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The Fossil Flora of the Wengen Formation (Ladinian) in the Dolomites (Italy)

by

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Contents

Abstract

Fossil plants from the Wengen Formation (Ladinian, MiddleTriassic) in the Dolomites (Italy) have been known for over 100 years. The best remains originate from the Zoldo Valley, from Corvo Alto near Cortina, Prags, Ritjoch near Wengen, Col Alto near Corvara and the Gröden Valley. The floral composition is remarkably different from that of other European contemporaneous floras such as in Austria, Germany and France.

The main floral components in the Wengen Formation are several *Voltzia* species, including the new species *Voltzia ladinica* n. sp., *Voltzia pragsensis* n. sp. and especially *Voltzia dolomitica* n. sp., followed by the conifer *Yuccites vogesiacus* and the seedfern *Ptilozamites heeri. Equisetites arenaceus*, the most common plant in the German Keuper flora, is very rare in the Dolomites just as *Pterophyllum jaegeri* (a cycadophyte abundant in the Lunz flora in Austria and common in Germany). Several fern species occur e.g. *Anomopteris mougeotii* (also known from the Buntsandstein of France), *Cladophlebis leuthardtii* and *Neuropteridium grandifolium.* Cycadophytes are further represented by *Bjuvia dolomitica* n. sp., *Taeniopteris* sp. and *Sphenozamites wengensis* n. sp. A single specimen of the conifer genus *Elatocladus* has been recorded as well.

Zusammenfassung

Fossile Pflanzen aus der Wengen Formation (Ladin, Obertrias) der Dolomiten (Italien) sind seit 100 Jahren bekannt. Als Hauptfundorte gelten das Zoldo Tal, Corvo Alto neben Cortina, Prags, Ritjoch bei Wengen, Col Alto bei Corvara und das Grödnertal. Die Pflanzengemeinschaft unterscheidet sich in vielerlei Belangen von anderen gleichaltrigen in Österreich, Deutschland und Frankreich.

Die Pflanzengemeinschaft aus der Wengen Formation setzt sich vor allen Dingen aus mehreren *Voltzia*-Arten, mit den neuen Arten *Voltzia ladinica* n. sp., *Voltzia pragsensis* n. sp. und vor allen Dingen *Voltzia dolomitica* n. sp. zusammen. Weiters finden sich die Konifere *Yuccites vogesiacus* und der Samenfarn *Ptilozamites heeri. Equisetites arenaceus*, die häufigste Pflanze aus dem deutschen Keuper, sowie *Pterophyllum jaegeri* (eine häufig gefundene Cycadophytenart aus Deutschland, sowie der Lunzer Flora in Österreich) ist in der Wengen- Formation sehr selten. Verschiedene Farne wie zum Beispiel *Anomopteris mougeotii* (bekannt vom Buntsandstein aus Frankreich), *Cladophlebis leuthardtii und Neuropteridium grandifolium* wurden darüberhinaus noch gefunden. An Cycadophyten wurden noch *Bjuvia dolomitica* n. sp., *Taeniopteris* sp. und *Sphenozamites wengensis* n. sp. gefunden. Nur ein einziges Stück der Koniferengattung *Elatocladus* ist belegbar.

1. Introduction and Geology

The Wengen Formation, named by WISSMANN (1841) after the place Wengen in the Gader Valley, encompasses various vulcanic deposits with changing amounts of tuffs, clays and limestones. They have often

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been preserved in easy to split layers. Their colour is usually darkbrown to grayish. Most of the sediments are of vulcanic origin; however, in the upper layers carbonate breccies are present as well. In the uppermost parts, the terrigene sediments disappear rapidly and finer sediments increase.

The Wengen group encompasses an area of 30 x 40 km, reaching from the Fassa Valley in the west to the Zoldana Valley in the southeast and Prags and Toblach in the north. The layers in the type locality at Wengen are built on top of the Buchensteiner agglomerates, and consist mainly of limestones embedded in greenish-gray to brown tuffs.

Well-preserved plant fossils occur in the Zoldo Valley, at Corvo Alto near Cortina, Prags, Ritjoch near Wengen, Col Alto near Corvara and the Gröden Valley.

The fauna of the Wengen Formation is dominated by the mollusc *Daonella lommeli*, found in mass-occurrences throughout the whole Formation, also accompanying the plant remains. These shells can be up to 10 cm long and are characterized by a radial structure. Another common mollusc is *Posidonia wengensis* which reaches a length of ca. 1 cm. Ammonites are more rare, and belong to the *Protrachyceras archelaus*-Zone; *Protrachyceras archelaus, P. ladinium, P. regoledanum, Trachyceras doleriticum, Monophyllites wengensis* and *Orthoceras campanile* are the most common ones. They can reach considerable lengths, up to 30 cm.

The Wengen Formation (*Daonella*-Zone and *Protrachyceras archelaus*-Zone) is ranked in the Late Ladinian (Longobardian)(De Zanche et al., 1995). A Longobardian age is also supported by the megaspore assemblage with *Dijkstraisporites beutleri* and *Maexisporites meditectatus* (Kozur, 1972).

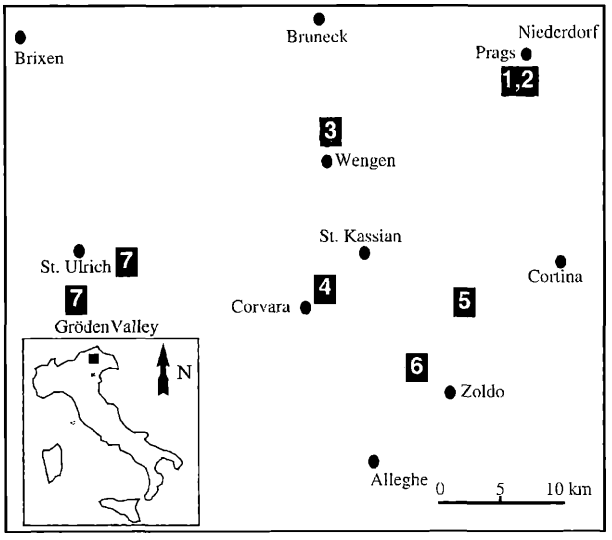

Figure 1: Map of the area showing the various localities. 1–Prags Seewald, 2–Prags Innerkohlbach, 3–Wengen Ritjoch, 4–Corvara, 5–Cortina, 6–Zoldo Valley, 7–Gröden Valley.

2. Historical Overview

The study of the fossil plant material has always been difficult or neglected, contrary to that of the marine fauna. While the cephalopods were already well-known through Mojsisovics' work (1879) and parts of the stratigraphy and tectonics had also been studied (Pia 1937), the fossil plants were only mentioned occasionally. Mojsisovics (1879) listed the following plants from Idria in Istria and Corvara (Badia Valley), without indicating which species came from which locality; *Equisetites arenaceus, E. meriani, Neuropteris* cf. *ruetimeyeri, N. gaillardoti, N. elegans, Sagenopteris lipoldi, Pecopteris triasica, P. gracilis, Chiropteris lipoldi, C. pinnata, Thinnfeldia richthofeni, Pterophyllum giganteum, P. jaegeri, Asplenites* cf. *roesserti, Danaeopsis marantacea, Taeniopteris* sp., *Voltzia* sp., *Lycopodites* sp.

Gordon (1927) listed from Corvara: *Taeniopteris angustifolia, Zamites* sp. indet., *Nilssonia* sp. indet., *Voltzia* sp.; from Gröden *Frenelopsis hoheneggeri, Voltzia* cf. *recubariensis, Voltzia* sp. indet., and from the Buchenstein strata from Puflatsch (actually also Wengen Formation) *Pecopteris* sp. indet., *Zamites* sp. indet., *Nilssonia* sp. indet., *Pterophyllum brevipenne* and *Voltzia recubariensis.*

Mutschlechner (1932) mentioned *Zamites* sp., *Voltzia* sp. and pinnules of ferns indetermined from Ciablun.

Leonardi (1953) discussed the plant remains found so far and included some new material, mainly from the Zoldo Valley, belonging to the genera *Cladophlebis, Neuropteridium, Pecopteris,* cf. *Lomatopteris,* ? *Thyrsopteris, Pagiophyllum* cf. *massalongi, Voltzia zoldana* and *Pagiophyllum foetterli.* From the village Cercená and the waterfall descending from Spiz Zuel into the Valley, he investigated *Neuropteridium* sp., *Pecopteris sulzensis, Cladophlebis ruetimeyeri, C. leuthardti, Pecopteris reticulata, Pterophyllum jaegeri, Voltzia* sp. and *Voltzia zoldana.* From Gröden, he described specimens found by the private collector Heinrich Moroder: *Pterophyllum* sp., *Cycadeoidea moroderi, Yuccites vogesiacus* and *Pagiophyllym foetterlii.*

Collectors from Cortina discovered material near Corvo Alto; *Cladophlebis leuthardtii, C.denticulata, Palaeocycas* sp., *Voltzia* sp., and near Forcella Giau *Neuropteridium grandifolium*; all these specimens are stored in the Museo delle Regole at Cortina d'Ampezzo.

Collectors from Gröden discovered near Puflatsch *Elatocladus* sp. and many more plant fossils from the Gröden Valley that are all kept at the Heimatmuseum Gröden.

Calligaris (1986) described a new cycad species (*Braiescycas leonardii*) from Prags, and also specimens of *Equisetites, Neuropteridum, Pecopteris, Cladophlebis, Yuccites, Voltzia* and *Pagiophyllum.*

In the last few years more material from the Wengen Formation was collected, due to a.o. the opening up of some mountain areas by means of forest roads, esp. near Prags, and Wengen. The new plant material will be described in this paper, and some of the previously described material will be discussed as well. It encompasses *Equisetites arenaceus, Anomopteris mougeotii, Neuropteridium grandifolium, Cladophlebis leuthardtii, Ptilozamites heeri, Sphenozamites wengensis* sp.nov., *Bjuvia dolomitica* sp. nov., *Taeniopteris* sp., *Pterophyllum jaegeri, Dioonitocarpidium* sp., *Elatocladus* sp., *Yuccites vogesiacus, Voltzia dolomitica* sp. nov., *Voltzia pragsensis* sp. nov. and *Voltzia ladinica* sp. nov. No profiles have been made yet for the new localities. The present paper deals exclusively with morphological descriptions.

3. Material and methods

The material originates from the following localities (see fig. 1).

Prags; there are two localities near Prags: **Prags Seewald** is situated near the end of the forest road from Bad Neuprags (Seminar) in the direction of Seewald, where the forest road opens up the Wengen Formation in a sharp bend to the left, at a height of ca. 1750 m above sea-level. Many well-preserved conifer remains have been collected at this locality, and also *Yuccites* leaves and to a lesser extent *Ptilozamites*. Some up to 2 cm thick layers of gypsum in the section indicate that a regression of the sea took place during short time intervals.

Prags Innerkohlbach (at a height of ca. 1650 m) is situated at the righthand bank of the small stream called Innerkohlbach that runs through the Seewald area. This locality yielded many conifer and *Yuccites* remains.

Wengen; the majority of the fossil plants was collected in the upper layers on the mountain ridge of the Ritjoch. Especially the topridge of the Ritjoch is very rich in plant material such as various conifers, the seedfern *Ptilozamites heeri*, the horsetail *Equisetites arenaceus*, the fern *Anomopteris mougeotii* and some Cycadophytes (*Bjuvia dolomitica* and *Sphenozamites wengensis*). The species diversity is the largest at this locality.

Col Alto near Corvara; mainly conifers have been collected around Col Alto, where the Wengen Formation surfaces in a larger area.

Corvo Alto, Forcella Giau, Mondeval and Fonderval near Cortina; this is a rich area where especially ferns and cycads have been found (e.g. the holotype of *Bjuvia*, exhibited in the Museo delle Regole in Cortina).

Zoldo Valley; plant fossils can be found near the village Cercená, near the waterfall descending from Spiz Zuel near Dont into the Zoldo Valley and Spiz Aguelesso.

Gröden Valley; the private collector Heinrich Moroder collected plant material on the Scagul-Alm and Puflatsch, mainly conifers, *Bjuvia* and *Pterophyllum jaegeri*. The specimens are kept in the Heimatmuseum Gröden (Ortisei). The specimens stored at the museums of Cortina and Gröden do not have any specimen numbers.

The specimens have been studied with the aid of a dissecting microscope, and when possible, cuticle preparations were made. For this purpose they were macerated in Schulze's Reagent ($KClO_3$ and 30% HNO_3) and neutralized with 5% ammonia. The cuticles were mounted in glycerin jelly and sealed with paraplast. The specimens (unless stated otherwise above) are partly stored in the Natural History Museum Bozen (Bolzano) and partly in Wachtler's private collection at Innichen (San Candido), both in Italy. The specimen codes for the museum in Bozen are: WRI – Wengen Ritjoch, WSW – Prags Seewald and WIK – Prags Innerkohlbach.

4. Systematic part

4.1. Sphenophyta

Equisetites STERNBERG 1833

Equisetites arenaceus (JAEGER 1827) SCHENK 1864

(Plate 1, figs. 1, 2)

1827 *Calamites arenaceus* JAEGER – JAEGER, p. 37; pl. 1, 2, 3, 4, figs. 1-7, 9, pl. 5, 6

1864 *Equisetites arenaceus* (JAEGER) SCHENK – SCHENK, p.9; pl. 7, fig.2

for further references see:

1998 *Equisetites arenaceus* (JAEGER) SCHENK – KELBER & VAN KONIJNENBURG-VAN CITTERT, p.3; pls. 1 -7.

Description: There is a specimen from Wengen (WRI 044) which is an apical stem fragment (pl. 1, fig. 1), 26 cm long (43 mm wide below, 27 mm above) consisting of many nodes and internodes (distances between nodes varying from 7 15 mm). Each node carries a leaf-sheath with the typical apical leaf teeth with their thorn-like appendages (KELBER, 1992).

A second specimen (WRI 043; pl. 1, fig. 2) from the same locality shows an apical fragment 36 mm long and up to 13 mm wide with 3 nodes (distance between nodes resp. 11 and 13 mm).

