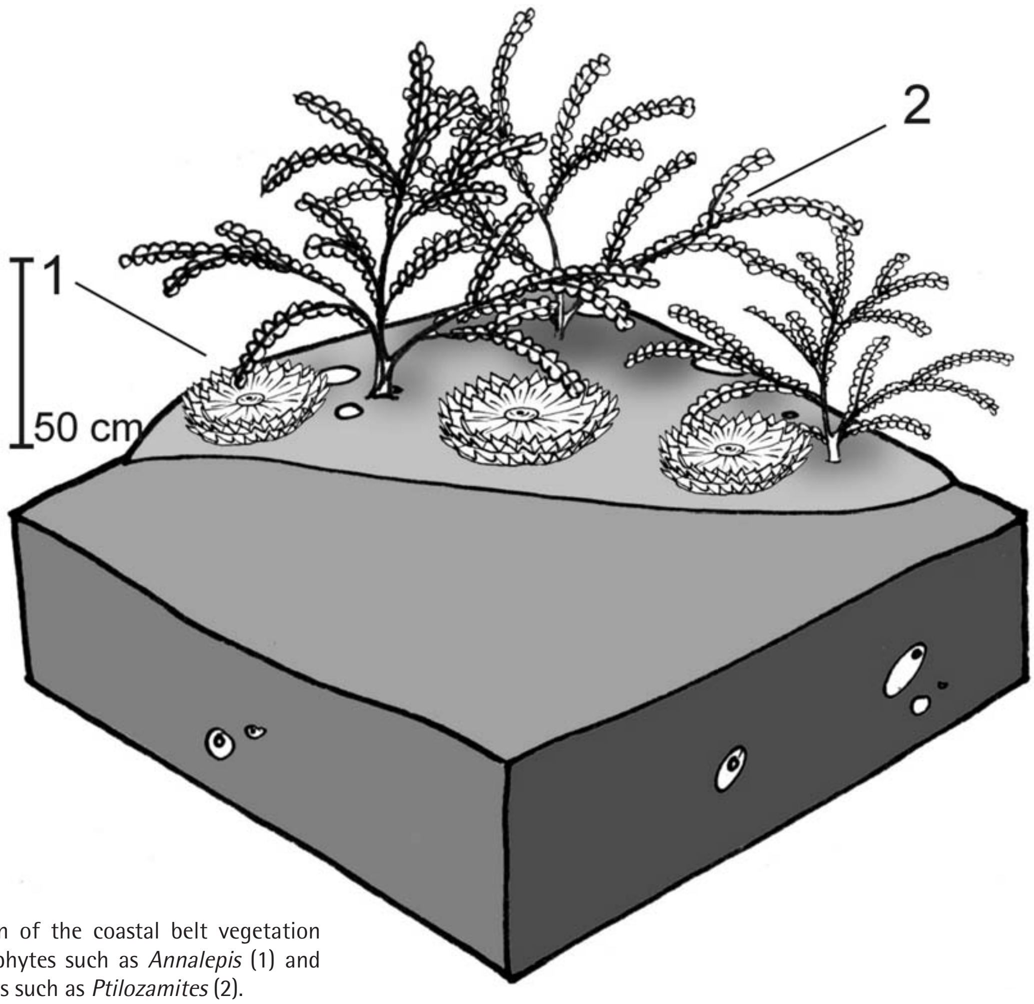

Fig. 5: Reconstruction of the coastal belt vegetation with halophytic lycophytes such as *Annalepis* (1) and shrubby pteridosperms such as *Ptilozamites* (2).

