BioOne COMPLETE

The Ferns of the Late Ladinian, Middle Triassic Flora from Monte Agnello, Dolomites, Italy

Authors: Kustatscher, Evelyn, Dellantonio, Elio, and Cittert, Johanna H.A. Van Konijnenburg-Van

Source: Acta Palaeontologica Polonica, 59(3) : 741-755

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2012.0076

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

The ferns of the late Ladinian, Middle Triassic flora from Monte Agnello, Dolomites, Italy

EVELYN KUSTATSCHER, ELIO DELLANTONIO,
and JOHANNA H.A. VAN KONIJNENBURG-VAN CITTERT



Kustatscher, E., Dellantonio, E., and Van Konijnenburg-van Cittert, J.H.A. 2014. The ferns of the late Ladinian, Middle Triassic flora from Monte Agnello, Dolomites, Italy. *Acta Palaeontologica Polonica* 59 (3): 741–755.

Several fern remains are described from the para-autochthonous early late Ladinian flora of the Monte Agnello (Dolomites, N-Italy). The plants are preserved in subaerially deposited pyroclastic layers. Some ferns, known already from the Anisian and Ladinian of this area, are confirmed (*Neuropteridium elegans*), but several taxa are described for the first time (*Phlebopteris fiemmensis* sp. nov., *Cladophlebis ladinica* sp. nov., *Chiropteris monteagnellii* sp. nov.). *Cladophlebis* sp. and some indeterminable fern remains cannot yet be assigned to any family. *Phlebopteris fiemmensis* is now the oldest formally established species in the genus. The fern family Dipteridaceae (*Thaumatopteris* sp. and some fragments probably belonging to the Dipteridaceae because of their venation) has not been recorded previously from European sediments as old as the Ladinian. Although stratigraphically attributed to the late Ladinian, the flora is markedly distinct from other Ladinian floras of the Dolomites and the Germanic Basin. The flora from Monte Agnello shows a higher diversity in ferns than coeval floras from this area although characteristic elements of the Ladinian of the Dolomites such as *Anomopteris* and *Gordonopteris* are missing. The new flora misses also the Marattiales (e.g., *Danaeopsis*, *Asterotheca*) and other elements such as *Sphenopteris schoenleiniana*, typical for the Ladinian of the Germanic Basin.

Key words: Dipteridaceae, Matoniaceae, *Phlebopteris, Cladophlebis, Chiropteris*, *Thaumatopteris*, plant fossils, Ladinian, Triassic, Southern Alps, Italy.

Evelyn Kustatscher [evelyn.kustatscher@naturmuseum.it], Naturmuseum Südtirol, Bindergasse 1, 39100 Bolzano, Italy; Elio Dellantonio [elio.dellantonio@mtsn.it], Museo Geologico delle Dolomiti, Piazza SS. Filippo e Giacomo 1, 38037 Predazzo (TN), Italy;
Johanna H.A. van Konijnenburg-van Cittert [Han.Konijnenburg@naturalis.nl, j.h.a.vankonijnenburg@uu.nl], Naturalis Biodiversity Center, PO Box 9517, 2300 RA Leiden, The Netherlands; and Laboratory of Palaeobotany and Palynology, Budapestlaan 4, 3584 CD Utrecht, The Netherlands.

Received 4 June 2012, accepted 23 October 2012, available online 23 October 2012.

Copyright © 2014 E. Kustatscher et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

Fossil plants of Ladinian age from the Dolomites have been known for over 150 years. The first fragment of a fern frond from the Ladinian of the Dolomites was figured by Wissmann and Münster (1841). Later, 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; Leonardi 1953, 1968; Calligaris 1982–1983, 1986; Jung et al. 1995); for a detailed historical overview see also Wachtler and Van Konijnenburg-van Cittert (2000), Kustatscher (2004), Kustatscher et al. (2004) and Kustatscher and Van Konijnenburg-van Cittert (2005). The "Buchensteiner Schichten" and "Wengener Schichten" are considered to belong respectively to the lower and upper Ladinian (Gianolla 1993). Later, Viel (1979a, b) proposed elevating the "Buchensteiner Schichten" and "Wengener Schichten" to group level and distinguishing several formations in each group: the Buchensteiner Group includes the Buchenstein Formation, the Zoppè Sandstone and the Acquatona Formation and the Wengen Group includes the Fernazza Formation and the Wengen Formation (Gianolla 1993). These groups are no longer used in contrast to the formations. The occurrence of plant fossils in the Fernazza Formation and Wengen Formation (both late Ladinian) was confirmed recently by three floras with well-defined geographic and stratigraphic positions (see also Kustatscher 2004). The stratigraphic attribution of the historical collections is often complicated or even impossible. The common feature of all of these Ladinian floras from the Dolomites is

 http://dx.doi.org/10.4202/app.2012.0076

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

a dominance of the conifers (*Voltzia*, *Pelourdea*), while cycadophytes, seed ferns, ferns, horsetails, and lycophytes are much rarer. This was related to climatic conditions (an arid climate on the mainland), edaphy (immature soil), or taphonomy (caused by selection during transport; Kustatscher and Van Konijnenburg-van Cittert 2005). Since the palynological analyses of some of the localities suggested a generally warm and humid climate, the composition of the flora was related mostly to taphonomy (for more details see Kustatscher and Van Konijnenburg-van Cittert 2005). Thus the discovery of a para-autochthonous flora from the early late Ladinian of Monte Agnello is of special interest. Because of the shorter transport of the plant remains the flora is much more diversified and composed of several ferns (discussed here), seed ferns (e.g., *Scytophyllum*), cycadophytes (e.g., *Bjuvia*, *Nilssonia* and *Apoldia*), and conifers (e.g., *Voltzia*).

This paper discusses the geology and stratigraphy of the new plant fossil locality and focuses on the ferns of this flora since the Triassic is an important period for the appearance of some leptosporangiate fern families such as the Dicksoniaceae, Matoniaceae, Dipteridaceae, and Hymenophyllaceae (Taylor et al. 2009). Indeed some taxa of the new flora represent some of the oldest representatives of the Matoniaceae and Dipteridaceae and give, thus, new insights in the first appearance of these families in the fossil record, especially in Europe.

Institutional abbreviations.—MGP, Museo Geologico delle Dolomiti, Predazzo. Specimens occurring on the same rock slab are identified by different capital letters following the catalogue number.

Geological setting

During the early late Ladinian, the Dolomites were subjected to significant volcanic activity. The volcanic complexes were mostly submarine although locally, such as in the area of Predazzo, subaerial eruptive centres also existed. In the north-eastern sector of the Fiemme Valley, a central vent volcanic complex was created (Hoernes 1912; Leonardi 1968) that was subjected to a series of caldera collapses, which gave origin to annular and semi-annular intrusive complexes in the central part (Monte Mulat). Metamorphic aureoles were associated with such intrusions. Monte Agnello (Fig. 1) represents an area that was only marginally influenced by these events and, therefore, the stratigraphic succession is well preserved there (Fig. 2).

An approximately 250 metres thick volcanic succession overlies a carbonate platform of late Anisian to Ladinian age (Sciliar Dolomite). The volcanic succession is composed of "explosion breccia" at the base, succeeded by lava breccia and alternations of lava flows and tuffs (Calanchi et al. 1977, 1978; Lucchini et al. 1982). The "explosion breccia", as figured in the geological map of Vardabasso (1930), comprises greyish-greenish clastic rocks. The lithic fragments are represented—in order of distribution—by calcareous, volcanic and metamorphic fragments, clastic rocks and isolated crystals, all related to the Permo-Triassic volcano-sedimentary succession and the underlying metamorphic basement. The components of the breccia are bound by carbonate and/or chlorite-serpentine cement (Calanchi et al. 1977). The thickness of this explosion breccia varies between 25 metres at the Monte Agnello and 10 metres at Censi (Fig. 2).