Discussion: This is the first definite record of this horse-tail species from the Wengen Formation. MOJSISOVICS (1879) mentioned already the presence of *E. arenaceus* but it was not clear if this species was

recorded from Idria in Istria or from Corvara in the Dolomites. LEONARDI (1953:8) described 2 specimens as *Neocalamites* or *Equisetites*. However, his specimens are so small and badly preserved that it is not even certain that they belong to a horse-tail. CALLIGARIS (1986) gave *Equisetites* sp. in a species list from Prags and figured a possible diaphragm that certainly does not belong to *E. arenaceus* as it demonstrates 'spokes' like in *E. laterale* (see HARRIS, 1961) and is not smooth as is common in *E.arenaceus* (see KELBER & VAN KONIJNENBURG-VAN CITTERT, 1998). The present authors have never found *E. arenaceus* at Prags so far.
E. arenaceus is a typical Triassic species, well-known from a.o. Franconia, Baden-Würtenberg and Neue Welt near Basel.
Localities: Wengen-Ritjoch (2 specimens)

4.2. Pterophyta

Anomopteris BRONGNIART 1828

Anomopteris mougeotii BRONGNIART 1828

(Plate 1, figs. 4, 5)

1828 *Anomopteris mougeotii* BRONGNIART – BRONGNIART, p.258; pl. 79, 81

for further references see:

1980 *Anomopteris mougeotii* BRONGNIART – GRAUVOGEL-STAMM & GRAUVOGEL, p.61, pl. 1-6

references from the Dolomites:

1953 cf. ? *Pecopteris sulzensis* SCHIMPER – LEONARDI, p.10, pl. 1, fig.14
1953 *? Cladophlebis ruetimeyeri* HEER – LEONARDI, p.10, pl. 1, fig. 15; non pl. 3, fig. 6
1953 *Neuropteridium* sp. – LEONARDI, p.8, pl. 1, figs. 3-7
1986 *Pecopteris* sp. – CALLIGARIS, p.9, fig. A48
1998 *Anomopteris mougeotii* BRONGNIART –STINGL & WACHTLER, p.80, fig. on p. 81.
1998 *Neuropteridium* sp. – STINGL & WACHTLER, p. 82

Description: In the Wengen Formation, the species is common at Ritjoch, but most specimens are only small pinna fragments; the best one measures 8 cm in length (WRI 072; pl. 1, fig. 4). The venation is clear, however, and resembles that of the young leaf form best.
The specimen (pl. 1, fig. 5) formerly described and figured as *Pecopteris* cf. *reticulata* (LEONARDI 1953, STINGL & WACHTLER 1998) proved to be a well-preserved specimen of *A. mougeotii* on re-examination (compare GRAUVOGEL-STAMM & GRAUVOGEL (1980:pl. 6, figs. 7, 8).
Discussion: *Anomopteris mougeotii* (both sterile and fertile) is a typical fossil in the Upper Bundsandstein (Scythian) of the Vosges, but has also been recorded from Germany and China (GRAUVOGEL-STAMM, 1978). *Anomopteris mougeotii* is a fern with large (up to 1.5-2 m long and 50 cm wide) bipinnate leaves. The pinnules often overlap, are normally ca. 3-3.5 mm long and 2-3 mm wide and are characterized by a small basal lobe and a typical neuropterid venation. The veins are so distinct that they are often the only thing remaining in badly preserved specimens (when the lamina has disappeared). GRAUVOGEL-STAMM & GRAUVOGEL (1980) also included the sterile *Pecopteris sulziana* Brongniart (see a.o. GRAUVOGEL-STAMM, 1978), without the typical basal pinnule lobe in the species as the leaf shape of young leaves. GRAUVOGEL-STAMM (1978) describes and figures (pl. 2, fig.3) also *Neuropteridium elegans* (BRONGNIART) SCHIMPER & MOUGEOT from the same bed in the Vosges, that resembles *Anomopteris mougeotii* in shape and venation but is only once pinnate. As the Wengen material consists only of pinna fragments it is possible that it may belong to *Neuropteridium elegans* instead of *Anomopteris mougeotii* but as the first species is less well known than *Anomopteris mougeotii* we prefer to include the material from the Dolomites in the latter with which it shares all characters of the young sterile leaves except the bipinnate state. Moreover, GOTHAN (1937) mentioned that the two species are similar differing mainly in size, and might even be conspecific.
Localities: Wengen-Ritjoch (common), Prags Seewald (1 specimen), Corvo Alto (common), Zoldo Valley (common).

Neuropteridium SCHIMPER 1891

Neuropteridium grandifolium (SCHIMPER et MOUGEOT 1844) SCHIMPER 1891

(Plate 2, fig. 1)

1844 *Neuropteris grandifolia* SCHIMPER & MOUGEOT – SCHIMPER & MOUGEOT, pl. 36, fig. 1 (subgenus *Neuropteridium*)

1891 *Neuropteridium grandifolium* (SCHIMPER & MOUGEOT) SCHIMPER – SCHIMPER, p. 113

Description: *Neuropteridium grandifolium* is not a common fossil in the Wengen Formation. Only one specimen (from Forcella Giau) is described and figured here. It is an apical pinna fragment, ca. 6 cm long. The pinnules are attached with their whole base; the length of the lower pinnules is 14 mm, diminishing rapidly to ca. 8 mm more apically. The width decreases from 5 mm below to 4 mm distally. The midrib is clear, the secondary veins are crowded, usually twice forked and the vein concentration at the margin is around 20/cm.
Discussion: The species is known from the Buntsandstein (Scythian) and the Keuper (Ladinian and Carnian) of France and Germany.
Localities: Forcella Giau (1 specimen); LEONARDI (1953) records *Neuropteridium* sp. from Zoldo Valley (Cercená).

Cladophlebis BRONGNIART 1849

Cladophlebis leuthardtii LEONARDI 1953

(Plate 1, fig. 3)

1953 *Cladophlebis leuthardti* LEONARDI – LEONARDI, p.11, pl. 2, figs. 1-5
1986 *Cladophlebis* sp. – CALLIGARIS, p. 9, fig. B29

Description: The pinna fragments found are only short (20-25 mm long) and demonstrate slightly falcate pinnules. These are attached with their whole base and are usually ca. 2.2 mm long and 2.5 mm wide. The venation is indistinct, except for the midrib, which ends long before the pinnule apex.
Discussion: *Cladophlebis leuthardtii* occurs in 4 localities in the Wengen Formation, although it is not a common fossil with the exception of Cortina Corvo Alto. LEONARDI (1953) described this species from 5 small fragments from Cercená (Zoldo Valley) which where characterized by the small size of their falcate pinnules, and by a more or less pecopterid to neuropterid venation (the midrib ends long before the pinnule apex). CALLIGARIS (1986) mentioned it as well. LEONARDI (1953) discussed the similarity of *C. leuthardtii* to the specimen of *Pecopteris ruetimeyeri* HEER figured by LEUTHARDT (1903-1904, pl. XXIV) from the Neue Welt flora near Basel, but there is a difference in pinnule shape between both species.
Localities: Cortina Corvo Alto (common), Zoldo (4 specimens), Prags Innerkohlbach (1), Ritjoch Wengen (1).

4.3. Pteridospermae

Ptilozamites NATHORST 1878

Ptilozamites heeri NATHORST 1878

(Plate 2, figs. 2-9)

1878 *Ptilozamites heeri* NATHORST – NATHORST, p. 24; pl. III, fig.9
1914 *Ptilozamites heeri* NATHORST – NATHORST, p. 12; pl. 2, fig.2, pl. 3, figs. 1-3, 12

Description:Leaf fragments or almost complete leaves are quite common at Wengen Ritjoch, and occur at two other localities (Prags Seewald and Zoldo) as well. In one leaf the petiole is present. It is 2.5 mm wide. The longest leaf fragment is ca. 11.5 cm long (WRI 053; pl. 2, fig. 2), but leaf fragments are usually shorter; their width is quite uniform: ca. 15 mm below and 10 mm near the leaf apex. The pinnae are in all leaf fragments oppositely to suboppositely arranged, and are ca. 8 mm long and 6-8 mm wide in the lower part of a leaf (pl. 2, fig. 4). They diminish in size towards the leaf apex (pl. 2, fig. 3). The veins arise almost perpendicularly from the rachis at a concentration of 7-9/cm, and run parallel to the rounded margin; they do not seem to fork. The leaf substance is quite thick, mainly because the cuticles are thick.
The leaf is amphistomatic, but the majority of the stomata is situated on the lower cuticle. Upper cuticle ca. 5-7 µm thick, consisting of irregular polygonal epidermal cells with occasional stomata between. No indication of veins in the cuticle. Lower cuticle ca. 8 µm thick, also consisting of irregular polygonal cells. Stomata occurring in irregular rows; several (usually 2-4) rows tending to form a stomatal band. Epidermal cells in the non-stomatal bands (indicating veins ?) not more elongated than those within the bands (pl. 2, fig. 7). Stomata irregularly spaced within the bands but never sharing subsidiary cells. Stomata usually longitudinally oriented; guard cells sunken, surrounded by 5-7 thickly cutinized subsidiary cells (pl. 2, figs. 8, 9), sometimes forming papillae overhanging stomatal pit. Occasionally large seeds (or cupulae with or without seeds) have been found associated with the leaves. They are ca. 3 cm long and ca. 1 cm (seeds) to ca. 3 cm (cupulae) wide. The seeds often show a mass of longitudinal fibres (WRI 069; pl. 2, fig. 6), the substance of the presumed cupulae is more dense but does not show any details (WSW 069; pl. 2, fig. 5).
Discussion: This is the first time that this species has been recorded from the Dolomites or even outside Sweden. The macromorphology of the material from the Dolomites is similar to *P. heeri* as described by NATHORST (1878, 1914) from the Rhaetian of Sweden. In both cases, the leaves are long and narrow, and the rachis is broad and undivided (quite a few *Ptilozamites* species have a once forked rachis, e.g. *P. nilssonii, P. fallax*). The shape and size of the pinnae is similar, but in the Swedish material the veins tend to fork sometimes, while we did not observe this feature in the material from the Dolomites. NATHORST (1914) gave a brief description of the cuticle which agrees with the one given here in general. Its main character is the absence of a clear indication of the veins in the cuticle, and the rather irregular distribution of the stomata. According to Nathorst they are equally distributed over the lower cuticle, while we found that they are more or less confined to stomatal bands but these are by no means well-defined.
Despite these small differences in macro- and cuticular characters and the time gap (Ladinian versus Rhaetian), we feel confident to place the material from the Dolomites in *P. heeri.*
Localities: Ritjoch Wengen (common), Prags Seewald (4 specimens), Gröden (3).

4.4. Cycadophyta

Sphenozamites BRONGNIART 1849

Sphenozamites wengensis n. sp.

(Plate 3, figs. 1, 2)

Description: Two leaf fragments have been found belonging to this genus; a larger one from Prags Seewald and a smaller one (a young leaf or a leaf apex ?) from Ritjoch Wengen.
The larger one (WSW 049; pl. 3, fig. 1) is ca. 12 cm long and 9.5 cm wide at its base. It then tapers towards a width of possibly 3-4 cm apically (apical part is not well preserved). The Ritjoch specimen (WRI 041; pl. 3, fig. 2) is 5.5 cm long. Its total width was ca. 5 cm basally, ca. 3 cm apically.
The Prags specimen demonstrates a ca. 6 mm wide rachis with (sub)oppositedly arranged pinnae that are probably inserted on the other side of the rachis than exposed, as none of the narrow pinna bases can be seen clearly. They seem to be ca. 5 mm wide, and immediately widen to 1-1.5 cm; they retain this width almost over their whole preserved length. The lower pinnae measure ca. 45 x 15 mm; pinna apex is rounded. The veins originate from the attachment area, fork in the lower and middle part of the pinna and reach the outer margin at a concentration of 16 / cm. No cuticle could be recovered. The Ritjoch specimen has an axis of only 2 mm wide, the pinnae appear to be inserted on this side of the rachis; the lower pinnules measure 30 x 11 mm. The vein concentration is also 16 / cm.
Discussion: *Sphenozamites* has been mainly recorded from the Triassic of the USA (Wesley 1958, 1974) but a *Sphenozamites* sp. is common in the Carnian of Mount Pora (Bergamascer Alps, Northern Italy), although the material probably belongs to a different species as the pinnae are much larger (> 15 cm long; 1-4 cm wide) (Passoni, 1996, unpublished thesis).
Sphenozamites resembles the living cycad *Zamia* quite closely in leaf shape, but as nothing is known of the Italian Triassic cuticles (both from the present material and from the Carnian of the Bergamascer Alps) and/or fructifications there is no certainty that both these fossil *Sphenozamites* species may be attributed to the cycads. It is quite well possible that they belong to Bennettitales instead. The leaf shape of *Eoginkgoites sydneyi* from the Late Triassic of the USA is quite similar as well, and this species has a bennettitalean cuticle (Axsmith et al. 1995). It differs clearly from both Italian *Sphenozamites* species in its venation as in *E. sydneyi* the veins fork and anastomose, while anastomoses have never been encountered in either Italian Triassic species. Wesley (1958, 1974) records two species of *Sphenozamites* from the Liassic of Northern Italy, which are recognized as bennettitalean leaves on the basis of their cuticle; *Sphenozamites geylerianus* Zigno has quite small pinnae (up to 2 cm long and just under 1 cm wide), even smaller than in the material from the Dolomites, with entire margins, while *S. rossii* Zigno is at once distinguished by coarsly dentate pinnae margins; each tooth is prolonged into a spine. Wesley (1958) gave an emended diagnosis for the genus *Sphenozamites* restricting it to those species of which a bennettitalean affinity is certain because of their cuticle; macromorphologically they do not have one terminal pinna but two. He made the new genus *Apoldia* for those species hitherto described as *Sphenozamites* that demonstrate a cycadalean cuticle and have one terminal pinna (*Apoldia tener* (Compter) Wesley; see also Linnell (1932), but he does not erect a new genus for those *Sphenozamites* species that do not yield a cuticle as is the case in both Triassic Italian species, the one described by Passoni from the Carnian of Mount Pora and the one described here from the Ladinian of the Wengen Formation.
So, the botanical affinity of those Triassic *Sphenozamites* species remains uncertain until their cuticle has been recovered; moreover, we do not have the leaf apex in those species, so we cannot deduce if there is one terminal pinna or two (a pair) (NB. The living cycad *Zamia* does not have one apical pinna but two; so this is not a character to distinguish between Cycadales and Bennettitales). We prefer to attribute our material to the genus *Sphenozamites* because many species have been described from this genus of which the affinity is unknown.
Diagnosis: *Sphenozamites* species with pinnae attached (sub)oppositely to the upper side of the broad rachis. Pinnae relatively small (up to 5 cm long, 1.5 cm wide), base contracted to ca. 5 mm; apex rounded. Veins arising from the narrow base, forking in the lower and middle part of the pinnae and reaching the margin at a concentration of ca. 16 per cm. Cuticle unknown.
Holotype: pl. 3, fig. 1 (WSW049) Natural History Museum of Bolzano (Bozen)
Paratype: pl. 3, fig. 2 (WRI 041, 042; part and counterpart) Natural History Museum of Bolzano (Bozen)
Derivatio nominis: from the Wengen Formation.
Localities: Prags Seewald (1), Ritjoch Wengen (1).
Stratum typicum: Wengen formation, Ladinian.

Bjuvia Florin 1933

Bjuvia dolomitica n. sp.