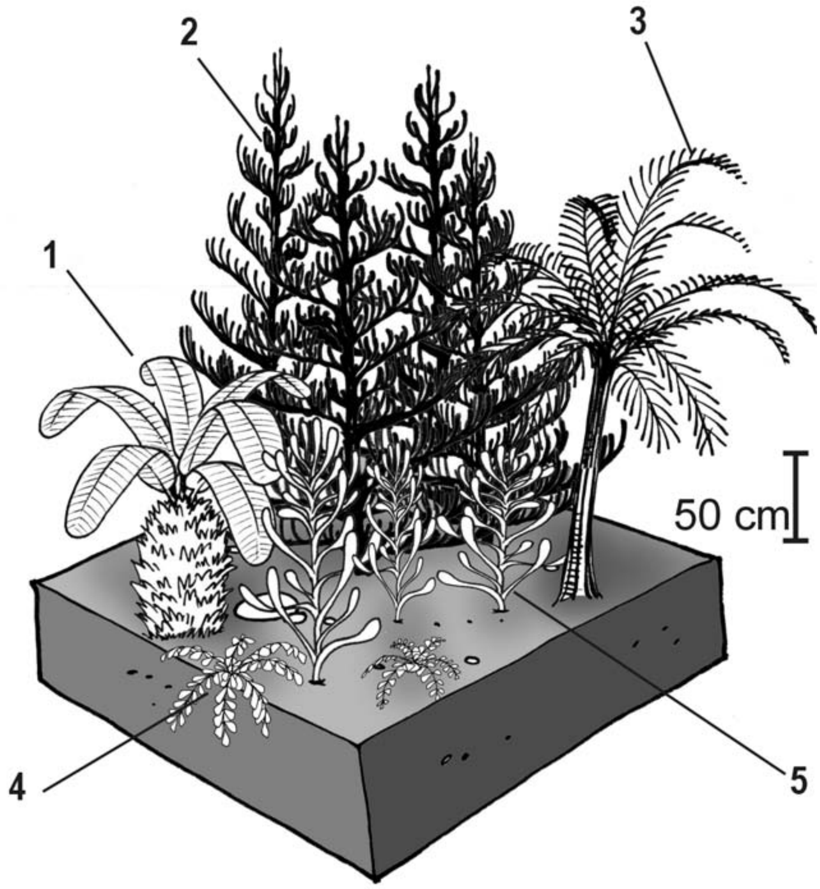

Fig. 6: Reconstruction of the more arid 'hinterland' vegetation with herbaceous (*Sphenozamites*, 1) and arboreous cycads (*Bjuvia*, 4), high stemmed Bennettitales (*Pterophyllum*, 3), shrubby (*Pelourdea*, 5) and arborescent conifers (*Voltzia*, 2).

have grown as well (Frentzen, 1933; Mägdefrau, 1948, 1953; Kelber & Hansch, 1995; Kelber, 1999; Gall & Grauvogel-Stamm, 2000).

6. Discussion

Quantitative variations of organic material (both plant fossils and palynomorphs) within an outcrop depend on various factors. For those observed between the three studied plant deposits two different hypotheses have been proposed; climatic oscillations of reduced time extension, or oscillations of the sea level and, therefore, of the relative distance between the coast line and the point of deposition.

Throughout the Ritberg section and between the Seewald and the Innerkohlbach sections, compositional variations have been observed (Tables 2-5). However, the outcrops of Seewald and Innerkohlbach, since they consist of one horizon only, do not permit to extrapolate any climatic considerations. It is possible that the increase of the spores and algal cysts and decrease of pollen and acritarchs at Innerkohlbach compared to Seewald is due to an increase of humidity, or an approach of the coastal line to the depositional area. The reduction of the acritarchs in favour of the algal cysts, however favours more the second hypothesis, variations of the sea level, as would a comparison with the sequence stratigraphy. The Seewald outcrop is positioned at the top of the Fernazza Formation, corresponding to the HST (Highstand Systems Tract) of the depositional sequence La3, composed of the basinal Zoppè Sandstone, the Acquatona and the Fernazza Formation and the Sciliar 3 platform (De Zanche et al., 1993; Gianolla, 1993). Innerkohlbach, on the other hand, belongs to the base of the La Valle / Wengen Formation, and is, therefore, corresponding to the LST (Lowstand Systems Tract) and TST (Transgressive Systems Tract) of the following depositional sequence (Car1, *sensu* De Zanche *et al.*, 1993; Gianolla, 1993), to which also the base of the S. Cassian Formation and the Cassian Dolomite 1 platform belong. The lowering of the sea level between these two depositional events could be, therefore, the principal factor of the observed quantitative variation between these two outcrops.

At the outcrop of Ritberg, on the other hand, the four samples indicate an increase of pollen grains throughout the section (Table 2), and also an increase of the Coastal SEG, corresponding to a decrease of the Lowland and River SEGs (Table 5). Also in this case the most accredited hypothesis is a transgression. This hypothesis is confirmed by the increase of the acritarchs, especially at Ritberg 4 (Table 2). These (para)autochtonous marine palynomorphs seem quite sensible to bathymetric and salinity variations, but not to climatic variations.

7. Conclusions

The study of historical and inedited material stored in various collections of Italian and international Museums and Institutions gives new insights into the composition of the Ladinian macroflora of the Dolomites.