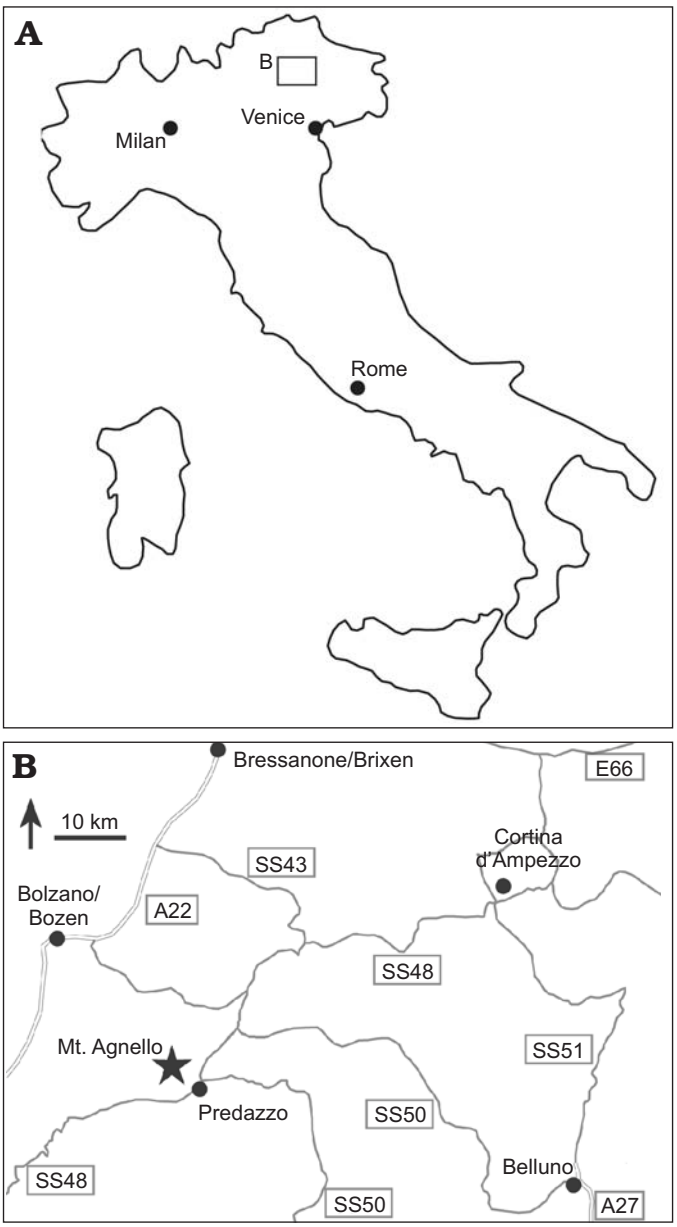


Fig. 1. **A**. Map of Italy indicating the location of the Monte Agnello area (Dolomites, N-Italy). **B**. Map of the Predazzo area indicating the position of Monte Agnello.

The deposit accumulated in an essentially subaerial environment. The depositional characters (e.g., bomb sags, antidunes, accretionary lapilli) can be attributed to falls and surges deposited in sandwave and massive facies. These are related to explosive phreatic activity (Calanchi et al. 1977;

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

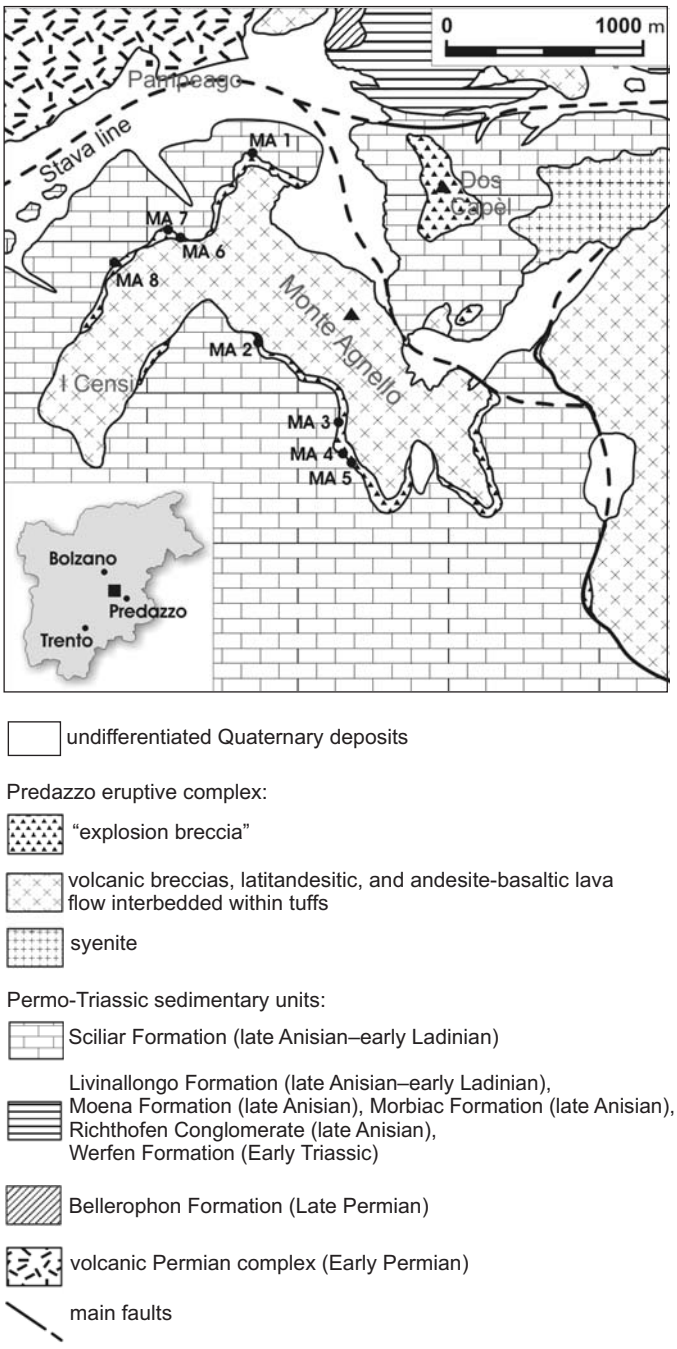


Fig. 2. Geological sketch of the Monte Agnello area (Dolomites, N-Italy), modified from Vardabasso (1930). MA1–MA8, fossil sites.

Lucchini et al. 1982). The flora described herein was preserved in the tuffs below the "explosion breccia" of the volcanic succession at Predazzo (sensu Calanchi et al. 1977).

Material and methods

The new locality crops out on the northwestern slope of M. Agnello-Censi (Fig. 2). About 1000 specimens have been collected from 8 distinctive sites denoted by the prefixes MA1–MA8. The detailed stratigraphic analyses of the fossiliferous outcrops show a carbonate platform covered by clay of variable thickness (from ca. 10 to more than 60 cm) of variable colour (yellow, red, brown, dark grey). This is succeeded by about 50 cm of tuffs (both coarse and fine-grained), locally rich in accretionary lapilli or, more rarely, small lithic lapilli. Higher in the succession are beds of lapilli-tuff with angular clasts up to several centimetres in diameter (lithofacies B2). The plant fossils are concentrated in the tuff interval (lithofacies B1) near the base of the depositional sequence, directly in contact with the clay bed or only slightly above it (within 50 cm of the clay bed).

The plants occur in several decimetre-long fragments; almost complete leaves are also present. The plant remains are preserved mostly as detailed impressions. The casts are almost three-dimensional even when the organic material is completely degraded, and veins are preserved as impressions rather than organic material. In some cases the leaves, especially *Chiropteris*, are characterized by "holes" related to the lapilli present in the rock.

Ferns are mostly preserved as frond or pinna fragments. The venation is well preserved in some cases, but in most taxa the venation can only be distinguished in a few specimens whereas the majority of the remains are only preserved as casts or strongly carbonised material. Thus no in situ spores could be extracted from the pinnules.

Systematic palaeontology

Division Pteridophyta Schimper, 1879

Order Osmundales Link, 1833

Order Osmundaceae Berchtold and Presl, 1820

Genus *Neuropteridium* Schimper in Schimper and Schenk, 1879

Type species: *Neuropteridium voltzii* (Brongniart, 1828) Schimper, 1879; Vosges (France); Grès bigarre (Buntsandstein, early Anisian).

Neuropteridium elegans (Brongniart, 1928) Schimper in Schimper and Schenk, 1879

Fig. 3A.

1828 *Nevropteris elegans* Brongniart; Brongniart 1928b: 54 (name only).
1828 *Nevropteris elegans* Brongniart; Brongniart 1828a: 247, pl. 74: 1, 2.
1844 *Neuropteris elegans* Brongniart subgenus *Neuropteridium* Schimper; Schimper and Mougeot 1844: 80, pl. 39.
1879 *Neuropteridium elegans* (Brongniart) Schimper; Schimper, and Schenk 1879: 117.
1978 *Neuropteridium elegans* (Brongniart) Schimper et Mougeot; Grauvogel-Stamm 1978: 26, pl. 2: 3.
2006 *Neuropteridium elegans* (Brongniart) Schimper; Van Konijnenburg-van Cittert et al. 2006: 946–948, pl. 1: 1, 2, 8, text-fig. 5A (see for more exhaustive synonymy).

Material.—MGP 191/35, 194/83A–B, two basal frond fragments belong to this species (in one case with the counterpart as well); Monte Agnello (Dolomites, N-Italy), early late Ladinian.

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Description.—The frond fragments reach 65 mm length and 18 mm width (MGP 194/83, Fig. 3A). Roundish pinnules (7–9 mm long and 5–7 mm wide) arise from the rachis (3.5–4 mm wide). The pinnules have a typical neuropterid venation pattern.

Discussion.—Three species are distinguished in the Triassic of Europe; *Neuropteridium elegans, Neuropteridium voltzii* (Brongniart, 1828) Schimper in Schimper and Schenk, 1879 and *Neuropteridium grandifolium* (Schimper and Mougeot, 1844) Compter, 1883 (for more discussions see Van Konijnenburg-van Cittert et al. 2006). *Neuropteridium elegans* is characterized by the smallest fronds, *N. grandifolium* is distinguished by its large, obtuse pinnules (50 × 25 mm) with an auriculate basis and *N. voltzii* has a broad rachis (10 mm) and relatively long pinnules (40–50 [max 80] mm × 10 mm).