(Plate 4, figs. 1-3, Plate 5, figs. 1-5)

1927 ? *Nilssonia* sp. – Gordon, p.68, pl. 8, fig.6
1953 ? *Pterophyllum* sp. – Leonardi, p.13, pl. 3, fig. 2

Description: Leaves of this genus can attain a length of 1 m and a width of over 30 cm. Those leaves are in principle entire with a strong midrib and secondary veins that arise almost perpendicularly, but they are often secondarily torn like we see in recent *Musa* leaves (banana).
Macrotaeniopteris-type leaves have been found at Corvara, Fonderval (Cortina) and Ritjoch Wengen. The largest specimen (pl. 4, fig. 1, pl. 5, fig. 1) originates from Cortina and is an almost complete leaf, ca. 60

cm long and 16 cm wide. The petiole is almost 12 cm long and 5-6 mm wide and continues as the rachis, which is partly torn; the lamina widens gradually from its base to its maximum width of 16 cm. The secondary veins arise almost perpendicularly from the rachis and run parallel, without forking to the margin; the concentration of the veins at the margin is 14-18 / cm. The leaf is seen from below.

Another large (ca. 40 cm long, 12 cm wide) specimen (pl. 4, fig. 2) is housed in the Heimatmuseum Gröden (Ortisei), together with a smaller fragment; both originate from Gröden.

The Ritjoch specimen (WRI 046) is only a leaf fragment (pl. 4, fig. 3); half of the lamina is 65 mm wide, resulting in a possible leaf width of 13 cm or more. The length of the fragment is only 42 mm, so nothing can be said of the total leaf length. This specimen is seen from above where the two halves of the lamina are joined together and the midrib cannot be see at all. The vein concentration is again 14-18 per cm. This specimen yielded fragments of a thin, amphistomatic cuticle.

The upper cuticle is 1 µm thin, consisting of more or less rectangular epidermal cells with straight to slightly wavy outlines (pl. 5, fig. 4). Veins indicated by more elongated cells. Stomata (pl. 5, fig. 5) occur in the intervenal areas, sparcely spaced in irregular rows.

Lower cuticle ca. 2 µm thick. Normal epidermal cells of the same type as in the upper cuticle. Venal and intervenal areas more clearly defined (pl. 5, fig. 2). Stomata arranged in 2-4 rows, much more crowded than in the upper cuticle. Stomata haplocheilic; guard cells slightly sunken; subsidiary cells usually 4-6, forming a thickened ring around the stomatal pit (pl. 5, fig. 3). No trichome bases nor papillae have been observed, no cell measurements are given as they vary considerably.

Discussion: *Macrotaeniopteris* is a formgenus for entire-shaped large leaves, and the present material was first assigned to this genus. In the majority of its species a cuticle is not preserved and they may even belong to the ferns; some demonstrate a bennettitalean cuticle (e.g. *M.magnifolia*) and are then sometimes included in *Nilssoniopteris* (FLORIN 1933; BARNARD & MILLER, 1976). Others have a cycadalean cuticle, e.g. *M.* cf. *gigantea* (HARRIS, 1932) and are then included in either *Rhabdotaenia* or *Doratophyllum* (see BARNARD & MILLER, 1976). The material described here has a cuticle that is in principal cycadalean, but it is amphistomatic, contrary to normal hypostomatic cycad cuticles. Therefore, we cannot include this material in the hypostomatic genus *Rhabdotaenia. Doratophyllum* is also hypostomatic and moreover characterized by a very special type of stomata with a ring of ca. 8 thickly cutinized subsidiary cells (HARRIS, 1932). This type of stoma is not present in our material.

FLORIN (1933) described *Bjuvia simplex* (together with the female fructification *Palaeocycas integer*) from the Rhaetian of Bjuv (Sweden). This plant had formerly been designated as *Macrotaeniopteris gigantea* SCHENK by NATHORST (1878) but does not belong to this species. This plant is the most similar to our material (it is probably amphistomatic), differing in the following characters; the width of the leaf is over 20 cm wide, according to FLORIN, while in our material the width varies between 13 and 16 cm, but this is not decisive. The rachis, however, of *Bjuvia simplex* is over 1 cm wide in lower parts of the leaf and diminishing to 7 mm more apically; a petiole is so far unknown in *Bjuvia.* In our material the petiole and the midrib retain the same width throughout the leaf (5-6 mm). The veins of *Bjuvia simplex* may fork once near the rachis, the veins of the new species remain unforked throughout; the vein concentration is 12-14 / cm in *Bjuvia* simplex and 14-18 in our material. The cuticle of *Bjuvia simplex* is quite similar to the cuticle of *Bjuvia dolomitica,* although FLORIN is not sure if the leaves are amphi- or hypostomatic, although he believes them to be amphistomatic. He described the lower cuticle only, where the stomata occurred according to him in broad bands. We observed a difference in the stomatal frequency and arrangement between upper and lower cuticle. Moreover, the ring built by the subsidiary cells around the stomatal pit is more pronounced in *Bjuvia simplex* than in our material, and stomata occur occasionally over the rachis in *B. simplex* while we did not find them over the rachis in our material.

We describe, therefore, our material as a new species of *Bjuvia, Bjuvia dolomitica.*

Similar material is known from the Lunz flora; KRASSER (1909) described several *Macrotaeniopteris* species, but according to FLORIN (1933) these belong in all probability to the Bennettitales. The three *Macrotaeniopteris* species mentioned by de ZIGNO (1865) from the Lower Jurassic are quite badly known (de ZIGNO did not figure them, and since then nobody re-examined the material); according to SCHIMPER (1869) they might belong to one species (they come from the same locality near Verona), and FLORIN (1933) considered them too imperfectly known to say anything about them at all.

GORDONS's (1927) material of *Nilssonia* sp. originates from Corvara as well and belongs possibly to *Bjuvia dolomitica* but the fragment is too small to be sure.

LEONARDI (1953) described and figured a specimen from Scagul as *Pterophyllum* sp. but this leaf fragment resembles more a small part of our *Bjuvia* than a pinna of *Pterophyllum.*

Diagnosis: Leaf large, estimated length over 60 cm, width around 15 cm. Petiole ca. 12 cm long, 5-6 mm wide just as the rachis which remains unchanged in width throughout the preserved leaf fragments; lamina widening gradually from its base, apex unknown. Secondary veins arising almost perpendicularly from the rachis, unforked; vein concentration at the margin

14-18 / cm. Leaf amphistomatic. Upper cuticle 1 µm thin, consisting of more or less rectangular epidermal cells with straight to slightly wavy outlines. Veins indicated by more elongated cells. Stomata occurring in the intervenal areas, sparcely spaced in irregular rows. Lower cuticle ca. 2 µm thick. Normal epidermal cells of the same type as in the upper cuticle. Venal and intervenal areas more clearly defined. Stomata arranged in 2-4 rows, more crowded than in the upper cuticle. Stomata haplocheilic; guard cells slightly sunken; subsidiary cells usually 4 – 6, forming a thickened ring around the stomatal pit. No trichome bases nor papillae.
Holotype: pl. 4, fig. 1, pl. 5, fig. 1, Museo delle Regole Cortina
Paratype: pl. 4, fig. 3 (WRI 046, 047; part and counterpart) Natural History Museum Bozen (Bolzano)
Derivatio nominis: after the region
Localities: Cortina (1), Ritjoch Wengen (1), Corvara (1), Gröden (2), Prags Seewald (1).
Stratum typicum: Wengen formation, Ladinian.

Taeniopteris BRONGNIART 1828

Taeniopteris sp.

(Plate 6, fig. 1)

1927 ? *Taeniopteris angustifolia* SCHENK – GORDON, p.67, pl. 8, fig.2

Description: Some leaf fragments of a *Taeniopteris* (WSW 049; pl. 6, fig. 1) have been found, both at Ritjoch Wengen and Prags Seewald. The fragments are only small (length around 4 cm, longest 9 cm; width 2 to 3 cm) with a sometimes forking parallel venation (vein concentration 18-24 / cm) and no cuticle.
Discussion: We can only say that we are dealing with a *Taeniopteris* but not with which species. As sometimes the veins are occasionally forking, we are probably not dealing with a *Nilssonia* sp. but a *Nilssoniopteris*; but some of the specimens are so badly preserved that this feature is not clear everywhere. Therefore, we simply include the specimens in the formgenus *Taeniopteris*. GORDON (1927) described and figured a specimen of *Taeniopteris angustifolia* from Corvara; this specimen is ca. 8 cm long and 2 cm wide, and may be conspecific with our material.
Localities: Ritjoch Wengen (rare), Prags Seewald (rare).

Pterophyllum BRONGNIART 1828

Pterophyllum jaegeri BRONGNIART 1828

(Plate 3, figs. 3, 4)

1828 *Pterophyllum jaegeri* BRONGNIART – BRONGNIART, p.95
1953 *Pterophyllum jaegeri* BRONGNIART – LEONARDI, p.13, pl. II, fig. 12
1967 *Pterophyllum jaegeri* BRONGNIART – LEONARDI, p.176, pl. XXVIII fig. 4

Description: The best specimen (pl. 3, fig. 3) has been found at Gröden (Scagul). It is 33 cm long, 6 cm wide almost complete with a petiole ca. 4 cm long and a well-preserved lower and middle part of the leaf. Only the apical part is missing. The pinnae are more or less rectangularly inserted on the 4 mm wide axis and are in the middle part 4-5 cm long and ca. 4 mm wide. Venation is parallel. A smaller specimen in the Heimatmuseum Gröden (Ortisei) consists only of an axis with a few pinnae on both sides but it demonstrates the venation and the insertion of the pinnae quite well (pl. 3, fig. 4)
Discussion: *Pterophyllum jaegeri* is, contrary to the floras from Lunz and Stuttgart, a rare fossil in the Wengen Formation. This material is so completely in agreement with *Pterophyllum jaegeri* as it is well known, esp. from the Lunz flora, that we do not hesitate to attribute it to the species, although our material did not yield any cuticle.
Localities: Cercená (Zoldo Valley; 1), Gröden Scagul (2), Corvara (1).

Dioonitocarpidium LILIENSTERN 1928

Dioonitocarpidium sp.

(Plate 6, fig. 2)

1953 *Cycadeoidea* (?) *moroderi* LEONARDI – LEONARDI, p.14, pl. II, figs. 6-8
1967 *Cycadeoidea (?) moroderi* LEONARDI – LEONARDI, p.176, pl. XXVIII, fig. 4

Description: There is only one specimen known, which is just over 18 cm long and just under 3 cm wide. The longitudinally grooved rachis is 9 mm wide and the lamina segments arise from the distal part at an angle of ca. 70° The lower part of the fertile organ (which is about half of the size of the total specimen) should contain the seeds, but it is too badly preserved to be able to see those.
Discussion: LEONARDI (1953) described and figured a new species of a cycadophytic fertile organ from Val Gardena. He considered it to have bennettitalean affinities, but in our opinion it resembles more the cycad fructifications described so far in the genus *Dioonitocarpidium* (see KELBER 1990).
We are not even sure if it is a species of its own, as it resembles *D. pennaeformis* from the German Keuper closely (KELBER 1990), therefore, we describe it as *Dioonitocarpidium* sp.
Locality: Gröden Valley (1).

4.5. Coniferophyta

Elatocladus HALLE 1913

Elatocladus sp.

(Plate 6, fig. 3)

1967 *Pterophyllum* sp. LEONARDI– LEONARDI, p.176, pl. XXVIII, fig. 2
1996 *Pterophyllum* sp. LEONARDI – BOSELLINI, p.121, fig. 13.8

Description: There is one specimen in the Museum at Gröden that was originally designated as *Pterophyllum* sp. Re–examination of the 17 cm long, 7 cm wide fragment (pl. 6, fig. 3) showed that we are dealing with a branch of *Elatocladus*. The spirally arranged needles are flat, 2.0 - 3.5 cm long and 1.5 - 2 mm wide with a rounded apex and a contracted base. The midrib is indistinct. The specimen did not yield a cuticle.
Discussion: This material resembles several Jurassic *Elatocladus* sp. such as *E. laxus* and *Marskea jurassica* (HARRIS 1969), but we do not know of any Triassic species that is so stout as the one described and figured here. When more material preferably with cuticles could be found, it will almost certainly turn out to be a new species.
Locality: Puflatsch (1).

Yuccites SCHIMPER et MOUGEOT 1844

Yuccites vogesiacus SCHIMPER et MOUGEOT 1844

(Plate 6, figs. 4, 5)

1844 *Yuccites vogesiacus* SCHIMPER et MOUGEOT – SCHIMPER & MOUGEOT, p.42, pl. XXI
1953 *Yuccites vogesiacus* SCHIMPER et MOUGEOT – LEONARDI, p.15, pl. II, figs. 9, 11; pl. III, figs. 3-5
1986 *Yuccites* sp. - CALLIGARIS, p.15, figs. B21, 42

for further synonymy, see:

1978 *Yuccites vogesiacus* SCHIMPER et MOUGEOT – GRAUVOGEL-STAMM, p.31, pl. 3, fig.1

Description: The leaf fragments vary in length between 8.5 and 15 cm in length, and 15-22 mm in width and an obtuse apex. Their parallel venation is usually clear (WRI 048; pl. 6, fig. 4).
Discussion: *Yuccites vogesiacus* is a common fossil in the Wengen Formation, esp. at Prags (WSW 050; pl. 6, fig. 5), where it occurs together with *Voltzia* sp. and *Ptilozamites heeri* but leaf fragments occur at Ritjoch Wengen and Corvara as well. Although *Yuccites vogesiacus* is a common species in the Wengen Formation, no stems or fructifications have been found. The species is considered to belong to the conifers, based on the female fructification described by SCHLÜTER & SCHMIDT (1927). Their reconstruction of the species is still used in all palaeobotanical textbooks as no new data have been found since then. It is especially well-known from the Bundsandstein of the Vosges.
Localities: Prags (both localities; abundant), Ritjoch Wengen (common), Corvara (2).

Voltzia BRONGNIART 1828

Conifer remains of the *Voltzia*-type are the most common fossils in the Wengen Formation, especially *Voltzia dolomitica* sp. nov. can be found at almost every locality. In the past various *Voltzia* and *Pagiophyllum* species have been described from the area (GORDON (1927) *Voltzia recubariensis*, *Voltzia* sp. and *Frenelopsis hoheneggeri;* LEONARDI (1953) *Pagiophyllum* (?) *massalongi, P.* cf. *foetterlei*, *Voltzia* sp. and *Voltzia zoldana*; CALLIGARIS (1986) *Voltzia* sp., *Pagiophyllum* cf. *massalongi, P.* cf. *foetterlei* and *Pagiophyllum* sp.) but none of these yielded cuticles, nor were they accompanied by reproductive organs. Most of the remains are quite small fragments, and it is often difficult to assign those to known species.
We describe three new *Voltzia* species from the Wengen formation, known from large branched fragments; *Voltzia dolomitica* is common throughout the whole formation; the material includes a stem, branched shoots with preserved cuticles, a possible male cone and female fructifications, although the latter are not too well preserved. *Voltzia pragsensis* is only known so far from Prags; the material consists of large branched shoots and two badly preserved female cones. Moreover, we describe a third *Voltzia* species: *Voltzia ladinica* consisting of branched shoots with preserved cuticles and male and female cones. The type locality is Wengen Ritjoch, but it occurs at Prags Seewald as well.
Voltzia zoldana as described by LEONARDI (1953:19, pl. 4, fig. 1) consists only of one specimen from Wengen which is less than 5 cm long. The leaves are spirally arranged and ca. 8 mm long and only 1 mm wide; no cuticle is known. We do not dare to identify one of our species with this fragment. The only species it resembles to some extent is *V. ladinica* but we cannot be sure about a possible conspecifity without having been able to study the specimen in detail. Therefore, we describe our material as *V. ladinica* but when in the future it might be able to identify *V. zoldana* with it, then of course the species should be named *V. zoldana*.