The palaeoenvironmental reconstruction based on both macro- and microfloral data shows more or less expanded carbonate or volcanic islands divided into various environments: the coastal belt and the so-called 'hinterland'; the latter subdivided into more humid and more arid areas.

Additionally, the integrated quantitative analyses (macro- and microfloral) suggest that the dominance of the conifers results mostly from taphonomic selection. The flora probably grew under environmental stress due to salted spray, immature soils and shallow water level, but in a locally humid climate.

Quantitative palynological analysis suggests also that the variations in frequency between spores and pollen or algal cysts and acritarchs are probably closer related to sea level changes than to climatic changes. At present the limited extensions of the fossil horizons do not permit to exclude the possibility of climate changes.

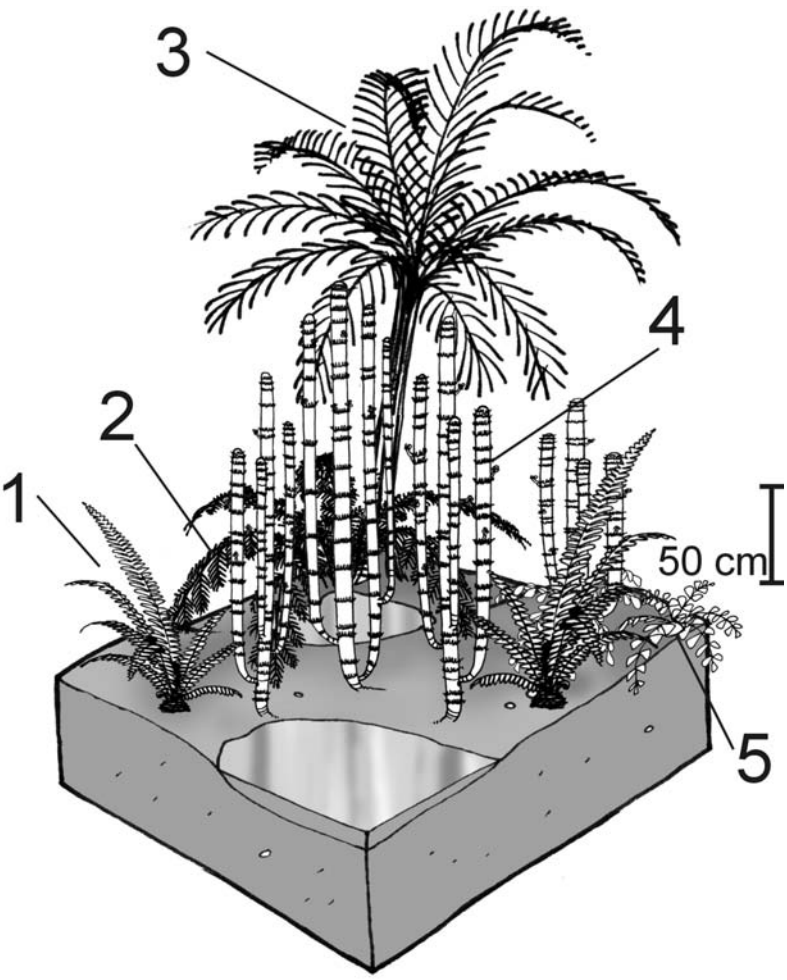

Fig. 7: Reconstruction of the more humid flora of the 'hinterland' environment with high stemmed Bennettitales (*Pterophyllum*, 3), arboreous horsetails (*Equisetites*, 4) and herbaceous ferns (*Neuropteridium*, 1; *Gordonopteris*, 2) and cycads (*Sphenozamites*, 5).