Stratigraphic and geographic range.—Early Anisian (Buntsandstein) of the Germanic Basin (e.g., Brongniart 1828a, b; Blanckenhorn 1886; Gothan 1937; Grauvogel-Stamm 1978), Pelsonian (late Anisian) to late Ladinian of the Dolomites (Kustatscher and Van Konijnenburg-van Cittert 2005; Van Konijnenburg-van Cittert et al. 2006).

Order Filicales Bower, 1899

Family Matoniaceae Presl, 1847

Genus *Phlebopteris* Brongniart, 1836

Type species: *Phlebopteris polypodioides* Brongniart, 1828; Scarborough (Yorkshire, England); Jurassic.

Phlebopteris fiemmensis sp. nov.

Figs. 3B–F, 4A.

Etymology: In reference to the geographic position, the Monte Agnello belongs to the Fiemme Valley.

Type material: Holotype: MGP 191/11B, almost entire pinnae with preserved vein structure, here designated (Fig. 3B). Paratypes: MGP 181/57B, fertile specimen; MGP 181-57A, palmate structure of the frond, here designated (Fig. 3C, D).

Type locality: Monte Agnello, Dolomites, N-Italy.

Type horizon: A tuff layer in the basal part of "explosion breccia" of the volcanic succession of Predazzo (sensu Calanchi et al. 1977), Ladinian, Middle Triassic.

Material.—MGP 63/70, 181/57A–C, 191/11A–B, all from type locality and horizon.

Diagnosis.—Pedate (palmately dissected) frond with at least 14 pinnae. Pinnae lanceolate with longest pinnules in the middle part, proximally pinnules almost fusing. Pinnules lanceolate to falcate, arising at c. 70–80°. Midvein distinct, slightly wavy, secondary veins distant, delicate, arising at an acute angle, bifurcating once or simple. Sporangia arranged in circular sori in two rows along the midrib consisting of a receptaculum surrounded by a ring of sporangia. No indusium present.

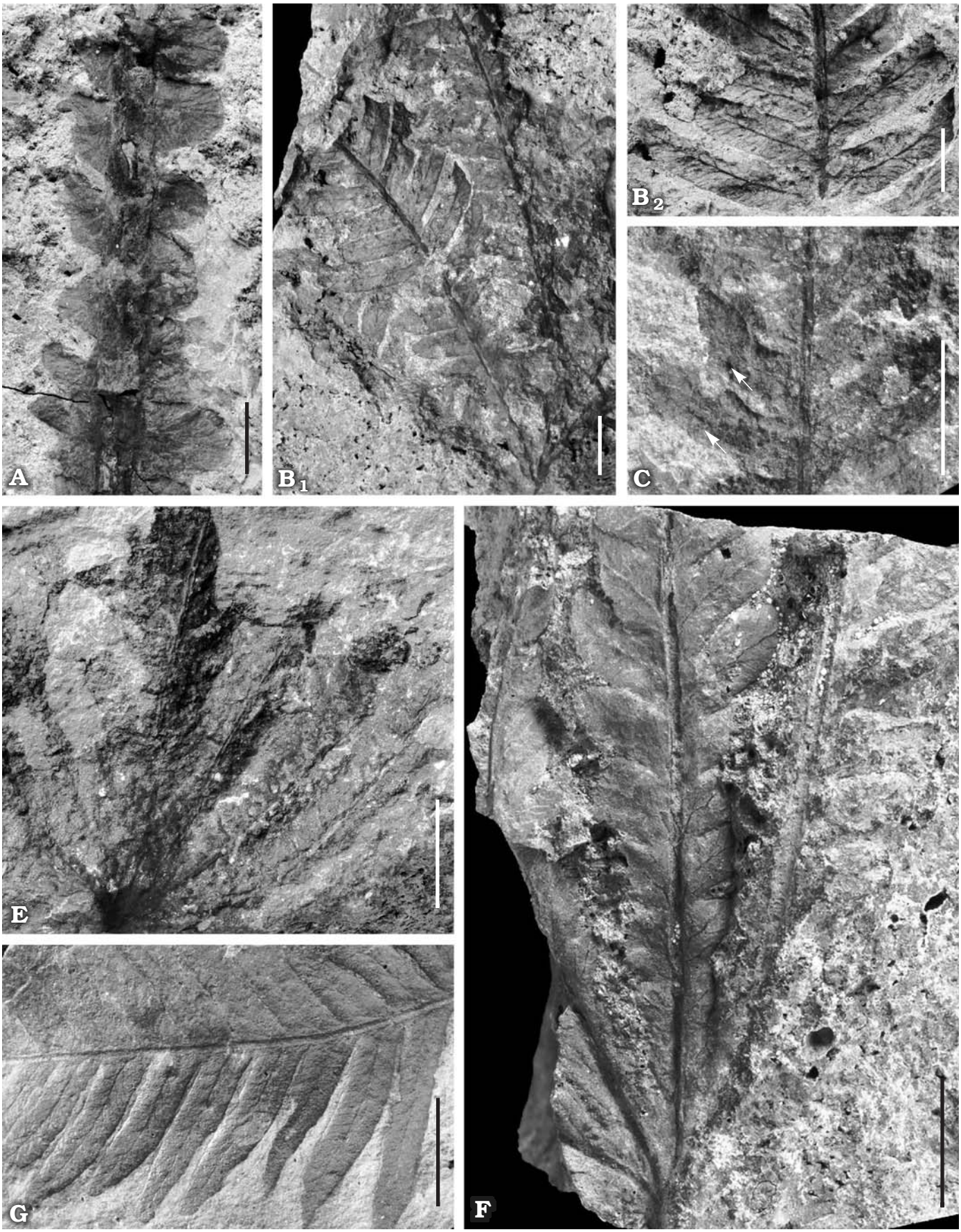
Description.—The frond fragments are up to 70 mm long and 60 mm wide (MGP 191/11A, 191/11B; Fig. 3B). Six to fourteen pinna fragments have been counted arising from the main rachis (1–2 mm), from two short arms (MGP 181/57A; Fig. 3D). The pinna fragments are lanceolate, up to 70 mm in length and about 20 mm in width (MGP 191/11A; Fig. 3F). The pinna fragments are inserted closely. The proximal pinnules are almost fused with each other (MGP 63/70; Fig. 3E). The lanceolate to falcate pinnules with a pointed apex arise alternately at an angle of 70–80°. The base is broadly attached to the rachis, connecting the adjacent pinnules. They increase in length throughout the proximal half of the lamina, from about 5 mm long and 2 mm wide at the base, up to 8–11 mm long and 3 mm wide in the middle part of the frond. Apically the pinnules decrease again in size (MGP 191/11B; Fig. $3B_2$). The midvein is distinct, slightly wavy in the apical part of the larger pinnules and straight in small pinnules. Secondary veins arise at an acute angle and are widely spaced. They are delicate, simple or bifurcate once near the base (MGP 63/70; Fig. 3E).

So far only a few fertile fragments have been found (MGP 181/57B–C; Fig. 3C). They have sori positioned on two sides of the midrib consisting of a small number of sporangia, probably around six sporangia (MGP 181/57B; Fig. 3C). No indusium is evident.

Comparison.—In *Phlebopteris* sp. from the late Ladinian of Thale (Germany), the pinnules are up to 25 mm long and 3–3.5 mm wide with a rounded apex arising perpendicularly from the rachis (2 mm wide). The secondary veins arise at 60–70°, forking once or twice and the sori consist of circa eight free sporangia (Kustatscher and Van Konijnenburg-van Cittert 2011). *Phlebopteris smithii* (Daugherty, 1941) Arnold, 1947 and its junior synonym *P. utensis* Arnold, 1956 (see Ash et al. 1982) from the Late Triassic of the USA differ because of the larger pinna dimensions (18 cm long), the more elongate pinnules (10–25 mm long) and its simpler lateral veins. In *P. crenulata* Weber, 2008 from the Late Triassic of Mexico, the margin of the lamina is crenulate and the venation is reticulate, both characters missing in *P. fiemmeae*. In *P. otongensis* Weber, 2008 from the Jurassic of Mexico, the pinnules are linear to triangular, smaller than in our material (5.5 x 1.5 mm), attached almost perpendicularly to the rachis and with crowded and in some cases anastomosing veins (Weber 2008). *Phlebopteris angustiloba* (Presl, 1838) Hirmer and Hörhammer, 1936 from the Rhaeto-Liassic of Europe has simple secondary veins arising at an angle of 70–90° which define "fields". *Phlebopteris muensteri* (Schenk, 1867) Hirmer and Hörhammer, 1936 from the Early

Fig. 3. Osmundaceae and Dipteridaceae from the tuff layer in the basal part of "explosion breccia" (late Ladinian, Middle Triassic) of Monte Agnello, → Dolomites, N-Italy. **A**. Frond fragment of *Neuropteridium elegans* (Brongniart, 1828) Schimper, 1879 (MGP 194/83A). **B**–**G**. *Phlebopteris fiemmensis* sp. nov. **B**. Holotype (MGP 191/11B), almost complete pinnae with vein structure preserved and attachment area visible (B_1), detail of the vein structure (B_2). **C**. Paratype, fertile frond fragment with sori on both sides of the midrib (arrow; MGP 181/57B). **D**. Paratype, detail of the palmate structure of the frond (MGP 181/57A). **E**. Pinnae with detail of the venation (MGP 63/70). **F**. Frond fragment (MGP 191/11A). Scale bars A, B_1, D, E 10 mm; B_2, C, F 5 mm.