Voltzia dolomitica n. sp.

(Plate 7, figs. 1-4, Plate 8, figs. 1-6)

1927 ? *Voltzia recubariensis* SCHENK GORDON, p.67, pl. 8, fig. 7
1953 ? *Pagiophyllum* (?) *massalongi* ZIGNO - LEONARDI, p.18, pl. 3, figs. 8, 10, pl. 4 fig. 2

1967 *Brachyphyllum* sp. - LEONARDI p.176, pl. XXVIII, fig.1
1986 ? *Pagiophyllum* cf. *massalongi* ZIGNO - CALLIGARIS, p.16, figs. A64, B6, 7, 11, 19, 27, 31
1998 *Voltzia* sp. - STINGL & WACHTLER, p.79 plus figure

Description: This is the main species in the Wengen Formation; it can be found in almost every locality (except Corvo Alto and Cortina), sometimes in large amount and sometimes as large specimens. The material includes stems (up to 3 m long and 10 cm in diameter), branched leafy shoot fragments (up to 30 cm long), many leafy shoots of the last order, male and female fructifications. No leaf dimorphism has been noticed in any of the specimens.

The holotype (WRI 029; pl. 7, figs. 1, 2) consists of a penultimate leafy shoot, ca. 34 cm long, with only 5 ultimate, slightly falcate shoots arising in the upper half of the shoot at an angle of about 45° Distance between ultimate shoots on one side of the penultimate shoot 3.5 - 4 cm. The ultimate shoots are 8 - 12 cm long and vary in width between 6 and 8 mm. Falcate leaves are spirally arranged and arise at an angle of ca. 60°, both on the penultimate and ultimate shoots. They partly overlap each other (especially on the ultimate shoots), are almost triangular in shape and vary in size between 6-10 mm x 3-5 mm on the penultimate shoot and 5-8 x 2-4 mm on the ultimate shoots. The apex is more or less acute. Other specimens are smaller, but demonstrate basically the same characters. Ultimate shoots always appear to be in one plane, and are sparsely spaced (pl. 7, fig. 2); distances between ultimate shoots on one side of a penultimate shoot vary between 2.5 -5 cm.

The cuticle is usually hypostomatic, ca. 2 µm thick and brittle. The adaxial cuticle shows relatively large, irregular, more or less isodiametric epidermal cells (pl. 8, fig. 4). Occasionally a stoma occurs. Abaxial cuticle with smaller, irregular, isodiametric epidermal cells. Stomata placed in short, irregular rows, usually sparcely spaced (pl. 8, fig. 5); never sharing subsidiary cells (pl.8, fig. 6). Guard cells sunken, surrounded by 4-7 subsidiary cells forming a slightly thickened ring around the stomatal pit. No papillae either on epidermal or subsidiary cells.

There is one possible male cone (WIK 003; pl. 7, fig. 4) (ca. 4.5 cm long; 1.2 cm wide) consisting of an axis with spirally arranged microsporophylls; the stalk is 6-7 mm long and the microsporophyll head ca. 1 mm wide and 1 mm long. No pollen sacs or pollen grains could be recovered. The cone was not attached, but based on association we attribute it provisionally to this species.

Female cones (WSW 0013; pl. 8, fig. 1) can be up to 7 cm long and 3 cm wide, but are usually just over 4 cm long and 2 cm wide (WRI 0013; pl. 7, fig. 3). They consist of spirally arranged bract / ovuliferous scale complexes that may be up to 1 cm wide, but normal dimensions are 5-7 x 4-7 mm. The ca. 5 mm long, 3 mm wide bracts are more or less rhomboidal in shape with an acute apex. Ovuliferous scales with 5 lobes (but not deeply lobed); usually up to 7 mm high and wide. So far only one or two seeds (up to 2 mm in diameter) per ovuliferous scale have been found, but because of the often detoriated nature of the cones this number is not clear. Detoriated cones (WIK 015; pl. 8, fig. 3) often only show a mass of bracts, ovuliferous scale remains and seeds. Ripe, detached seeds are round and ca. 3 mm in diameter.

Discussion: *Voltzia dolomitica* is distinguished from the well-known species *V. heterophylla* and *V. coburgensis* by not being heterophyllous (see e.g. SCHWEITZER, 1996). MILLER (1977) stated that all *Voltzia* species should have bract / scale complexes with 3 seeds, but SCHWEITZER (1996) demonstrated clearly that the older *Voltzia* species (e.g. the Permian species *V. hexagona* and *V. liebeana*) have only two seeds, and that the late Triassic *V. coburgensis* is the first species with 3 seeds per bract / scale complex. So far, we have not been able to detect more than 2 seeds in *V. dolomitica* but this might be due to the relatively poor preservation of the material.

Conifer fragments resembling *V. dolomitica* that have been described so far from the Wengen Formation were all small fragments and were partly attributed to *Voltzia* sp., partly to *Pagiophyllum* cf. *massalongi* and partly to *Voltzia recubariensis*. The last two are conspecific (SCHENK, 1868), and the name *Voltzia recubariensis* (MASSALONGI) SCHENK has priority. Careful examination showed that although the shoots appear to be quite similar there are differences. The leaves are in general more sparsely spaced in *V. recubariensis* than in *V. dolomitica*, especially on penultimate shoots, and are often slightly larger. No cuticle is known so far from *V. recubariensis*. The main difference however lies in the female fructification; the larger seeds in *V. recubariensis* are, according to SCHENK (1868:87, pl. 11, fig. 1) winged while those in *V. dolomitica* (pl. 8, fig. 1a) do not show any trace of a wing. Moreover, they are elliptical and much larger, being ca. 8 mm long, while here the ripe seeds are round and ca. 3 mm in diameter.

Other conifer species that have been described from slightly younger sediments in Northern Italy (Raibl) are *V. raiblensis* and *V. foetterlei* (STUR, 1868) but none of these is well-known (no fructifications nor cuticles) and they appear to be heterophyllous as well.

Diagnosis: Conifer with penultimate leafy shoots with ultimate shoots in one plane. Penultimate and ultimate shoots of the same width; ultimate shoots arising mainly in the upper half of the penultimate shoots, at angles of about 45° Ultimate shoots of median length, longer in distal than apical part. Leaves spirally arranged, falcate, arising at an angle of ca. 60°, both on the penultimate and ultimate shoots, partly overlapping each other (especially on the ultimate

shoots), almost triangular in shape; apex more or less acute.
Cuticle usually hypostomatic. Adaxial cuticle with relatively large, irregular, more or less isodiamteric epidermal cells. Abaxial cuticle with smaller, irregular, isodiametric epidermal cells. Stomata in short, irregular rows, usually sparcely spaced; never sharing subsidiary cells; guard cells sunken, surrounded by 4-7 subsidiary cells forming a slightly thickened ring around the stomatal pit. No papillae either on epidermal or subsidiary cells.
Male cones consist of an axis with spirally arranged microsporophylls. No pollen sacs or pollen grains known.
Female cones consisting of spirally arranged bract/ ovuliferous scale complexes. Exact structure of the bract/ovuliferous scale complexes not clear. Seeds ca. 3 mm long, round, without wing.
Holotype: pl. 7, figs. 1, 2 (WRI 029) Natural History Museum Bolzano (Bozen)
Paratypes: pl.8, fig. 2 (WSW 008, shoots with cuticle), pl. 8, fig. 1 (WSW 001, 045; part and counterpart, female cone), pl. 8, fig. 3 (WIK 005, 015; part and counterpart, detoriated female cone), pl. 7, fig. 4 (WIK 003, male cone), all in the Natural History Museum Bolzano (Bozen)
Derivatio nominis: from the Dolomites, the region in which this species occurs.
Localities: Almost all localities; good specimens originate from Prags (both localities and from Ritjoch Wengen (including the Holotype).
Stratum typicum: Wengen formation, Ladinian.

Voltzia pragsensis n. sp.

(Plate 9, figs. 1, 2)

1927 ? *Voltzia* sp. – GORDON, p.69, pl. 8, fig. 8
1953 ? *Voltzia* sp. – LEONARDI, p.19, pl. 4, fig. 8
1953 ? *Pagiophyllum* cf. *foetterlei* – LEONARDI, p.19, pl. 4, fig. 6, 7, 9
1986 ? *Pagiophyllum* cf. *foetterlei* – CALLIGARIS, p.17, figs. A58, B3, 20, 33

Description: There is another *Voltzia* sp. that resembles *V. dolomitica* in first view but differs in several characters.
The holotype (WIK 009; pl. 9, fig. 1) is around 27 cm long and consists of a penultimate, leafy shoot with 14 ultimate shoots, all in one plane. The penultimate shoot is ca. 1 cm wide, and the ultimate shoots arise at angles of about 30-45° from it; they are quite densely placed in the distal part with distances of only 1.2-2 cm; in the more apical part the distance between the ultimate shoots may be as much as 4-7 cm. The ultimate shoots are quite long, esp. in the distal part where they can reach a length of almost 20 cm. The most apical ones are only 4-5 cm long. They are all 8-10 mm wide. The leaves are spirally arranged, both on the penultimate and the ultimate shoots; they are usually 6 mm long and 2 mm wide and do not curve outwards but are appressed to the stem. The apex is acute. No cuticles have been recovered.
The male cones are unknown, but two badly preserved female cones have been found, one on the holotype and on the paratype (WSW 004; pl. 9, fig. 2) that consist of an axis with spirally arranged bract / scale complexes around them. No details could be seen.
Discussion: Because of the presence of those badly preserved female cones, we attribute this species to the genus *Voltzia*, although details fail. *V. pragsensis* is distinguished from *V. dolomitica* first of all by its different leaf shape and size: the leaves in *V. pragsensis* are distinctly smaller than in *V. dolomitica* and are appressed to the stem, while those in *V. dolomitica* are falcate and arise at an angle of ca. 60° Moreover, the ultimate shoots in *V. pragsensis* are quite densely placed in the distal part of the ultimate shoot and more widely in the apical part, while in *V. dolomitica* it is the other way round.
Diagnosis: Conifer with penultimate, leafy shoots with ultimate shoots in one plane. Penultimate shoots and ultimate shoots of the same width: ca. 1 cm; ultimate shoots arising at angles of about 30-45°, quite densely placed in the distal part and more sparsely in the apical. Ultimate shoots quite long, esp. in the distal part. Leaves spirally arranged, both on the penultimate and the ultimate shoots, appressed to the stem; apex is acute. Cuticle unknown.
Male cones unknown; female cones consisting of an axis with spirally arranged bract / scale complexes around them. No more details known.
Holotype: pl. 9, fig. 1 (WIK 009, 029; part and counterpart), Natural History Museum Bozen (Bolzano)
Paratype: pl. 9, fig. 2 (WSW 004), Natural History Museum Bozen (Bolzano)
Derivatio nominis: from Prags where the specimens were found
Localities: Prags Seewald and Prags Innerkohlbach.
Stratum typicum: Wengen formation, Ladinian.

Voltzia ladinica n. sp.

(Plate 10, figs. 1-5, Plate 11, figs. 1-5)

Description: There is a third species of *Voltzia*, a probably much smaller, bushy plant with more sparsely spaced leaves that are quite narrow. It occurs mainly at Wengen Ritjoch, where stems, penultimate and ultimate shoots occur, but two small specimens were found at Prags Seewald.
Stems have a diameter of up to 5 cm and are often not straight but mutilated.

The holotype (WRI 006; pl. 10, fig. 1) is an apical part of a penultimate shoot, 12 cm long, with four ultimate shoots (length ca. 5 cm) attached, arising at angles of ca 60° The distance between the ultimate shoots is usually 15-20 mm. Penultimate shoot and ultimate shoots have approximately the same width, ca. 6 mm. The falcate leaves on both shoot types are 3-4 mm long and only ca. 1 mm wide.

Other specimens have longer fragments (the longest shoot is ca. 34 cm long), with penultimate shoots up to 12 cm (distance between them 35-40 mm), but the width of the shoots remains 6-8 mm. Leaves on penultimate shoots are max. 6-8 mm long and 2 mm wide, leaves on ultimate shoots are usually 1 cm long (pl. 10, fig. 4) but on typical heterophyllous shoots they may be up to 25 mm (pl. 10, fig. 3). Their width is normally around 1 mm.

This species yielded good cuticles; the stem cuticle is ca. 5 µm thick and shows elongated epidermal cells and irregular rows of stomata (pl. 11, fig. 1). The guard cells are sunken and surrounded by 6-10 subsidiary cells that overhang the stomatal pit almost completely (pl. 11, fig. 2)

Leaf cuticles are amphistomatic, ca. 2-3 µm thick, with less stomata on the adaxial than on the abaxial cuticle. Normal epidermal cells more or less rectangular between stomatal rows, more isodiametric within stomatal rows. The stomata are arranged in rows (pl. 11, fig. 3), especially in the middle part of the leaf. They tend to avoid the margins. Within the rows they are often quite densely placed but they never share subsidiary cells. Occasionally stomata occur outside the stomatal rows. The guard cells are sunken and surrounded by 6-10 subsidiary cells that are heavily cutinized (pl. 11, fig. 4), and occasionally bear papillae but never overhang the stomatal pit so completely as on the stems.

Three male cones with spirally arranged microsporophylls have been found at Ritjoch, Wengen; one is 60 mm long and 12 mm wide (WRI 008; pl. 10, fig. 5), one 90 mm long and 10 mm wide, and one is only a fragment 40 mm long and 8 mm wide.

Only one terminal female cone has been found (WSW 002; pl. 10, fig. 2), that is not attached to a leafy shoot but lies immediately above it. It is ca. 7 cm long, and only 1.5 cm wide. It consists of an axis around 1 mm wide, with spirally arranged bract / ovuliferous scale complexes. Bracts are around 6-8 mm long, ovuliferous scales (8-10 mm long, 8-10 mm wide) appear to have five lobes with two (around 2 mm long) seeds per scale. We attribute the female cone to *V. ladinica* because of the association with the leafy shoot with the typical, only 1 mm wide, leaves of this species; these leaves are up to 10 mm long.