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	Mojsisovics, 1879	Ogilvie Gordon, 1927	Mutschlechner, 1932	P. Leonardi, 1953, 1968	G. Leonardi, 1964	Calligaris, 1983	Calligaris, 1986	Wachtler & Van Konijnenburg - Van Cittert 2000a, b	Kustatscher, 2004	Kustatscher *et al.*, 2004
Annalepis zeilleri Fliche									x	x
Anomopteris mougeotii Brongniart								x		
Asplenites roesserti Münster	cf.									
Bjuvia dolomitica Wachtler et Van Konijnenburg-Van Cittert								x	x	x
cf. *Bjuvia*									x	
Brachyphyllum sp.					x	x				
Braiescycas leonardii Calligaris							x			
Calamites meriani Brongniart	x									
Chiropteris lipoldi Stur	x									
Chiropteris pinnata Stur	x									
Cladophlebis gaillardoti Brongniart					cf.					
Cladophlebis leuthardti Leonardi,				x			x	x	x	x
Cladophlebis ruetimeyeri Heer				x					x	x
Cladophlebis ruetimeyeri Heer var. *heeri* Leonardi				x						
Cladophlebis sp.					x					
Dioonitocarpidium moroderi (Leonardi) Kustatscher *et al.*				cf.		cf.			x	x
cf. Cycadeoidea							x			
Cordaicarpus sp.					x					
Cycadeospermum sp.					x					
Cycadites rectangularis Brauns					cf.					
Danaeopsis marantacea (Presl) Schenk	x									
Dioonitocarpidium sp.								x		
Elatocladus sp.								x	x	x
Equisetites arenaceus (Jaeger) Schenk	x							x	x	x
cf. *Equisetites*									x	
Equisetites sp.					?		x			
?Equisetostachys					x					
Fern *incertis sedis*										x
?Filicales indet.									x	
Frenelopsis hoheneggeri Schenk		x								
Ginkgo sp.							x			
Lomatopteris sp.				x						
Lycopodites sp.	x									
?Neocalamites					x					
Neuropteris elegans Brongniart	cf.								x	x
Neuropteris gaillardoti Brongniart.	cf.									
Neuropteridium grandifolium (Schimper et Mougeot) Schimper								x		
Neuropteris ruetimeyeri Heer	cf.									
Neuropteridium sp.				x	x	x	x			
cf. *Neuropteridium*									x	
Nilsonia sp.		x								
Odontopteris sp.							x			
Pagiophyllum foetterlei Stur				cf.	cf.	x	cf.			
Pagiophyllum massalongi De Zigno				x		x	cf.			
Pagiophyllum peregrinum (Lindley et Hutton) Seward						x				
Pagiophyllum sp.							x			
Pecopteris (*Lonchopteris*) *reticulata* Leuthardt				cf.						
Pecopteris gracilis Heer	x									

Pecopteris sulzensis Schimper				**cf.**						
Pecopteris triascia Heer	x									
Pecopteris sp.							x			
Pelourdea vogesiaca (Schimper et Mougeot) Seward				x				x	x	x
Pelourdea sp.							x		x	
Pterophyllum brevipenne Kurr		x								
Pterophyllum giganteum Schenk	x									
Pterophyllum jaegeri Brongniart	x			x	**cf.**			x	x	x
Pterophyllum sp.				x	x				x	x
?*Pterophyllum* sp.									x	
Ptilozamites heeri Nathorst								x	x	x
Sagenopteris lipoldi Stur	x									
Scolopendrites sp.									x	x
Sphenozamites wengensis Wachtler et Van Konijnenburg-Van Cittert								x	x	x
Sphenozamites cf. *bronnii* Passoni et Van Konijnenburg-Van Cittert									x	x
Taeniopteris angustifolia Schenk		x								
Taeniopteris sp.	x			**cf.**				x	x	x
?*Taeniopteris* sp.									x	
Thinnfeldia richthofeni Stur	x									
?*Thyrsopteris*				x						
Tingia sp.							x			
Voltzia dolomitica Wachtler et Van Konijnenburg-Van Cittert								x	x	x
Voltzia cf. *dolomitica* Wachtler et Van Konijnenburg-Van Cittert									x	
Voltzia ladinica Wachtler et Van Konijnenburg-Van Cittert								x		x
Voltzia cf. *ladinica* Wachtler et Van Konijnenburg-Van Cittert									x	
Voltzia pragsensis Wachtler et Van Konijnenburg-Van Cittert								x	x	x
Voltzia cf. *pragsensis* Wachtler et Van Konijnenburg-Van Cittert									x	
Voltzia recubariensis Schenk		x								
Voltzia zoldana Leonardi				x					x	x
Voltzia sp.	x	x	x	x	x		x	x	x	x
?*Voltzia*							x			
Zamites sp.		x	**?**							
Sporofillo di cicadea o bennettitale				x						

Tab. 1. Plant fossils of Ladinian age described and figured in the literature (Mojsisovics, 1879; Ogilvie Gordon, 1927; Mutschlechner, 1932; P. Leonardi, 1953, 1968; G. Leonardi, 1964; Calligaris, 1983, 1986; Wachtler & van Konijnenburg - van Cittert 2000a, b; Kustatscher 2004; Kustatscher et al., 2004).