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use



Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Jurassic of Europe and Asia has larger pinnules (at least 60 mm × 4–5 mm), a thick midrib and simple to twice forked lateral veins with a higher vein concentration (30–40 per cm). *Phlebopteris muensteri* from the Late Triassic of Sweden (Pott and McLoughlin 2011) resembles the pinnule shape of Fig. 3E, but the pinnules of *P. fiemmensis* seem shorter with a denser venation. In *Phlebopteris formosa* (Givulescu and Popa, 1998) H.-J. Schweitzer, U. Schweitzer, Kirchner, Van Konijnenburg-van Cittert, Van der Burgh, and Ashraf, 2009 from the early Jurassic of Romania, the pinnules are bigger (80–150 mm long and 10–14 mm wide) with lateral veins arising at 2–3 mm interval and bifurcating often to form an almost fasciculate structure. *Phlebopteris tracyi* Ash, 1991 from the Jurassic of Oregon (USA) differs because of the reticulate structure of the lateral veins, larger pinnae (up to 50 cm long) and pinnules (40–60 × 3–7 mm). The new species differs from *P. polypodioides* Brongniart, 1836 and from *P. dunkeri* (Schenk, 1871) Schenk, 1875 from the Jurassic of Europe and Asia because of the typical anastomosing venation in the latter species (Van Konijnenburg-van Cittert 1993). *Phlebopteris fiemmeae* shows some resemblance to *P. woodwardii* Leckenby, 1864 from the Jurassic of Europe with its simple secondary veins; in the latter species the lateral veins arise almost perpendicularly. Anastomoses may also occur in *P. woodwardii* Leckenby, 1864 (Harris 1961). Additionally, the lamina of *P. woodwardii* is very thick and is commonly preserved as fusain.

Discussion.—Only one fragment shows the attachment of the pinnae. It seems that there are two short basal arms on which the pinnae are attached. Unfortunately, the fragment is small and may belong to an unexpanded leaf. The fertile material confirms the attribution to the genus *Phlebopteris*.

Phlebopteris is typically a Late Triassic–Jurassic genus. So far, the oldest species are known from the Carnian or Norian of North America (Chinle Formation, *P. smithii*) or Europe (*P. muensteri*), and it becomes widespread during the Jurassic and has its latest record in the Early Cretaceous (Van Konijnenburg-van Cittert 1993). Only a few fragments have been found in the Ladinian so far. Recently, fertile frond fragments were described as *Phlebopteris* sp. from the late Ladinian of Thale, Germany (Kustatscher and Van Konijnenburg-van Cittert 2011) because they were too badly preserved to identify them to species level. Thus, *Phlebopteris fiemmensis* from Monte Agnello is now the oldest formally established species in the genus, although the family seem to appear in the early Middle Triassic of Antarctica (Millay and Taylor 1990).

Stratigraphic and geographic range.—Late Ladinian of Monte Agnello, Dolomites, Italy.

Family Dipteridaceae

Genus *Thaumatopteris* Goeppert, 1841

Type species: *Thaumatopteris muensteri* Göppert, 1841; Bayreuth (Bavaria, Germany); Rhaetian (Late Triassic).

Thaumatopteris sp.

Fig. 4B.

Material.—MGP 63/80, pinna fragment, Monte Agnello, Dolomites, N-Italy, early late Ladinian.

Description.—One pinna fragment 55 mm long and 13 mm wide is characterized by a very distinct midrib and an entire margin (MGP 63/80; Fig. 4B). The lateral veins are distinctly reticulate with meshes that are coarser near the midrib (1–2 mm wide) and finer near the margin.

Discussion.—Unfortunately the fragment is small and does not provide any details on the frond and pinna morphology, thus attribution to a species is impossible. The venation pattern, however, attributes this specimen to *Thaumatopteris* (see e.g., Nathorst 1907; Schweitzer et al. 2009).

?Dipteridaceae indet.

Fig. 4C, D.

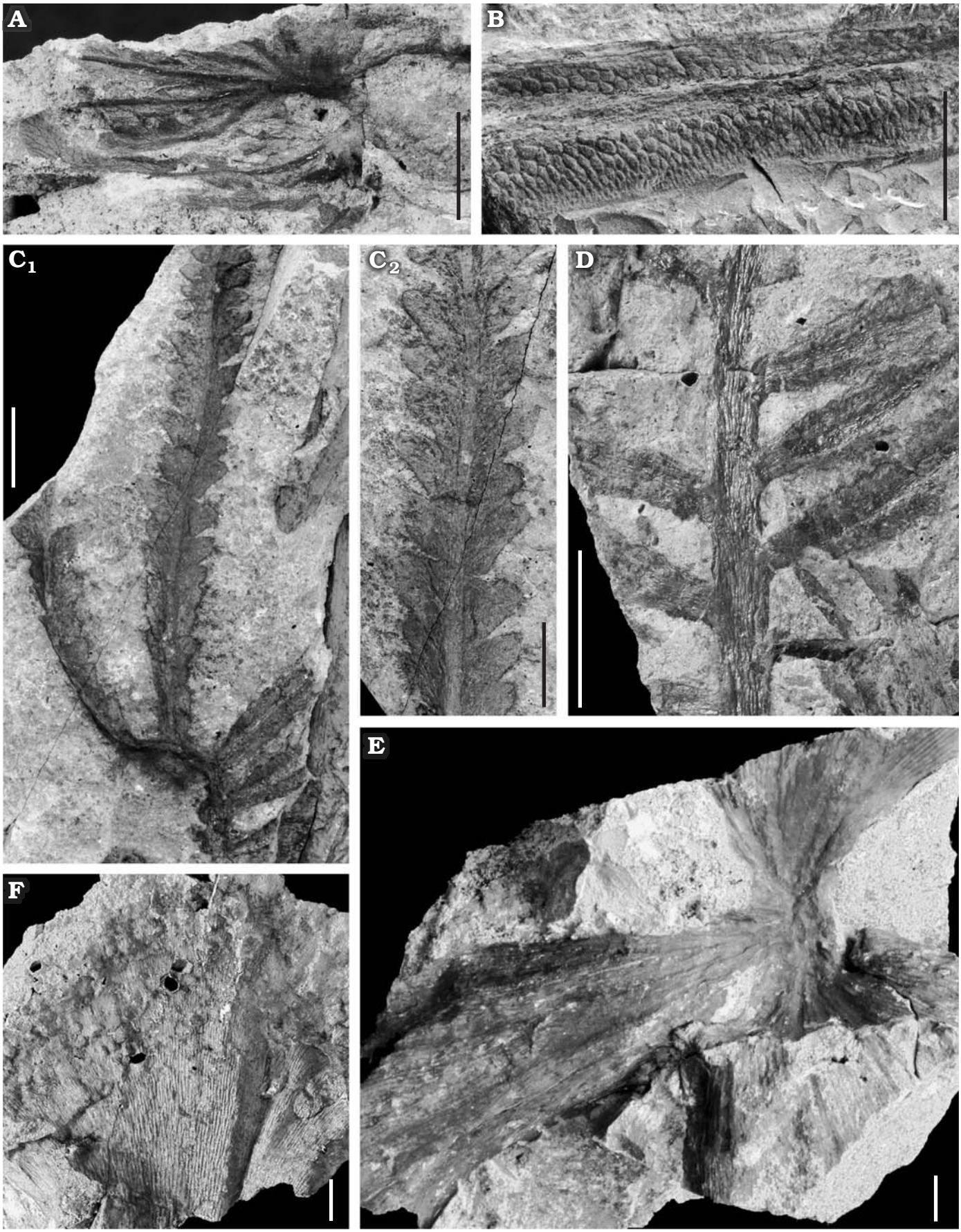
Material.—MGP 194/2A–B, 194/103, 196/41, frond fragments, Monte Agnello, Dolomites, N-Italy, early late Ladinian.

Description.—Frond fragments are up to 110 mm long and 70 mm broad. Pinnae arise alternately at c. 6 mm distance from a rachis of about 4 mm width (e.g., MGP 194/2A; Fig. 4D) The pinna fragments are 60 mm long and 10 mm wide, with a deeply incised lamina (MGP 194/2B; Fig. 4C). The lobes with a rounded apex are 3.5–7 mm long and—separated by sinuses—2.5–4 mm deep but the incisions never reach the midrib. The midrib is thick (~ 1 mm). The basal part of the pinnae and the rachis are characterized by longitudinal striae (MGP 194/2A; Fig. 4D). Each lobe has a distinct secondary vein; tertiary veins are indistinct in the lamina (MGP 194/2B; Fig. 4C_2).