Discussion: To date no material like this had been found in the Wengen Formation, or anywhere else. This conifer must have lived under stress judging from its often scruffy appearance. Its cuticle is also thicker than that of *V. dolomitica* and the stomata are more heavily protected, again pointing towards an existence in a more severe environment.

The three species from the Wengen Formation are compared in Table 1, the cuticles of *V. dolomitica* and *V. ladinica* are compared to that of the well-known species *V. coburgensis* in Table 2.

Diagnosis: Species of conifer with often mutilated stems, penultimate and ultimate leafy shoots.

Penultimate and ultimate shoots of the same width, ca. 6 mm. Ultimate shoots arising at angles of ca. 60°

Leaves spirally arranged, usually falcate and sparsely spaced; width only 1-2 mm, length 4-10 mm, but heterophyllous leaves up to 25 mm.

Stem cuticle ca. 5 µm thick with elongated epidermal cells and irregular rows of stomata. Guard cells sunken, surrounded by 6-10 subsidiary cells overhanging the stomatal pit almost completely.

Leaf cuticles amphistomatic, ca. 2-3 µm thick, with less stomata on the adaxial than on the abaxial cuticle. Normal epidermal cells more or less rectangular between stomatal rows, more isodiametric within stomatal rows. Stomata arranged in rows tending to avoid the margins. Stomata within the rows quite densely placed but they never sharing subsidiary cells. Occasionally stomata occurring outside stomatal rows. Guard cells sunken, surrounded by 6-10 are heavily cutinized subsidiary occasionally bearing papillae but never overhanging the stomatal pit completely.

Male cone with spirally attached microsporophylls. Length over 5 cm, width around or just over 1 cm.

Female cone terminal, consisting of an axis around 1 mm wide, with spirally arranged bract/ovuliferous scale complexes. Bracts around 6-8 mm long, ovuliferous scales (8-10 mm long, 8-10 mm wide) with five lobes and two (around 2 mm long) seeds per scale.

Holotype: pl. 10, fig. 1 (WRI 006, 007; part and counterpart), Natural History Museum Bozen (Bolzano)

Paratypes: pl. 10, fig. 2 (WSW 046, 047; part and counterpart) female cone, pl. 10, fig. 5 (WRI 008, 009; part and counterpart) male cone, Natural History Museum Bozen (Bolzano)

Derivatio nominis: from the Ladinian age of the fossils.

Localities: Wengen Ritjoch (common), Prags Seewald (3 specimens and the female fructification).

Stratum typicum: Wengen formation, Ladinian.

5. Discussion

The assemblages of the various localities are listed in table 3. Many specimens were collected without a good documentation of the exact finding location. It is therefore difficult to compare and discuss the localities more throughfully.

6. Acknowledgements

We want to thank the Heimatmuseum Gröden (Ortisei) and Cortina, and the University of Innsbruck for the possiblity to study their material. The Natural History Museum at Bolzano (Bozen) where the collection is housed, deserves our special thanks, just as the University of Ferrara where Prof. C. Broglio Lorigo, Miss Evelyn Kustatscher, and the photographer Mr. Brandoli gave a lot of assistance. We are grateful to the Geological Survey (Dr. Volkmar Mair) and the Cultural Institute (Dr. Lorenzo Dal Ri) of Bolzano (Bozen) for their financial support. Martin Schönegger made the majority of the photos for which we are thankful. Finally, we have to thank Fabian Pfeifhofer who presented us with some of the specimens.

character / species	*V. dolomitica*	*V. pragsensis*	*V. ladinica*
stem diameter	ca. 10 cm	unknown	ca. 5 cm
shoot thickness	6 - 8 mm	8 - 10 mm	ca. 6 mm
length of ultimate shoots	8 - 12 cm	up to 20 cm	ca. 5 cm
arrangement of ultimate shoots	mainly in upper part of penultimate shoot	mainly in distal part of penulimate shoot	along the whole of the penultimate shoot
distance between ultimate shoots on one side of penult. shoot	2.5 - 5 cm	ca. 2 cm	ca. 2 cm
leaf form and arrangement	falcate, crowded	appressed to stem, crowded	falcate, sparsely spaced
leaf length	5 - 10 mm	ca. 6 mm	ca. 10 mm (up to 25 mm)
leaf width	2 - 5 mm	2 - 3 mm	ca. 1 mm
female cone	ca. 5 cm long 2 - 3 cm wide	ca. 4 cm long 1.5 cm wide	ca. 7 cm long 1.0 - 1.5 cm wide
ripe seeds	round, ca. 3 mm in diameter, unwinged	unknown	elliptical, ca. 1.5 - 2 cm long, unwinged

Table 1. Comparison of the three *Voltzia* species from the Wengen-Formation.

character / species	*V. dolomitica*	*V. ladinica*	*V. coburgensis*
cuticle	hypostomatic	amphistomatic	amphistomatic
cuticle thickness	ca. 2 µm	2 - 5 µm	3 - 5 µm
normal epidermal cells	rel. large adaxially, smaller abaxially, isodiametric	rectangular between stom. rows, isodiametric within	relatively large, isodiametric
stomatal arrangement	short, irregular rows, sparcely spaced	longitudinal rows, densely spaced	longitudinal rows, densely spaced
subsidiary cells	4 - 7, forming a thickened ring	6 - 10, completely thickened	4 - 7, not thickened but with short papillae
papillae on epidermal cells	absent	absent	often present

Table 2. Comparison between the cuticles of *Voltzia dolomitica*, *V. ladinica* and *V. coburgensis*, the only other *Voltzia* species of which cuticles are known.

Species	Prags Seewald	Prags Innerkohl-bach	Wengen Ritjoch	Corvara	Cortina area	Zoldo Valley	Gröden Valley
Anomopteris mougeotii	+		+		+	+	
Bjuvia dolomitica	+		+	+	+		+
Cladophlebis leuthardtii		+	+		+	+	
Dioonitocarpidium sp.							+
Elatocladus sp.							+
Equisetites arenaceus			+				
Neuropteridium grandifolium					+	+	
Pterophyllum jaegeri				+		+	+
Ptilozamites heeri	+		+				+
Sphenozamites wengensis	+		+				
Taeniopteris sp.	+		+				
Voltzia dolomitica	+	+	+	+	+	+	
Voltzia ladinica	+		+				
Voltzia pragsensis	+	+					
Yuccites vogesiacus	+	+	+	+			

Table 3. Comparison between the assemblages found in the various localities.

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PLATE 1

Fig. 1 *Equisetites arenaceus* (JAEGER) SCHENK; largest specimen (WRI 044; Natural History Museum Bozen (Bolzano)); x 1

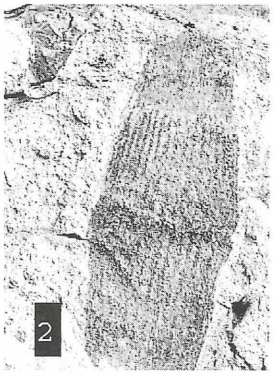
Fig. 2 *Equisetites arenaceus* (JAEGER) SCHENK; apical fragment (WRI 043; Natural History Museum Bozen (Bolzano)); x 1.6

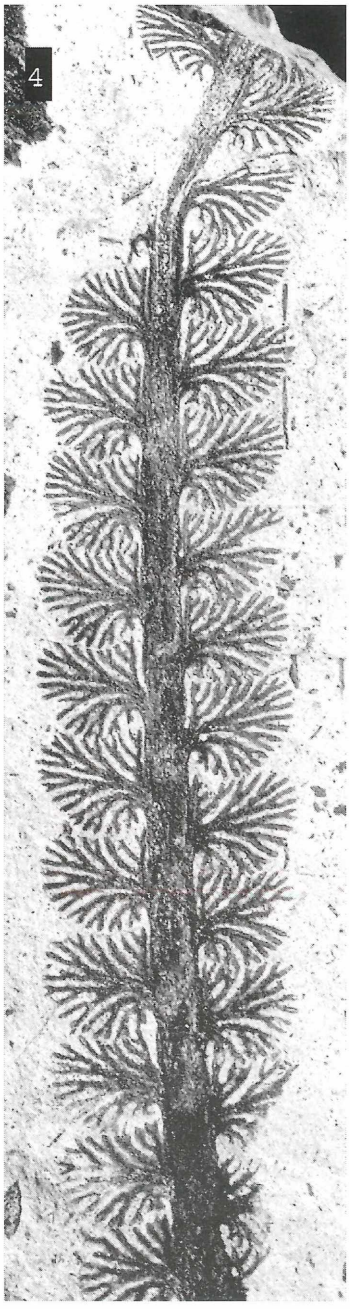
Fig. 3 *Cladophlebis leuthardtii* LEONARDI; typical apical pinna (Museo delle Regole Cortina); x 5

Fig. 4 *Anomopteris mougeotii* BRONGNIART; longest fragment with the typical venation (WRI 072; Natural History Museum Bozen (Bolzano)); x 2

Fig. 5 *Anomopteris mougeotii* BRONGNIART; a well-preserved specimen formerly described as *Pecopteris* cf. *reticulata*; (Museo delle Regole Cortina); x 2

PLATE 1





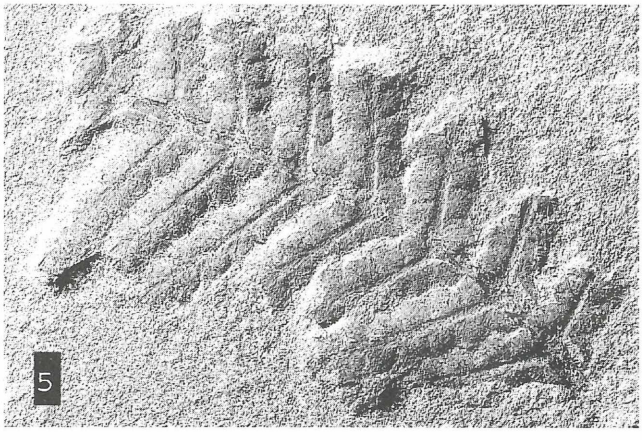


PLATE 2

Fig. 1 *Neuropteridium grandifolium* (SCHIMPER et MOUGEOT) SCHIMPER; apical fragment (Museo delle Regole Cortina); x 2

Fig. 2 *Ptilozamites heeri* NATHORST; longest fragment (WRI 053; Natural History Museum Bozen (Bolzano)); x 1

Fig. 3 *Ptilozamites heeri* NATHORST; fragment with pinnae diminishing in size towards the apex (WRI 056; Natural History Museum Bozen (Bolzano)); x 2

Fig. 4 *Ptilozamites heeri* NATHORST; typical fragment (WRI 055; Natural History Museum Bozen (Bolzano)); x 2

Fig. 5 Cupule possibly belonging to *Ptilozamites heeri*; (WSW 069; Natural History Museum Bozen (Bolzano)); x 1

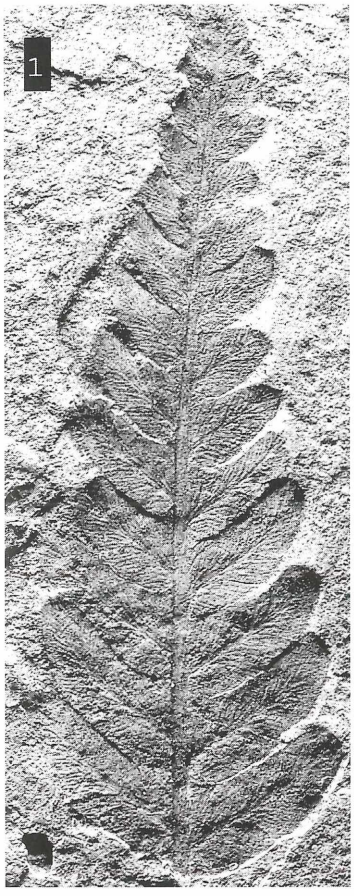
Fig. 6 Seed possibly belonging to *Ptilozamites heeri*; (WRI 069; Natural History Museum Bozen (Bolzano)); x 1

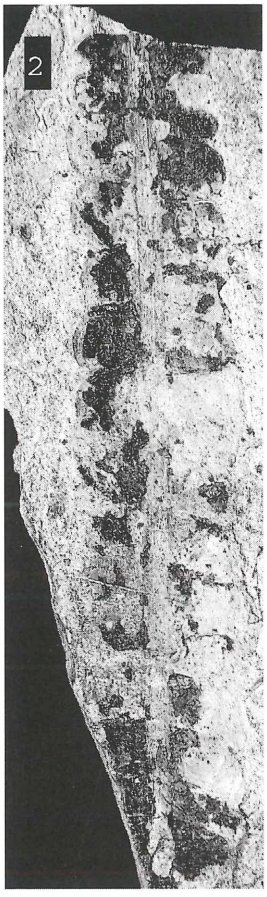
Fig. 7 *Ptilozamites heeri* NATHORST; part of upper cuticle showing a non-stomatal band; x 100

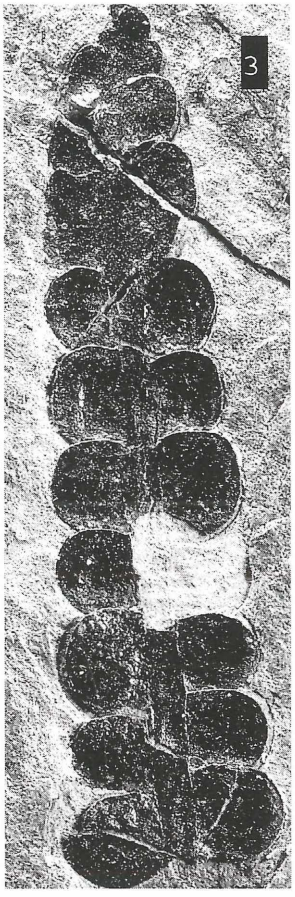
Fig. 8 *Ptilozamites heeri* NATHORST; part of upper cuticle showing a stoma; x 400

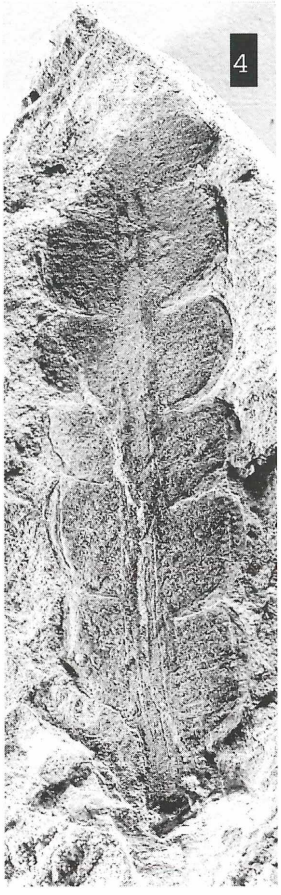
Fig. 9 *Ptilozamites heeri* NATHORST; part of lower cuticle showing several stomata; x 400