	SW %		**IK %**		**RI 1 %**	**RI 2 %**	**RI 3 %**	**RI 4 %**
spores	40.42		68.86		44.52	46.13	33.28	35.95
pollen	59.58		31.14		55.48	53.87	66.72	64.05
Algal cysts	1.48		3.99		4.75	7.83	3.35	2.85
acritarchs	7.94		0.74		5.73	1.60	5.71	15.25

Tab. 2: Relative abundance of the main palynomorph groups (SW = Seewald, IK = Innerkohlbach, RI 1-4 = Ritberg).

	SW %		IK %		RI 1 %	RI 2 %	RI 3 %	RI 4 %
A - monolete acavate spores	**0.00**		**0.00**		**0.00**	**0.00**	**0.00**	**0.00**
B - trilete acavate laevigate or apiculate spores	**24.84**		**66.53**		**47.20**	**47.09**	**30.74**	**29.49**
C - trilete acavate murornate spores	**1.27**		**1.77**		**1.44**	**2.69**	**0.67**	**1.15**
D - trilete cingulate and zonotrilete spores	**0.85**		**0.82**		**2.24**	**0.00**	**0.40**	**1.98**
E - *Aratrisporites* group	**0.21**		**0.14**		**0.64**	**0.45**	**0.13**	**0.33**
F - *Porcellispora* complex	**0.00**		**0.00**		**0.00**	**0.00**	**0.00**	**0.00**
G - monosulcate pollen grains	**0.21**		**0.14**		**0.00**	**0.15**	**0.00**	**1.48**
H - *Ovalipollis* complex	**13.59**		**13.47**		**22.72**	**20.48**	**28.05**	**18.95**
I - alete (proto)bisaccate pollen grains	**21.02**		**5.58**		**7.52**	**7.92**	**12.21**	**12.36**
J - *Samaropollenites*	**0.00**		**0.00**		**0.00**	**0.00**	**0.00**	**0.00**
K - taeniate (proto)bisaccate pollen grains	**3.61**		**0.14**		**1.28**	**0.60**	**1.48**	**2.47**
L - *Triadispora* complex	**31.00**		**6.53**		**9.12**	**13.90**	**20.40**	**26.36**
M - vesicante pollen grains	**0.00**		**0.00**		**0.00**	**0.00**	**0.00**	**0.00**
N - (proto)monosaccate pollen grains	**2.97**		**2.18**		**4.64**	**5.08**	**3.49**	**3.13**
O – *Circumpolles* group	**0.42**		**2.72**		**3.20**	**1.64**	**2.42**	**2.31**

Tab. 3. Palynological composition of the palynomorph groups proposed by Visscher & van der Zwan (1981); SW = Seewald, IK = Innerkohlbach, RI 1-4: Ritberg.

	SW 1%		IK 1%		RI 1%	RI 2%	RI 3%	RI 4%
Upland	8.4		5.5		7.4	7.3	6.6	4.5
Lowland	11.0		29.1		23.7	23.8	14.5	16.4
Coastal	34.0		9.0		14.6	16.3	25.7	29.4
River	13.4		37.9		23.9	24.9	16.3	17.9
Tidal	12.6		1.9		2.9	5.1	6.2	7.9
Ovalipollis	13.9		13.5		22.8	20.5	28.1	19.0
Not attributed	6.7		3.0		4.8	1.9	2.6	5.0
Lowland	**SW**		**IK**		**RI 1**	**RI 2**	**RI 3**	**RI 4**
“more humid”	10.82		27.22		19.23	20.39	13.32	13.22
“more arid”	0.22		1.92		4.49	3.45	1.21	3.14

Tab. 4. Abundance of the main floral groups within the microflora; SW = Seewald, IK = Innerkohlbach, RI 1-4: Ritberg.

	SW %		IK %		RI 1 %	RI 2 %	RI 3 %	RI 4 %
Lycophyta	3.3		17.1		12.2	16.9	7.4	7.1
Sphenophyta	0.0		0.1		0.5	0.1	0.1	0.2
Pteridophyta	20.9		50.8		35.5	32.5	23.1	21.7
Pteridospermae	17.9		2.6		5.0	5.7	9.4	13.2
Cycadophyta	0.0		0.1		0.8	0.0	0.1	1.3
Ginkgophyta	0.0		0.1		0.3	0.1	0.1	1.2
Ovalipollis	13.9		13.5		22.8	20.5	28.1	19.0
Coniferophyta	42.3		13.8		19.7	22.9	30.4	31.8
altro	1.7		1.8		3.2	1.0	1.1	4.5

Tab. 5. Relative abundance of the different SEGs within the plant deposits; SW = Seewald, IK = Innerkohlbach, RI 1-4: Ritberg.