Discussion.—These specimens show several characters of the Dipteridaceae, such as the partly pedate frond organization. But most of the pinnae are arranged pinnately, and no tertiary venation is visible that might render an assignment to this family possible. Dipteridaceae are characterized by a pedate (palmately dissected) frond arrangement with pinnae dissected to a certain degree, and it is the only fern family occurring in the Mesozoic in which all members are characterized by reticulate venation (see e.g., Wagner 1979). This is in contrast to some *Phlebopteris* species that show occasional anastomoses, but no completely reticulate venation.

Fig. 4. Fern remains from the tuff layer in the basal part of "explosion breccia" (late Ladinian, Middle Triassic) of Monte Agnello, Dolomites, N-Italy. → **A**. *Phlebopteris fiemmensis* sp. nov., young frond (MGP 181/57A). **B**. *Thaumatopteris* sp., pinnae fragment (MGP 63/80). **C**, **D**. ?Dipteridaceae indet. **C**. Frond fragment (MGP 194/2B) (C_1), detail of pinnae with secondary venation (C_2). **D**. Frond fragment with striate attachment area of the pinnae (MGP 194/2A). **E**, **F**. *Chiropteris monteagnellii* sp. nov. **E**. Holotype, most complete frond fragment (MGP 194/8A). **F**. Paratype, frond fragment with clear net venation (MGP 194/95B). Scale bars 10 mm, except E 5 mm.

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use



Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

It is an important fern family during the Late Triassic to Cretaceous with several genera (e.g., *Clathropteris*, *Dictyophyllum*, *Thaumatopteris*, *Camptopteris*, *Hausmannia*, *Goeppertella*) occurring worldwide (Tidwell and Ash 1994; Collinson 1996). The present material shows some resemblance to *Dictyophyllum* with its deeply divided lateral pinna segments and to the narrower pinnae of *Camptopteris* (Nathorst 1906). It might even be an aberrant specimen of *Thaumatopteris* or *Goeppertella*. But as long as no specimens with a clear venation have been found, the material cannot be attributed to a family or genus.

Order indet.

Family indet.

Genus *Chiropteris* Kurr in Bronn, 1858

Type species: *Chiropteris digitata* Kurr ex Bronn, 1858; Sinsheim near Heidelberg (Germany); Erfurt Formation (Longobardian, Middle Triassic).

Chiropteris monteagnellii sp. nov.

Figs. 4E, F, 5A, B.

Etymology: In reference to the geographic location of the fossils at the Monte Agnello.

Type material: Holotype: MGP 194/8A, most complete specimen, here designated (Fig. 4E). Paratypes: MGP 194/95B (reticulate vein structure), MGP 191/10A (several petioles coming together); both here designated (Figs. 4F, 5A).

Type locality: Monte Agnello, Dolomites, N-Italy.

Type horizon: A tuff layer in the basal part of "explosion breccia" of the volcanic succession of Predazzo (sensu Calanchi et al. 1977), Ladinian, Middle Triassic.

Material.—MGP 63/74, 63/75A–B, 171/25, 191/9A–D, 191/10A–C, 191/12, 191/17A–C, 191/19A–B, 191/29, 191/36, 191/77A–B, 191/78, 194/8A–B, 194/17, 194/90, 194/95A–B, 194/103, all from type locality and horizon.

Diagnosis.—Funnel-shaped leaves with elongate, thick petiole characterized by longitudinal striae. Lamina spathulate, probably only secondarily incised to form several lobes, characterized by anastomosing venation forming very narrow meshes without any "midrib". Margin entire.

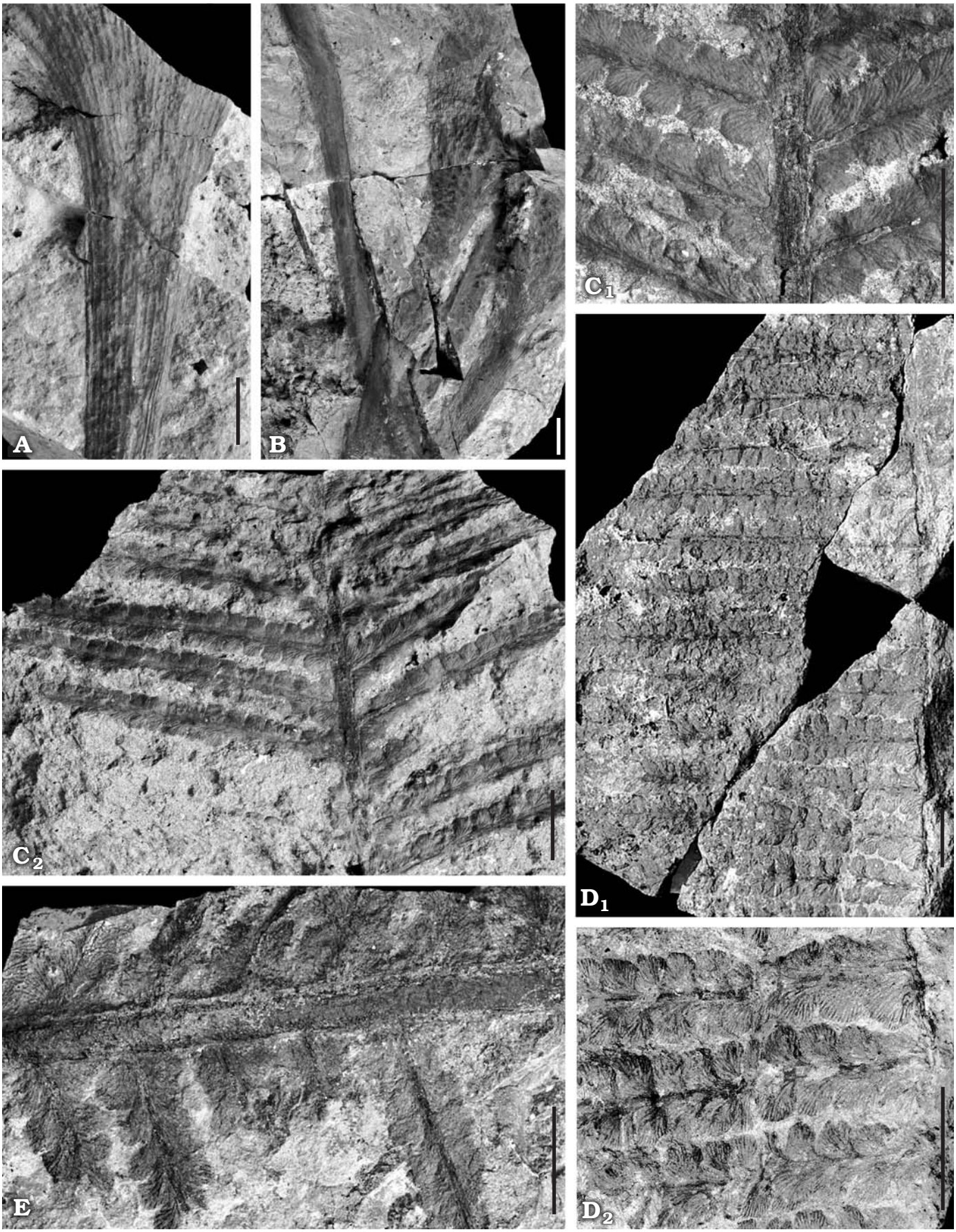
Description.—Thirteen rock samples contain leaf remains belonging to *Chiropteris*. Several slabs are compound and contain the fragments of more than one frond. The frond fragments are up to 200 mm long and 120 mm wide (MGP 194/8A; Fig. 4E). The frond was originally funnel-shaped, as is clearly shown in one specimen (MGP 194/8A; Fig. 4E); the incisions and division in lobes have been created secondarily by dissection of the lamina caused either by the age of the frond or by the transport and deposition of the specimen. The lamina is characterized by a coarse, loose net venation (MGP 191/9B, MGP 194/95B; Fig. 4F); no "midrib-like" structure can be distinguished as is typical for other species of this genus. In most cases the fragments belong to distal parts of the lamina, in some cases also part of the petiole is preserved (MGP 63/75A; Fig. 5A); the lamina reduces downwards to 30 mm and finally the petiole has a diameter of c. 8–15 mm. The petiole reaches more than 150 mm in length and is characterized by longitudinal striae reflecting probably the veins of the leaves (MGP 63/75A; Fig. 5B). In one specimen at least four different petioles merge together at the base almost as if attached to the same stem or rhizome (MGP 191/10A; Fig. 5B).