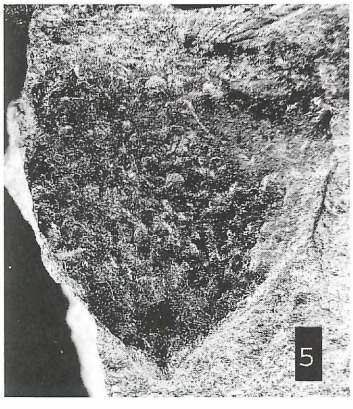
PLATE 2

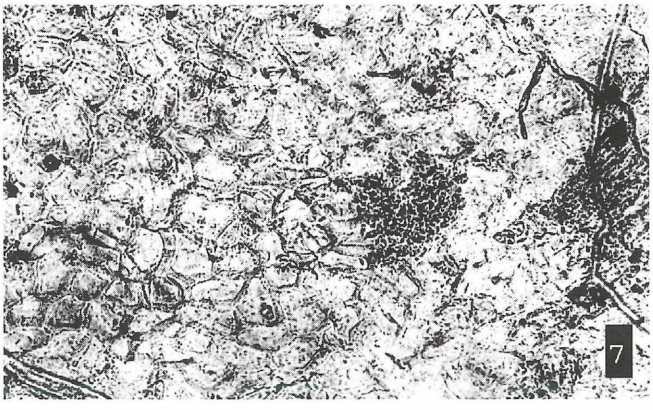


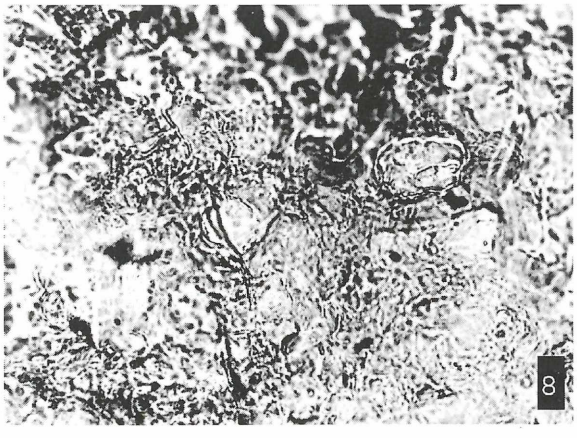












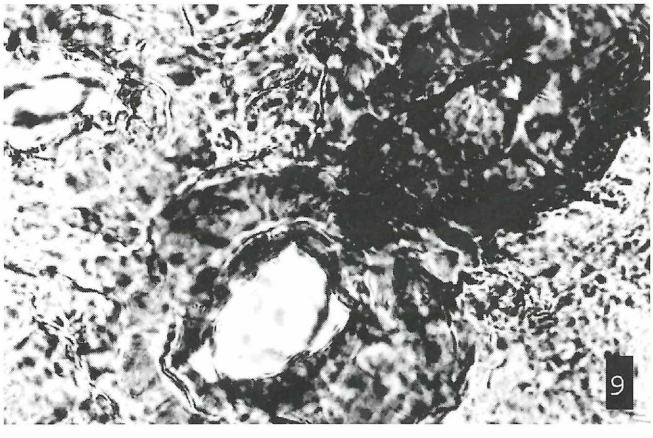


PLATE 3

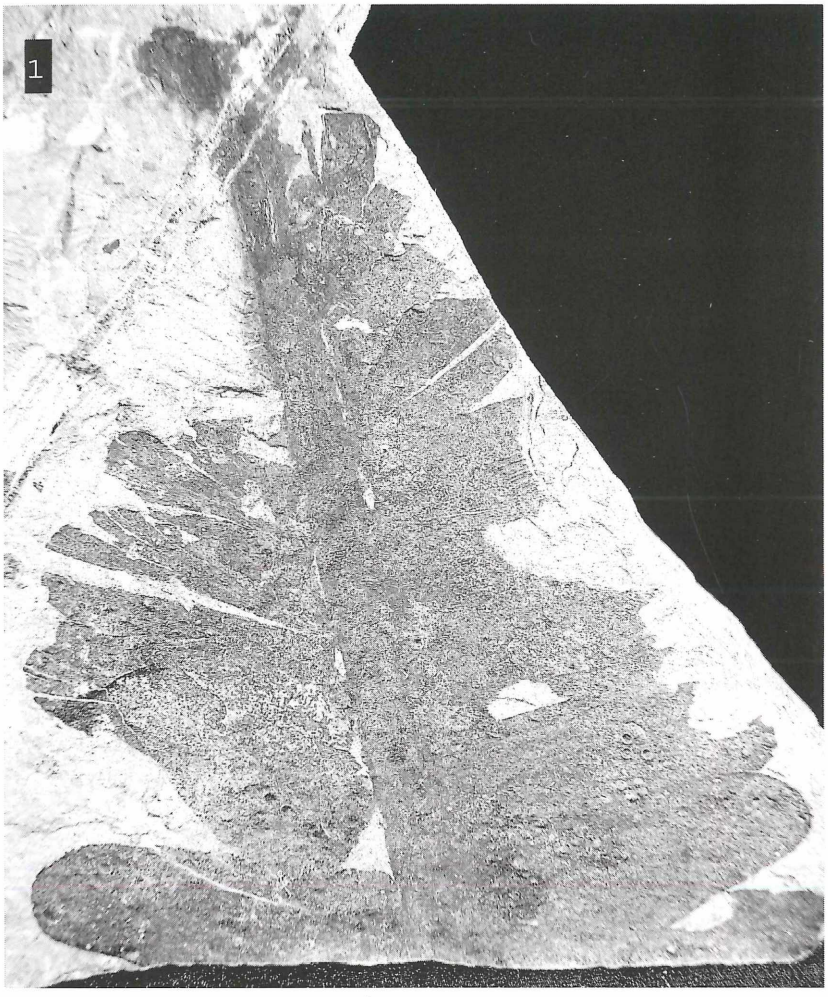
Fig. 1 *Sphenozamites wengensis* n. sp.; holotype (WSW 049; Natural History Museum Bozen (Bolzano)); x 1

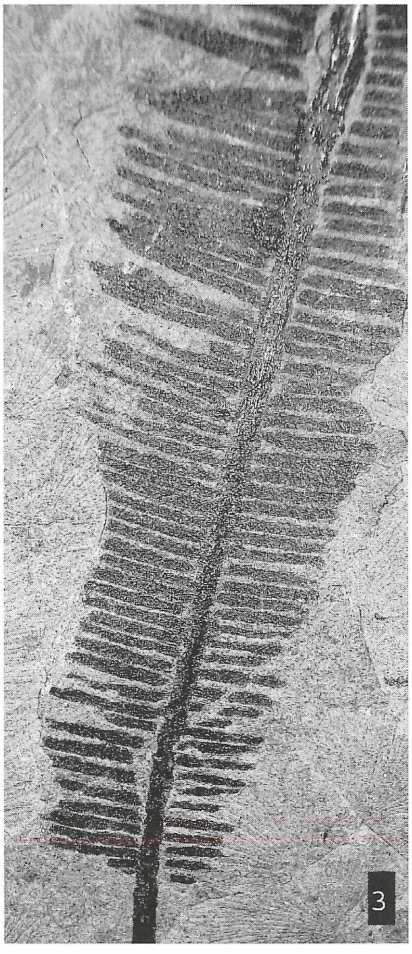
Fig. 2 *Sphenozamites wengensis* n. sp.; paratype (WRI 041; Natural History Museum Bozen (Bolzano)); x 1.5

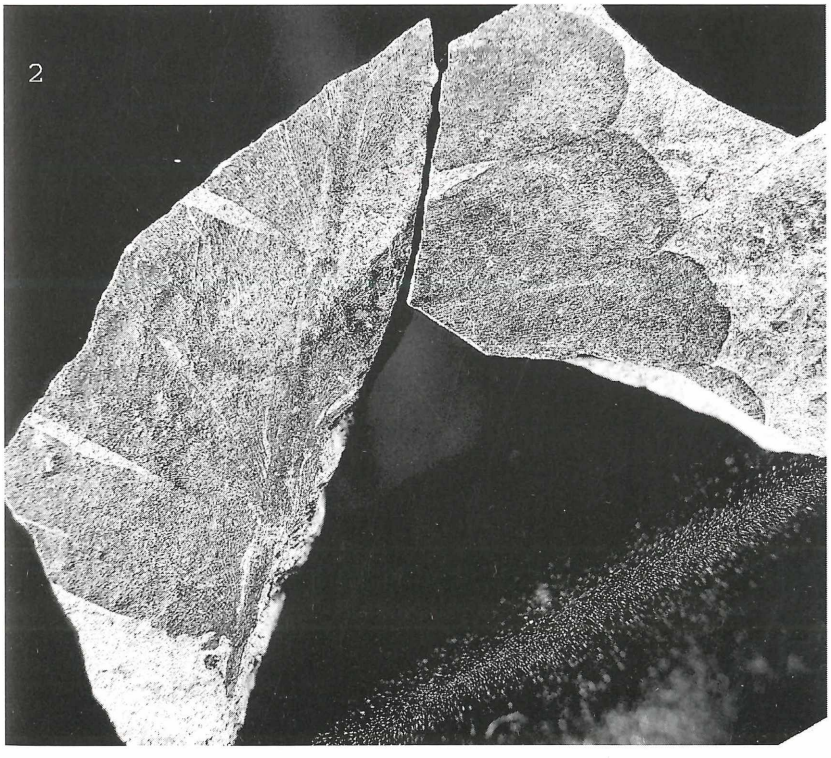
Fig. 3 *Pterophyllum jaegeri* BRONGNIART; typical specimen, Institute for Geology and Palaeontology, University of Innsbruck; x 1

Fig. 4 *Pterophyllum jaegeri* BRONGNIART; small specimen demonstrating the venation and pinna insertion; Heimatmuseum Gröden (Ortisei); x 2

PLATE 3







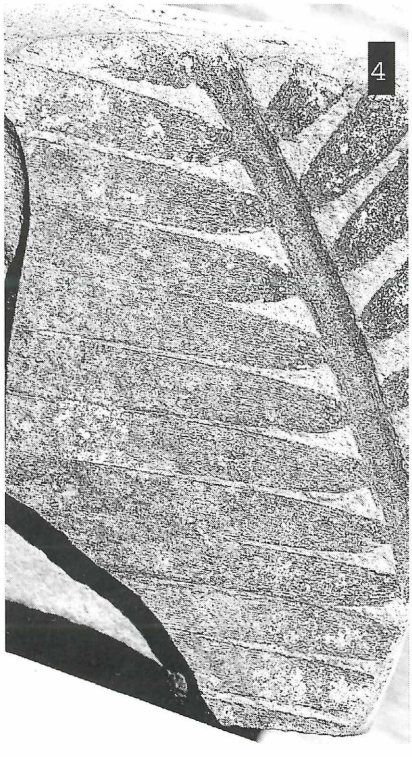


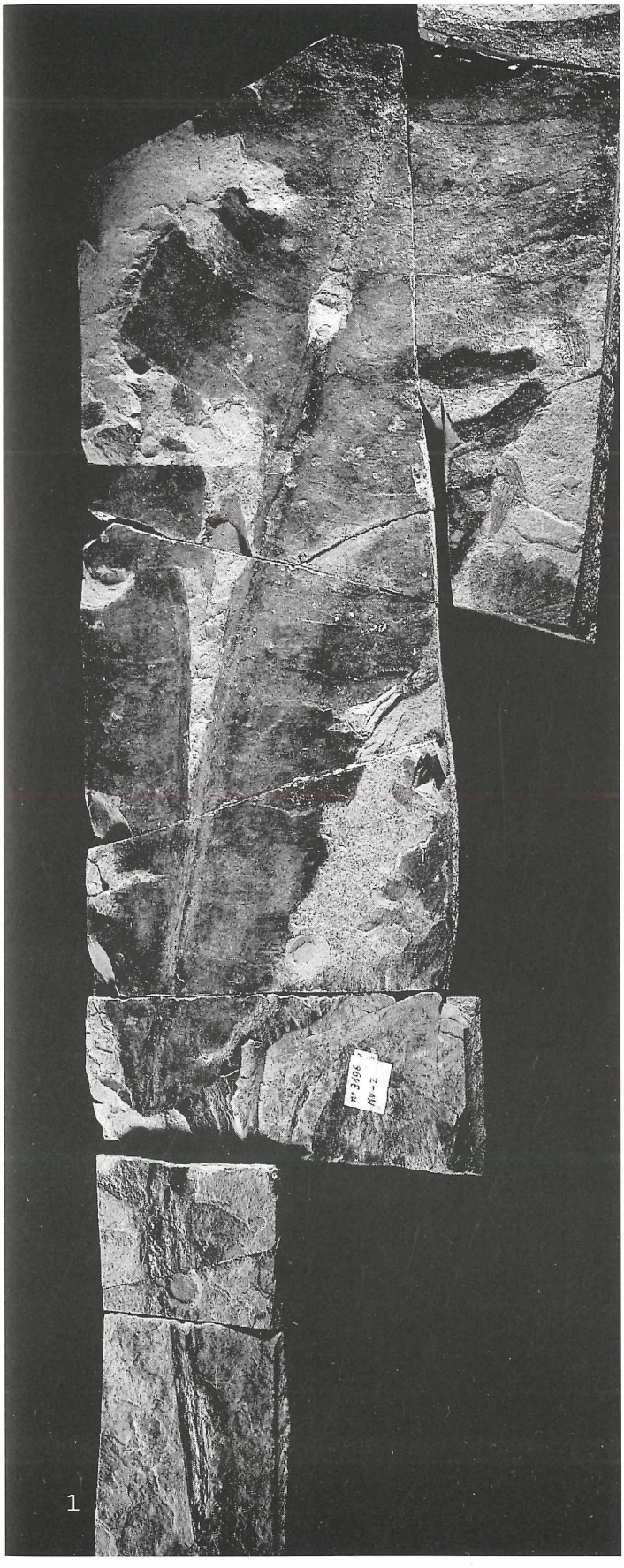
PLATE 4

Fig. 1 *Bjuvia dolomitica* n. sp.; holotype, Museo delle Regole Cortina; x 0.4

Fig. 2 *Bjuvia dolomitica* n. sp.; large specimen, Heimatmuseum Gröden (Ortisei); x 0.5

Fig. 3 *Bjuvia dolomitica* n. sp.; paratype, showing the venation quite clearly (WRI 046; Natural History Museum Bozen (Bolzano)); x 1

PLATE 4



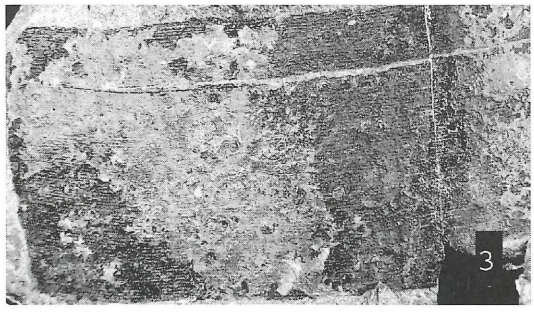


PLATE 5

Fig. 1 *Bjuvia dolomitica* n. sp.; counterpart of the holotype, showing the venation, Museo delle Regole Cortina; x 0.5