This species differs from *Chiropteris lacerata* (Quenstedt, 1885) Rühle von Lilienstern, 1931 in its larger frond dimensions, the absence of a midrib in our material and a clear division into lobes, apart from secondary incisions. Rühle von Lilienstern (1931a, b) considered the leaves of *C. lacerata* to be up to 20 cm wide with a narrow petiole up to 15 cm long; some of our fragments are larger than that. Although large frond fragments are preserved, there is no sign of a midrib. The leaves of *C. barrealensis* Frenguelli, 1942 from the Rhaetian of Barreal (Argentina), *C. tasmanica* Walkom, 1925 from the Mesozoic of Tasmania and *Chiropteris biloba* Bell, Harrington, and McKellar, 1956 from the Late Triassic of New Zealand are all smaller in dimensions (up to 30–40 mm long); the veins branch mostly dichotomously and anastomose only occasionally in the first two species, in the latter the leaves are deeply incised into two distinct segments. In *Chiropteris taizihoensis* Zhang in Zhang et al. (1980) and *Chiropteris yuanii* Sze, 1956 from the Late Triassic of China the leaves have even smaller dimensions (15–25 mm), whereas *Chiropteris kawasakii* Kon'no, 1972 from the Late Triassic of East Malaysia has reniform leaves with a slender petiole and an entire or slightly undulate margin. *Chiropteris zeilleri* Seward, 1903 from the Rhaetian of South Africa differs because of its orbiculate lamina and the polygonal meshes. *Chiropteris waitakiensis* Bell, 1956 from the Late Triassic of New Zealand differs because of the lamina's subdivision into four or more strap-like segments by repeated dichotomy, resembling more a ginkgophyte than a fern frond.

Chiropteris cuneata (Carruthers, 1872) Seward, 1903 from the Triassic of Queensland and *Chiropteris arberi* Rühle von Lilienstern, 1931 from the Rhaetian of New-Zealand differ in its delicate secondary veins, which in our specimen are coarse, and in the dentate margin of the latter species. Furthermore, *Chiropteris copiapensis* Steinmann and Solms-Laubach in Solms-Laubach and Steinmann, 1899 from the Rhaetian of Chile seems to be characterized by an irregularly undulate to laciniate margin and rhomboidal areolae (Frenguelli 1942). Additionally, these three species have

Fig. 5. Fern remains from the tuff layer in the basal part of "explosion breccia" (late Ladinian, Middle Triassic) of Monte Agnello, Dolomites, N-Italy. → **A**, **B**. *Chiropteris monteagnellii* sp. nov. **A**. Frond base with petiole (MGP 63/75A). **B**. Paratype, several petioles coming together (MGP 191/10A). **C**, **D**. *Cladophlebis ladinica* sp. nov. **C**. Holotype (MGP 194/6B), frond fragment (C_2), detail of basiscopic pinnules with the distinct venation (C_1). **D**. Paratype (MGP 194/65B), one of the largest frond fragments (D_1), detail of the rhomboidal pinnules with the distinct venation (D_2). **E**. Rachis showing a wing (MGP 197/69A). Scale bars 10 mm.

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use



Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

been now assigned to the genus *Rochipteris*, with a putative gymnosperm affinity, because of the non-petiolate, flabellate shape and slightly anastomosing venation (for more details see Barone-Nugent et al. 2003).

Chiropteris seems to be abundant and diverse globally during the Late Triassic (mostly Rhaetian), even if the type species *Chiropteris lacerata* (Quenstedt, 1885) Rühle von Lilienstern, 1931 comes from the late Ladinian of the Germanic Basin. The preservation of the new material is special. The veins must have been thick because they are very well preserved, different from most of the other fern taxa. The spathulate lamina of these leaves is locally interrupted by "holes" or characterized by undulations because of the presence of lapilli (e.g., MGP 194/95B; Fig. 4F).

The systematic position of *Chiropteris* is still unclear. Schimper (1869) evidenced the close resemblance in the net venation between *Chiropteris* and *Sagenopteris* (Caytoniales). The genera differ, however, in the leaf structure (funnel-shaped against two pairs of closely spaced leaflets) and venation (lateral veins are almost parallel to the midrib in *Chiropteris* against lateral veins arising at an acute angle from the midrib in *Sagenopteris*). Other fan-shaped, non-petiolate leaves with a slightly anastomosing venation and an entire to dissected apex belong to the genus *Rochipteris* Herbst, Troncoso, and Gnaedinger, 2001. The venation of this Late Triassic genus from Gondwana is, however, only sparsely reticulate, and the leaves are non-petiolate. Additionally they have a gymnosperm, possible ginkgoalean, affinity. *Kannaskoppifolia* Anderson and Anderson, 2003, also a putative ginkgophyte leaf, resembles the genus *Chiropteris* but has a cuneate to flabellate, entire to three times divided lamina and a forking to anastomosing venation; the leaves are irregularly attached on short shoots. *Batiopteris* Anderson and Anderson, 2003 with its species *Batiopteris pulchella* Anderson and Anderson, 2003 is characterized by a long, gracile petiole and a fan-shaped to auriculate and bifidly divided lamina with frequently anastomosing veins; this species has also been attributed to the gymnosperms (Anderson and Anderson 2003). In *Cetiglossa* Anderson and Anderson, 2003 with its species *Cetiglossa balaena* Anderson and Anderson, 2003, a putatively gnetophyte genus of the Carnian of the Karoo Basin, the leaves are elongated with a distinct midrib and a lateral net venation. *Gontriglossa* Anderson and Anderson, 2003 resembles *Sagenopteris* with its lanceolate to elliptic leaves and the distinct midrib from which the anastomosing secondary veins arise; the organisation and the shape of the leaves and the distinct midrib distinguish this genus from *Chiropteris*.

Because of its resemblance with *Ophioglossum palmatum* Linnaeus, 1753 various authors suggested an attribution to the Ophioglossaceae (e.g., Potonié 1899; Zeiller 1900; Frentzen 1922). Rühle von Lilienstern (1931b) considered some roundish structures on the lower side of the leaves to be sporangia and attributed the genus to the Matoniaceae or Dipteridaceae; the Dipteridaceae is the only Mesozoic fern family with reticulate venation. Some authors even consider it a ginkgoalean type of leaf (Taylor et al. 2009). We consider an attribution to the Dipteridaceae the most likely because of the leaf morphology and venation pattern.

Stratigraphic and geographic range.—Late Ladinian of Monte Agnello, Dolomites, N-Italy.

Genus *Cladophlebis* Brongniart, 1849

Type species: *Cladophlebis haiburnensis* (Lindley and Hutton, 1836) Brongniart, 1849; Hayburn Wyke, Yorkshire, England; Middle Jurassic.

Cladophlebis ladinica sp. nov.

Figs. 5C–E, 6A.

Etymology: In reference to the stratigraphic position.

Type material: Holotype: MGP 194/6B, specimen with clear venation and basiscopic pinnules, here designated (Fig. 5C). Paratype: MGP 194/65B, the largest specimen showing the pinna arrangement, here designated (Fig. 5D).

Type locality: Monte Agnello, Dolomites, N-Italy.

Type horizon: A tuff layer in the basal part of the "explosion breccia" of the volcanic succession of Predazzo (sensu Calanchi et al. 1977), Ladinian, Middle Triassic.

Material.—MGP 63/105, 191/10A–B, 194/3A–B, 194/4A–B, 194/5, 194/6A–B, 194/63B, 194/64A–B, 194/65A–C, 194/66, 194/84A–B, 194/85, 194/86, 194/102A–C, 194/109, 194/110, 197/17A–B, 197/67A–B, 197/68A–B, 197/69A–B, all from type locality and horizon.

Diagnosis.—At least bipinnate fronds with stout, winged rachis. Pinnae arising almost perpendicularly, without imbricating. Basiscopic pinnules enlarged, pinnules decreasing in size apically. Pinnules rhomboidal to falcate in shape; in some cases almost connate. Basal pinnae with fused pinnules. Pinnules without distinct midrib, several veins arising from the rachis, bifurcating up to three times.

Description.—The frond fragments are up to 165 mm long and 92 mm wide. The rachis (2.5–4.5 mm wide) shows a wing (MGP 197/69A; Fig. 5E). The pinnae arise at an angle of 70–90° and are up to 65 mm long and 8 mm wide. Proximally the pinnae reduce in size (22–55 mm long and 6.5–8 mm wide). No apical fragments have been found so far. The pinnae never overlap. The pinna rachis is up to 1 mm wide. The pinnules are rhomboidal to falcate in shape; in some cases they are almost connate (MGP 194/6B, MGP 194/65B; Fig. 5C, D). The pinnules are 3–4.5 mm long and 2.5–3.8 mm wide (MGP 194/6B; Fig. 5C) and inserted at an acute angle. The pinnules are largest at the base, with an enlarged basiscopic pinnule, and decreasing apically (MGP 194/65B; Fig. 5D). Pinnules in the basal pinnae are completely fused demonstrating a sort of fasciculate venation (MGP 194/4B; Fig. 6A). No midrib is present in the pinnules; several veins arise from the rachis and bifurcate up to three times (almost odontopterid venation).

The Middle and Late Triassic species *Todites gaillardotii* (Brongniart, 1834) Kustatscher and Van Konijnenburg-van Cittert, 2011 has roundish sterile pinnules with an apex curved slightly upwards, and a venation similar *Cladophle-*

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

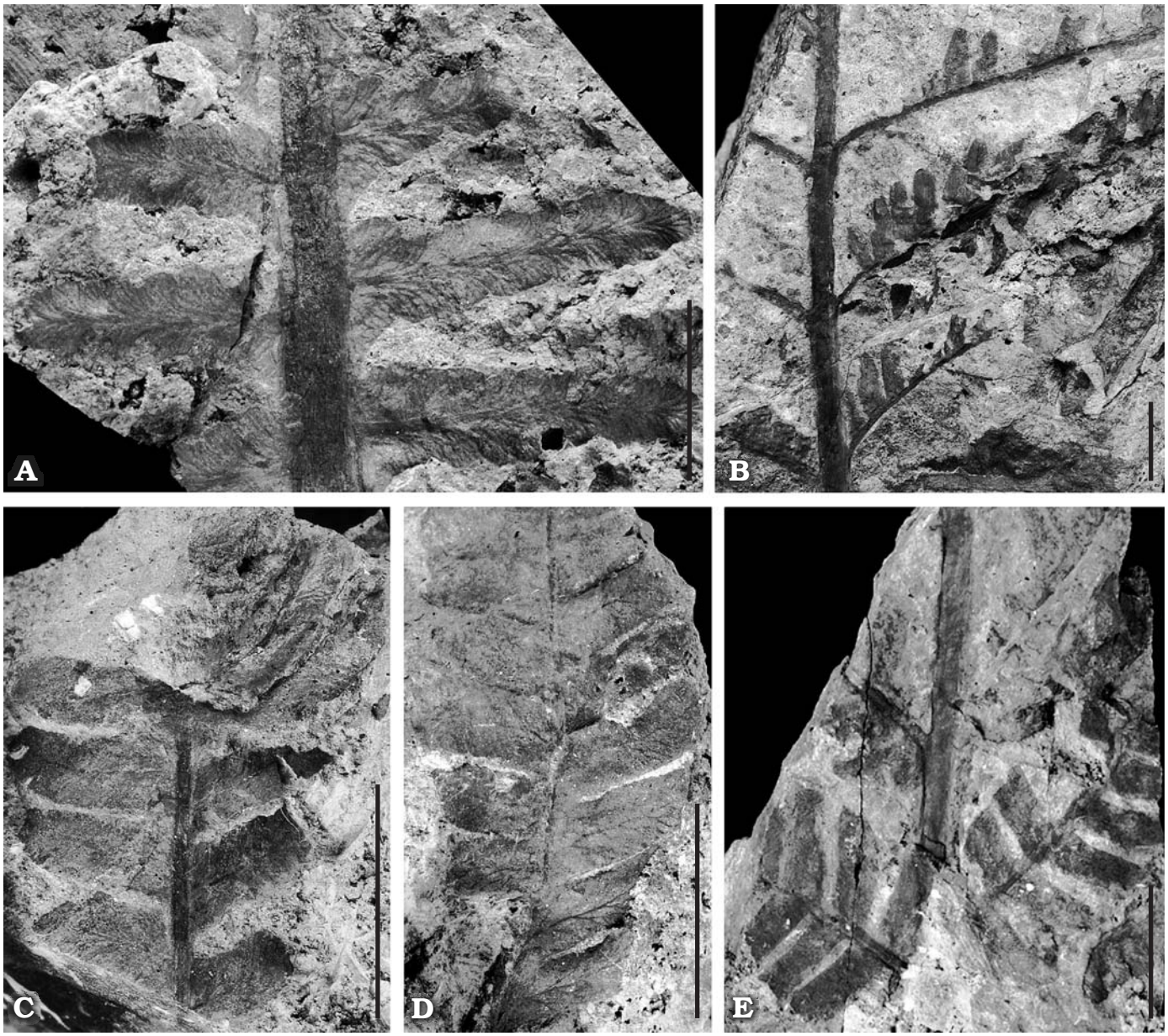


Fig. 6. *Cladophlebis* fronds from the tuff layer in the basal part of "explosion breccia" (late Ladinian, Middle Triassic) of Monte Agnello, Dolomites, N-Italy. **A**. *Cladophlebis ladinica* sp. nov., partially fused basal pinnules (MGP 194/6B). **B**–**E**. *Cladophlebis* sp. **B**. Bipinnate frond fragment (MGP 194/88). **C**. Pinnae with slightly falcate pinnules (MGP 194/87). **D**. Detail of the slightly imbricate pinnules (MGP 63/71). **E**. Possible basal pinnae with broad pinnules (MGP 194/89A). Scale bars 10 mm.

bis ladinica. The secondary veins fork 2–3 times, no midrib is present just as in *C. ladinica*. *Todites gaillardotii* differs from *C. ladinica* mainly in the absence of enlarged basiscopic pinnules; moreover, the pinnules in *T. gaillardotii* are always free up to their constricted bases (Kustatscher and Van Konijnenburg-van Cittert 2011). *Todites roessertii* (Presl in Sternberg, 1838) Krystofovich, 1912 from the Rhaeto-Liassic of Europe has larger pinnules with a neuropterid venation, and more importantly lacks specialized basiscopic pinnules.

Assignment of this taxon to an existing fossil genus for fern foliage is problematic because of two characters of this species; the specialized, enlarged first basiscopic pinnules and the radiating and forking venation lacking a clear midrib. We include the specimens in the morphogenus *Cladophlebis*, as no other genus combines all the characters of our material. Some *Cladophlebis* species have a more or less radiating venation (see below), some may have a more or less specialized basiscopic pinnule but to our knowledge, no existing species combines both characters. Hence, we establish the new species *Cladophlebis ladinica*. Three genera of fern foliage are similar in one aspect. *Mertensides* Fontaine, 1883 (with its type-species *Mertensides bullatus* [Bunbury, 1864] Fontaine, 1883) is characterized by a specialized basiscopic pinnule with radiating venation, but the other pinnules have a pecopterid gross morphology with

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

a distinct midrib, like almost all species of *Cladophlebis* (see e.g., Bock 1969). *Lobifolia* Rasskazova and Lebedev, 1968 is a morphogenus for sterile foliage of the type found in e.g., *Eboracia, Todites*, and *Cladophlebis* with enlarged basiscopic pinnules. These pinnules, are, however, usually divided into two lobes, and the venation incorporates a midrib in the majority of the species (see e.g., Boureau and Doubinger 1975). *Nymborhipteris* Holmes, 2003 is characterized by pinnules with a radiating and forked venation as in *Cladophlebis ladinica*, but it lacks enlarged basal pinnules.

The botanical affinity of *Cladophlebis ladinica* is not yet clear as no fertile material was found. Species with enlarged, or at least modified basiscopic pinnules are common in the Dicksoniaceae (see e.g., Schweitzer et al. 2009) but they also occur sparsely in other families, such as the Osmundaceae and Schizaeaceae (Kustatscher and Van Konijnenburg-van Cittert 2011; Van Konijnenburg-van Cittert 2002). Neuropterid venation as seen in *C. ladinica* occurs mainly in Osmundaceae and Dicksoniaceae, so those two families seem the most likely affiliates of the new taxon.

Cladophlebis sp.

Fig. 6B–E.

Material.—MGP 63/71, 194/87, 194/88, 194/89A–B, Monte Agnello, Dolomites, N-Italy, early late Ladinian.

Description.—The fronds are at least bipinnate. The fragments are up to 80 mm long and 55 mm wide (MGP 194/88; Fig. 6B). The primary rachis is 3–5 mm thick. Pinnae arise suboppositely and at an acute angle (45–50°) from the rachis, but then curve slightly outwards. Pinnae fragments are up to 55 mm long and generally 10–12 mm wide; just in one case the pinnae fragments are broader (MGP 194/89A; Fig. 6E). It could belong to a basal frond fragment. The rachis of the pinnae is 1–1.5 mm wide. The pinnules are lanceolate to slightly falcate with a rounded apex and a broad base. The pinnules are densely inserted alternately to suboppositely at an angle of 70–80°. The pinnules are 5–11 mm long and 2.5–4 mm wide (MGP 194/87; Fig. 6C). The midrib is distinct. The secondary veins arise at an acute angle (c. 50°), bifurcate once halfway along the lamina and perhaps once again near the margin (MGP 63/71; Fig. 6D).

Remarks.—These remains are very fragmentary and too badly preserved to be assigned to a new or established species. They resemble the Late Triassic species *Cladophlebis remota* (Presl, 1838) Van Konijnenburg-van Cittert, Van Konijnenburg-van Cittert, Kustatscher, and Wachtler, 2006, but in the latter species the pinnules are more closely inserted and the apex is acute. *Cladophlebis nebbensis* (Brongniart, 1828) Nathorst, 1876, a typical Rhaeto-Liassic species from Europe and Asia is similar in its once forked secondary veins and slightly restricted pinnule bases, but the pinnules dimensions in *C. nebbensis* are larger (around 15 mm long) and the rachis is relatively thin (Schweitzer et al. 1997).