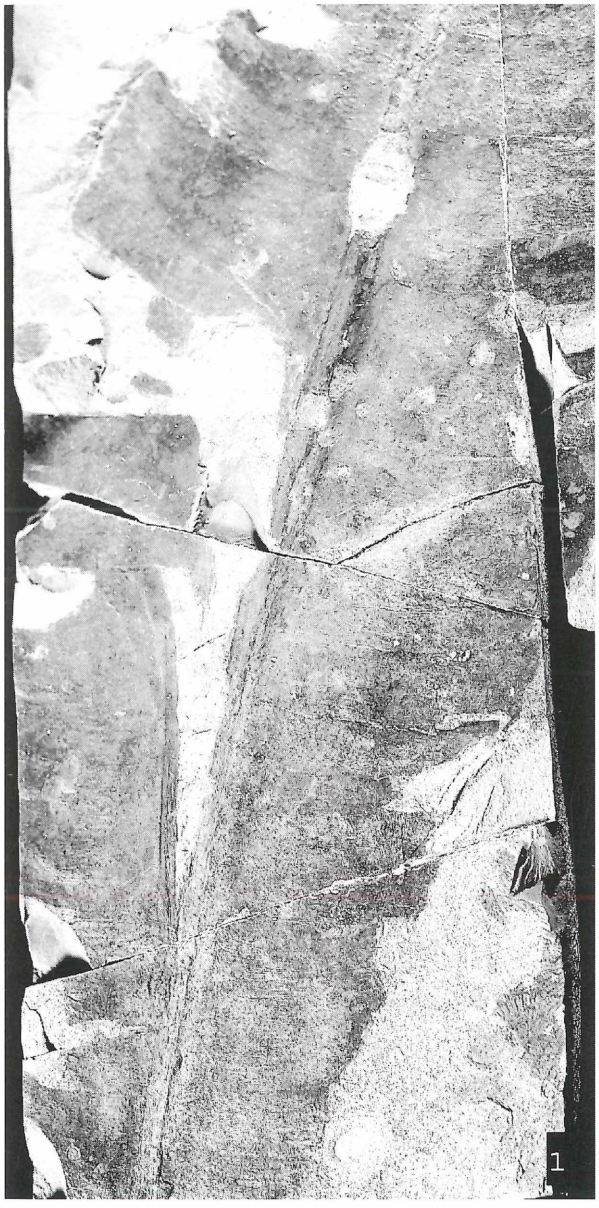
Fig. 2 *Bjuvia dolomitica* n. sp.; lower cuticle from the paratype (WRI 046) showing a stomatal zone; x 100

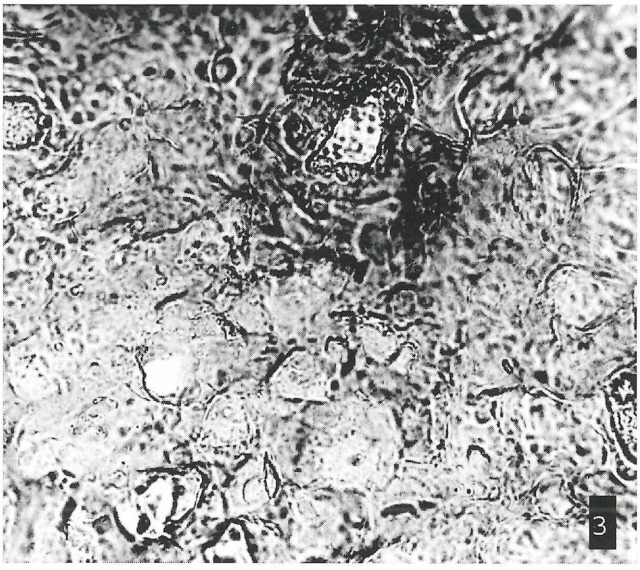
Fig. 3 *Bjuvia dolomitica* n. sp.; detail from Fig. 2 showing stomata; x 400

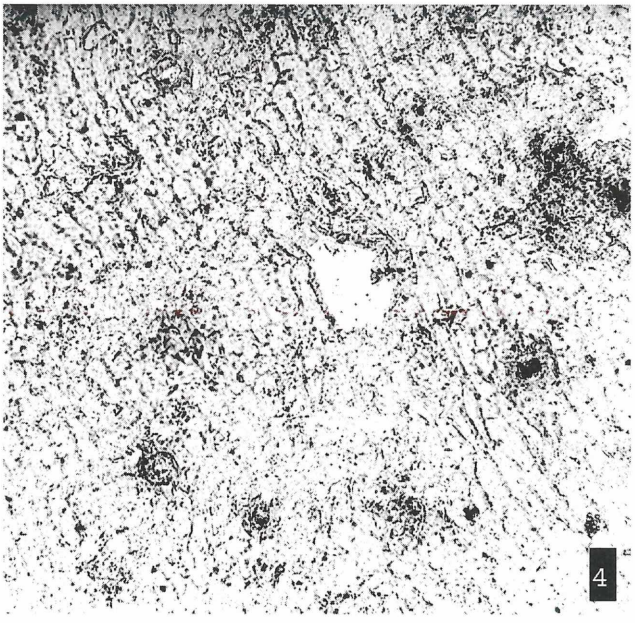
Fig. 4 *Bjuvia dolomitica* n. sp.; upper cuticle from the paratype (WRI 046); x 100

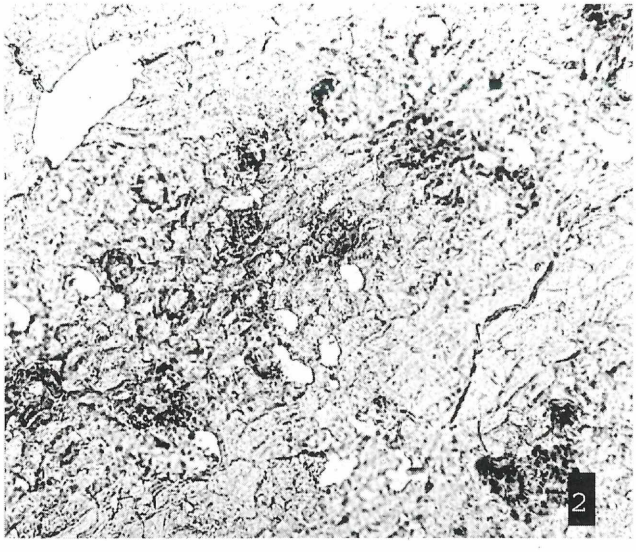
Fig. 5 *Bjuvia dolomitica* n. sp.; detail from Fig. 4 showing stomata; x 400

PLATE 5









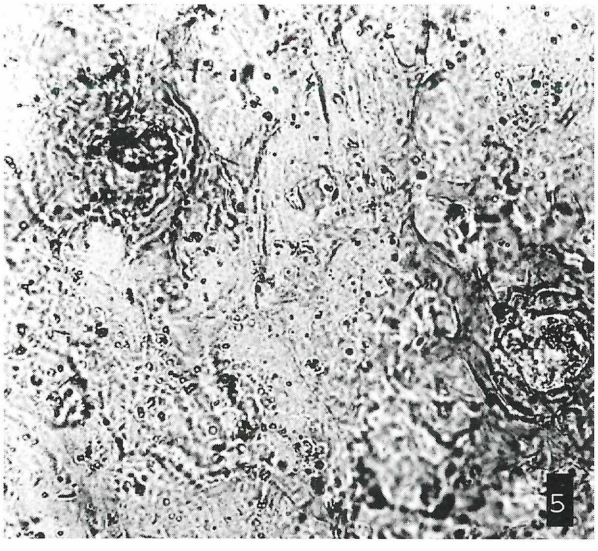


PLATE 6

Fig. 1 *Taeniopteris* sp.; small fragment (WSW 049; Natural History Museum Bozen (Bolzano)) x 1

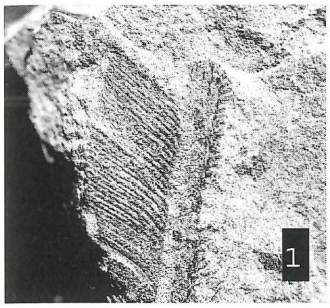
Fig. 2 *Dioonitocarpidium* sp.; specimen in the Heimatmuseum Gröden (Ortisei); x 1

Fig. 3 *Elatocladus* sp.; specimen in the Heimatmuseum Gröden (Ortisei); x 1

Fig. 4 *Yuccites vogesiacus* SCHIMPER et MOUGEOT; specimen showing venation (WRI 048; Natural History Museum Bozen (Bolzano)); x 1

Fig. 5 *Yuccites vogesiacus* SCHIMPER et MOUGEOT; typical leaf lying over another leaf at the base (WSW050; Natural History Museum Bozen (Bolzano)); x 1

PLATE 6



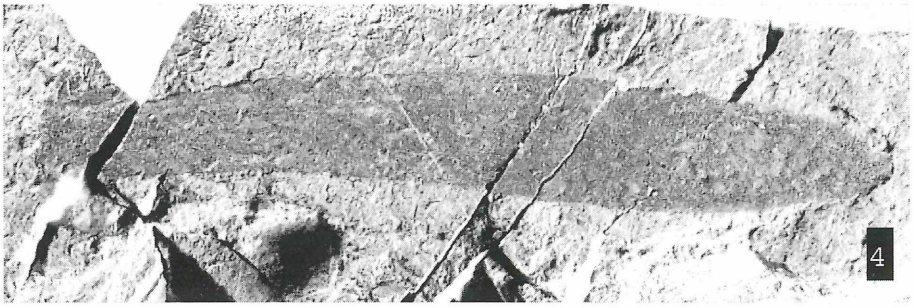


PLATE 7

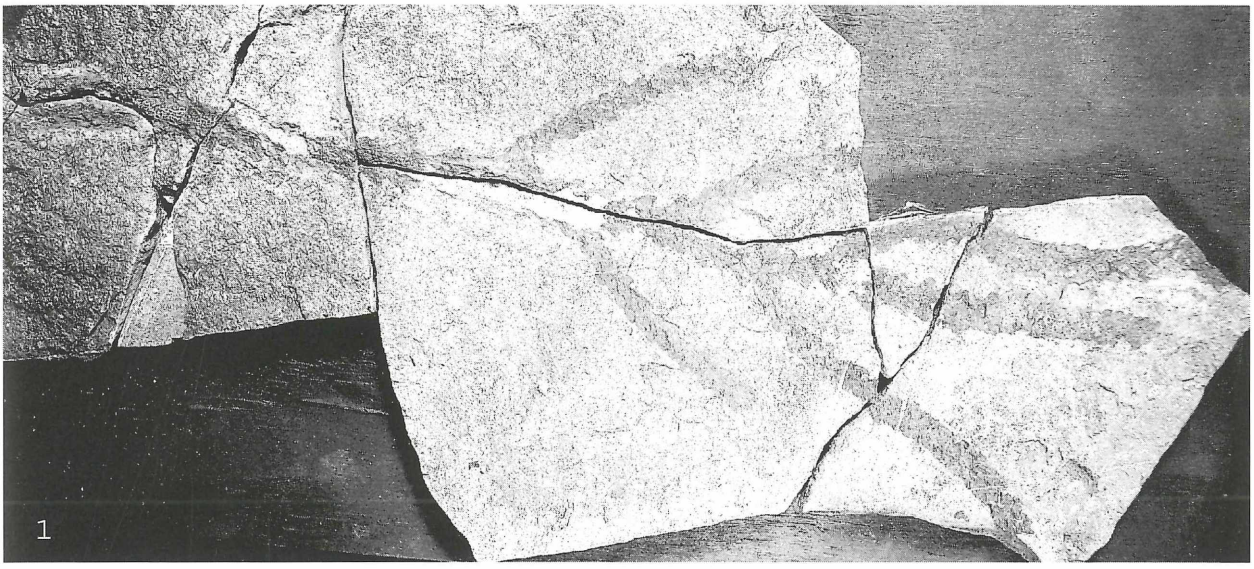
Fig. 1 *Voltzia dolomitica* n. sp.; holotype (WRI 029; Natural History Museum Bozen (Bolzano)) x 0.5

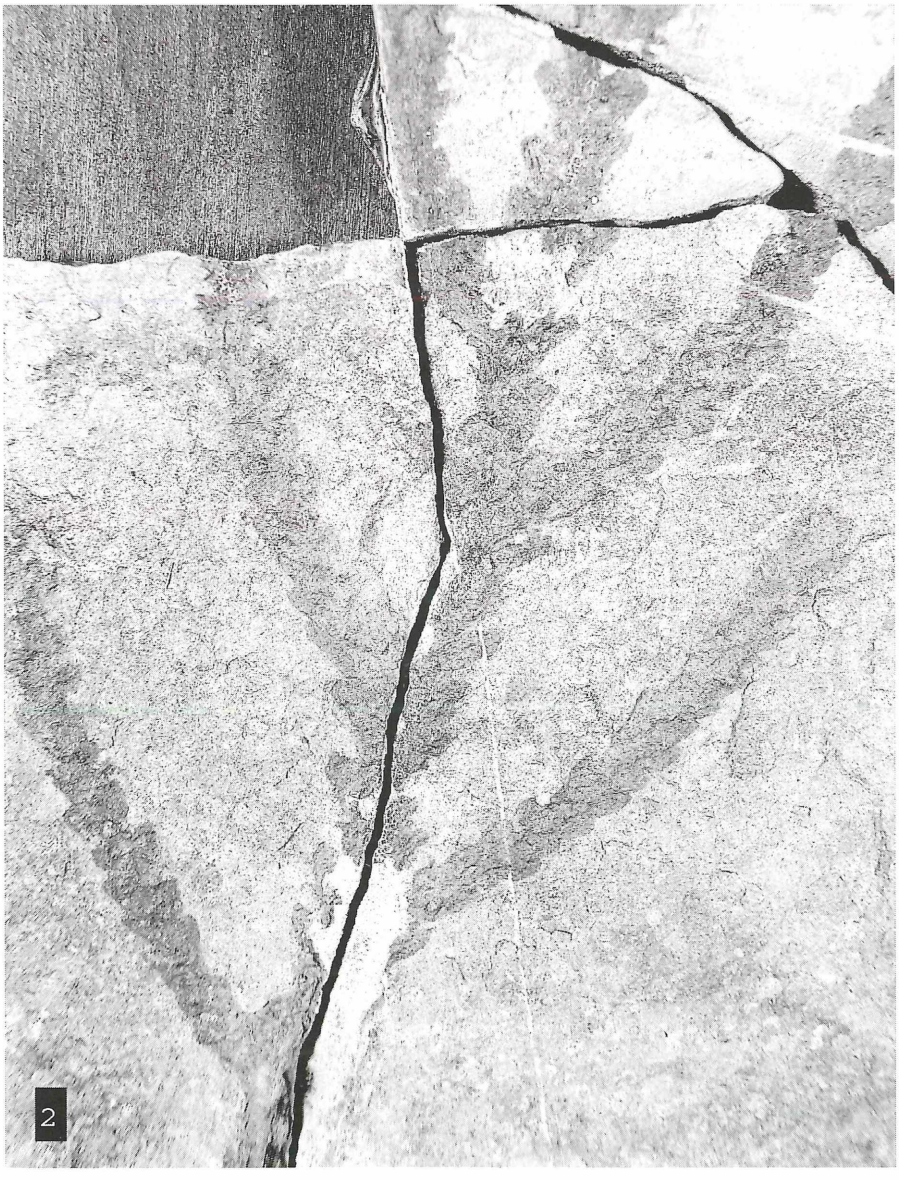
Fig. 2 *Voltzia dolomitica* n. sp.; detail from upper part of the holotype; x 1

Fig. 3 *Voltzia dolomitica* n. sp.; typical female cone (WRI 001; Natural History Museum Bozen (Bolzano)) x 1.5

Fig. 4 *Voltzia dolomitica* n. sp.; paratype, possible male cone (WIK 003; Natural History Museum Bozen (Bolzano)) x 1

PLATE 7





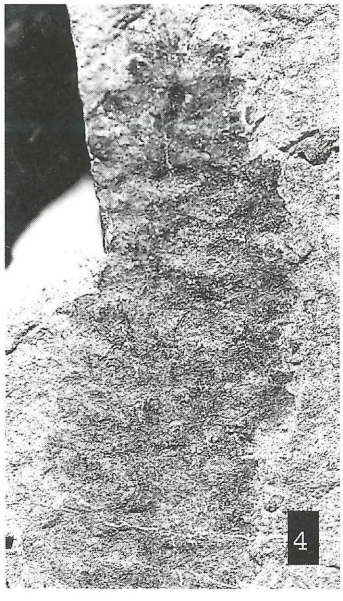


PLATE 8

Fig. 1 *Voltzia dolomitica* n. sp.; paratype, female cone (WSW001; Natural History Museum Bozen (Bolzano)) x 1.5

Fig. 1a *Voltzia dolomitica* n. sp.; an ovuliferous scale bearing only one seed (WSW023; Natural History Museum Bozen (Bolzano)) x 1.5

Fig. 2 *Voltzia dolomitica* n. sp.; paratype, shoot from which the cuticle preparations originate (WSW008; Natural History Museum Bozen (Bolzano)) x 1

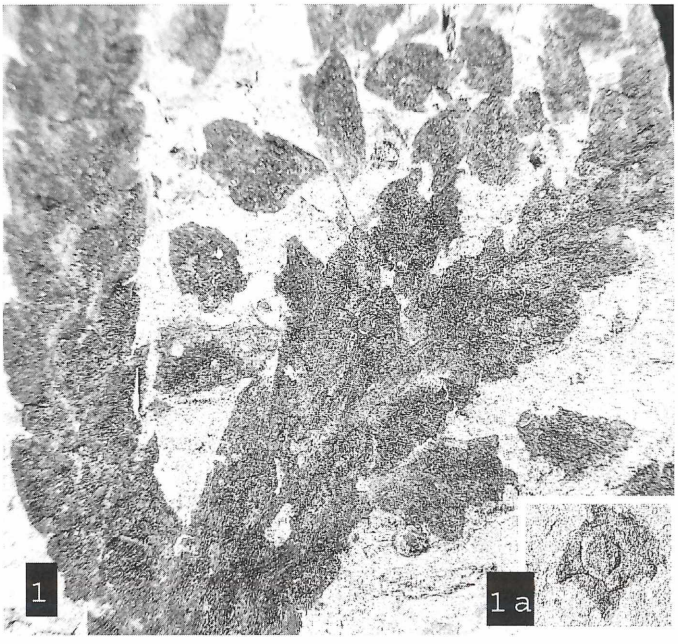
Fig. 3 *Voltzia dolomitica* n. sp.; paratype, detoriated female cone (WIK 015; Natural History Museum Bozen (Bolzano)) x 2

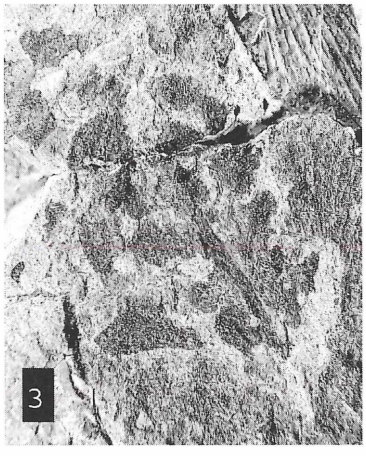
Fig. 4 *Voltzia dolomitica* n. sp.; upper cuticle from paratype WSW 008; x 100

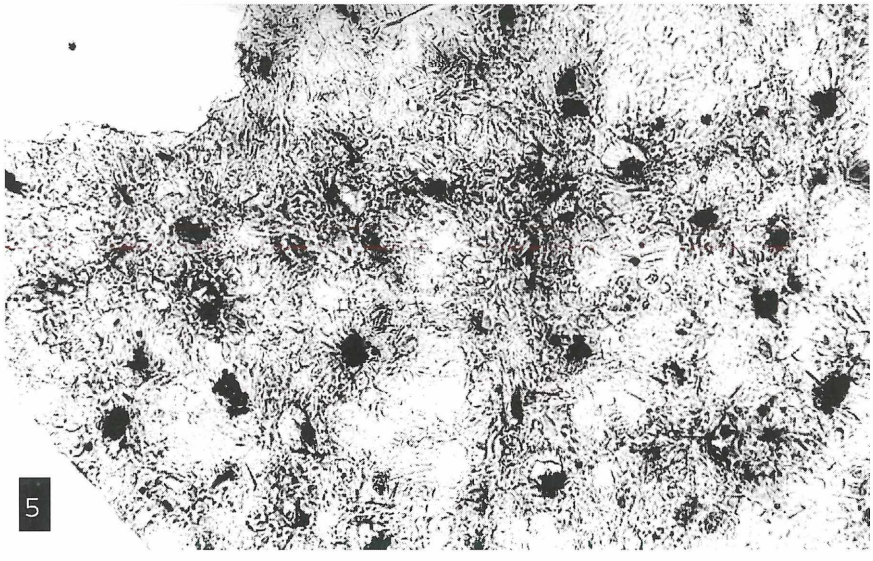
Fig. 5 *Voltzia dolomitica* n. sp.; lower cuticle from paratype WSW 008; x 100

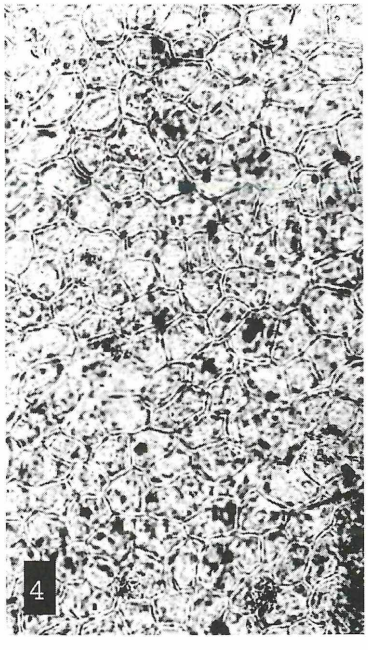
Fig. 6 *Voltzia dolomitica* n. sp.; detail from Fig. 5 showing stomata on lower cuticle; x 400

PLATE 8









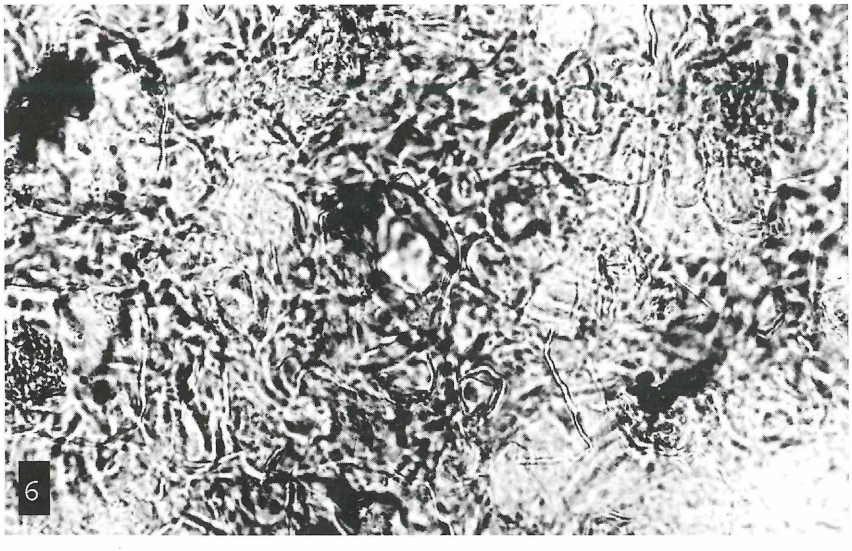


PLATE 9

Fig. 1 *Voltzia pragsensis* n. sp.; holotype (WIK 009; Natural History Museum Bozen (Bolzano)) x 1

Fig. 2 *Voltzia pragsensis* n. sp.; paratype with female cone (WSW 004; Natural History Museum Bozen (Bolzano)) x 1

PLATE 9

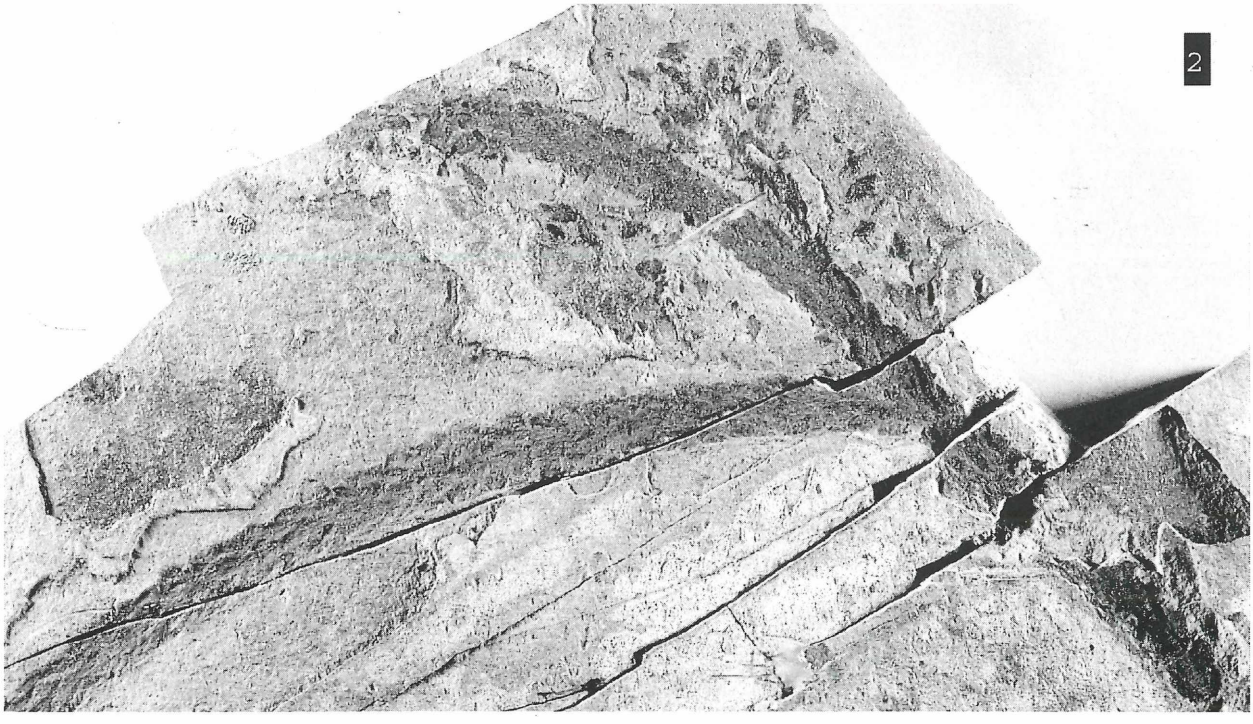


PLATE 10

Fig. 1 *Voltzia ladinica* n. sp.; holotype (WRI 006; Natural History Museum Bozen (Bolzano)) x 1

Fig. 2 *Voltzia ladinica* n. sp.; paratype, female fructification (WSW002; Natural History Museum Bozen (Bolzano)) x 1

Fig. 3 *Voltzia ladinica* n. sp.; heterophyllous ultimate shoot with the longest needles found; Heimatmuseum Gröden (Ortisei); x 1

Fig. 4 *Voltzia ladinica* n. sp.; typical heterophyllous shoot system; Heimatmuseum Gröden (Ortisei); x 1

Fig. 5 *Voltzia ladinica* n. sp.; paratype, male cone (WRI 008; Natural History Museum Bozen (Bolzano)) x 2

PLATE 10

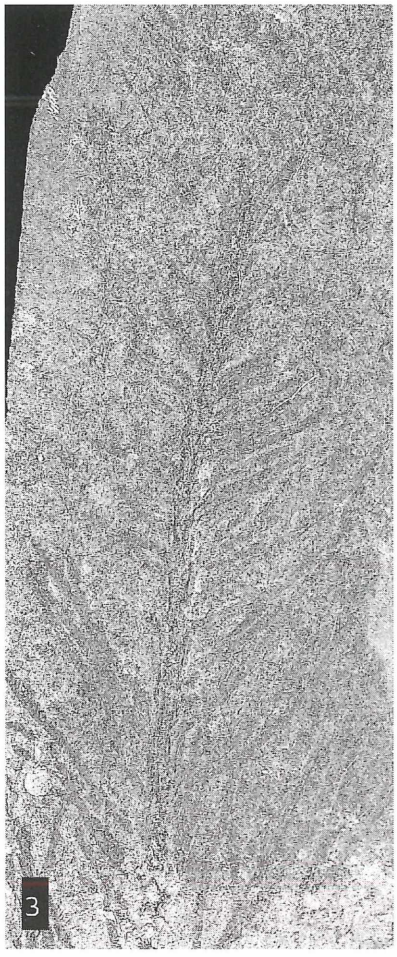


PLATE 11

Fig. 1 *Voltzia ladinica* n. sp.; cuticle from stem on the holotype, x 100

Fig. 2 *Voltzia ladinica* n. sp.; detail from Fig. 1 showing stoma; x 400

Fig. 3 *Voltzia ladinica* n. sp.; lower cuticle from a leaf on the holotype; x 100

Fig. 4 *Voltzia ladinica* n. sp.; detail from Fig. 3 showing stoma; x 400

PLATE 11