Discussion

The flora is characterized by a large number of ferns, as described above. Moreover, seed ferns are represented by leaf fragments of *Scytophyllum bergeri* Bornemann, 1856, cycads by leaf fragments with entire lamina probably belonging to the genera *Bjuvia* Florin, 1933, *Taeniopteris* Brongniart, 1828 and/or *Macrotaeniopteris* Schimper, 1869 and segmented leaves resembling *Nilssonia* Brongniart, 1828 and *Apoldia* Wesley, 1958. The conifers are represented mostly by shoots belonging to the genera *Voltzia* Brongniart, 1828 and *Pelourdea* Seward, 1917.

The ferns described in this paper can be assigned to the Osmundaceae (*Neuropteridium elegans*), Matoniaceae (*Phlebopteris fiemmensis* sp. nov.) and Dipteridaceae (*Thaumatopteris* sp.). The Matoniaceae, previously described only on the basis of a few specimens from the late Ladinian of the Germanic Basin (compare Kustatscher and Van Konijnenburg-van Cittert 2010), are now confirmed for the early late Ladinian. For the Dipteridaceae it is so far the oldest fossil record in the Northern Hemisphere. Previously the earliest appearances in Europe were given by the genera *Dictyophyllum* and *Clathropteris* in the Carnian of the Germanic Basin and Lunz (Austria, e.g., Corsin and Waterlot 1979). But in Gondwana the genus *Dictyophyllum* Lindley and Hutton, 1834 was present already during the Anisian–Ladinian (*D. davidii* Walkom, 1917, see Webb 1982). The *Cladophlebis* species (*C. ladinica* and *Cladophlebis* sp.) may have belonged to the Osmundaceae and/or the Dicksoniaceae but no definite assignment can be made until fertile material has been recovered. The attribution of *Chiropteris monteagnellii* sp. nov. remains unclear as is the affinity of the whole genus *Chiropteris* but it might have belonged to the Dipteridaceae.

Regarding the ecology of the taxa found in this assemblage, during the Mesozoic osmundaceous ferns probably grew in warm, humid environments either along river banks or even in fresh-water marshes where they locally even formed peat (resulting in coal) during the Liassic (Van Konijnenburg-van Cittert 2002). The ecology of the Matoniaceae was variable during the Mesozoic, varying from river banks, to understorey and drier habitats on slopes just as Dipteridaceae, which were mainly recorded from warm-temperate to subtropical zones and were commonly colonizers of disturbed sites (Collinson 1996; Van Konijnenburg-van Cittert 2002). Considering the similarities between the fossils and the extant forms and considering the demands of the extant genera *Dipteris* and *Matonia*, a warm, damp and shaded environment is postulated for the Mesozoic Dipteridaceae and Matoniaceae; they have likely thrived in constantly damp understorey (Corsin and Waterlot 1979). Unfortunately, although the transport must have been short, the flora is still not autochthonous and this considerably biases the ecological considerations. It enables, however, to infer a more complex flora for the late Ladinian of the Dolomites, which was dominated previously by conifers (*Voltzia* Brongniart, 1828; *Pelourdea* Seward, 1917) and seed ferns (*Ptilozamites* Na-

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

thorst, 1878). So far, the scarcity of "hygrophytic" elements such as ferns, lycophytes, and horsetails in the late Ladinian suggested a more arid climate or a strong taphonomic selection. Recently, a humid spell has been proposed for the late Ladinian of the Dolomites (Preto et al. 2010 and references therein). This suggested that the taphonomic selection (transport of the plant fossils to the marine basin) biased noticeably the knowledge on the Ladinian floras of the Southern Alp (e.g., Kustatscher and Van Konijnenburg-van Cittert 2005). The high variability of ferns of the flora from Monte Agnello corroborates the theory of a humid interval in the late Ladinian of the Southern Alps; for the first time the more humid elements of the Ladinian flora of the Southern Alps are preserved in the fossil record.

Several other floras have been described from both the late Anisian and the late Ladinian of the Dolomites, but so far the only early Ladinian flora of the Southern Alps comes from Monte San Giorgio (Stockar and Kustatscher 2010), thus filling the gap between the two floras. Unfortunately the latter flora was subjected to a prolonged transport and mainly conifers have been found. Thus, the flora from Monte Agnello is so far the only flora filling this gap.

The late Anisian floras from Kühwiesenkopf/Monte Prà della Vacca and Piz da Peres, are rich in fern remains (Broglio Loriga et al. 2002; Van Konijnenburg-van Cittert et al. 2006; Todesco et al. 2008) whereas their abundance is lower in the late Ladinian floras from the Dolomites (as discussed above). *Neuropteridium elegans* is common in both late Anisian localities and rare but at least recorded from some late Ladinian floras of the Dolomites. *Phlebopteris* and *Thaumatopteris* have never been recorded from other Triassic floras of the Southern Alps. On the other hand, typical Anisian elements of the Germanic Basin and the Dolomites such as *Anomopteris mougeotii* Brongniart, 1828, *Neuropteridium voltzii* (Brongniart, 1828) Schimper, 1879, *Scolopendrites scolopendrioides* (Brongniart, 1828) Van Konijnenburg-van Cittert, Kustatscher, and Wachtler, 2006 and *Scolopendrites grauvogelii* Van Konijnenburg-van Cittert, Kustatscher, and Wachtler, 2006 (e.g., Fliche 1910; Grauvogel-Stamm 1978; Van Konijnenburg-van Cittert et al. 2006) and also typical Anisian–Ladinian elements of the Dolomites, such as *Gordonopteris lorigae* Van Konijnenburg-van Cittert, Kustatscher, and Wachtler, 2006, *Sphenopteris schoenleiniana* (Brongniart, 1828) Presl in Sternberg, 1838 and *Cladophlebis remota* (Presl, 1838) Van Konijnenburg-van Cittert, Kustatscher, and Wachtler, 2006, are missing in the flora of Monte Agnello. Some of the taxa in the new flora can be assigned to the same genus although not to the same species of some Ladinian elements of the Germanic Basin, such as *Chiropteris lacerata*, or *Phlebopteris* sp. described recently from the late Ladinian of Thale (Kustatscher and Van Konijnenburg-van Cittert 2011). Other typical late Ladinian elements of the Germanic Basin such *Danaeopsis marantacea* (Presl, 1838) Schimper, 1869 and *Symopteris rumpfii* (Schenk, 1864) Kustatscher, Pott, and Van Konijnenburg-van Cittert, 2010 are missing in the new flora.

The new flora from Monte Agnello is the first Ladinian flora from the Southern Alps showing the "hygrophytic" vegetation elements of this flora. This is most likely an effect of their preservation in para-autochthonous assemblage. The study of the other groups of the flora is still pending and essential in understanding whether the conifers, seed ferns, and cycadophytes show also high diversity in this para-autochthonous flora or if the typically "hygrophytic" elements described above were contaminated during the transport.

Conclusions

In this study the fern remains of the flora from Monte Agnello (Dolomites, Italy) are surveyed. The plant remains have been deposited in volcanic tuff with lapilli commonly disrupting the plant surface. Organic material has not been preserved, but impressions of the veins can be observed. The remains do not show any orientation or sorting due to transport. They are commonly preserved at an angle to the bedding rather than compacted into a single horizon, indicating that the transport must have been short; thus the assemblage can probably be considered a para-autochthonous assemblage.

The ferns are represented by Osmundaceae (*Neuropteridium elegans*), Matoniaceae (*Phlebopteris fiemmensis* sp. nov.) and Dipteridaceae (*Thaumatopteris* sp.). The *Cladophlebis* species (*C. ladinica* and *Cladophlebis* sp.) may have belonged to the Osmundaceae and/or the Dicksoniaceae; also the attribution of *Chiropteris monteagnellii* sp. nov. remains unclear.

For the Dipteridaceae it is the so far oldest fossil record in Europe.

This work provides additional information on the "hygrophytic" elements of the Ladinian flora of the Southern Alps, previously considered almost completely dominated by conifers and seed ferns. The latter resulted from the reduced transport and taphonomic selection.

Acknowledgements

We thank Federica Angeli (Trento, Italy), Fulvio Boninsegna (Predazzo, Italy), Andrea Braito (Daiano, Italy), Daniele Ferrari (Museo Geologico delle Dolomiti, Predazzo, Italy), Christian Fontana (Vigo di Fassa, Italy) and Guido Roghi (Centro Nazionale di Ricerca and University of Padova, Italy) for their help during fieldwork and the preparation of the fossils. Special thanks goes to Daniele Ferrari for the photographs of the plants. The manuscript benefited greatly from the remarks and comments by Stephen McLoughlin (Swedish Museum of Natural History, Stockholm, Sweden) and Michael Krings (Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany). The work has been supported by the Comune di Predazzo (Provincia di Trento). The study of the material has partly been carried out in the project "The Permian–Triassic ecological crisis in the Dolomites: extinction and recovery dynamics in Terrestrial Ecosytems" financed by the Promotion of Educational Policies, University and Research Department of the Autonomous Province of Bolzano-South Tyrol.

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

References

Anderson, J.M. and Anderson, H.M. 2003. Heyday of the Gymnosperms: Systematic & Biodiversity of the Late Triassic Molteno Fructifications. *Strelitzia* 15: 1–398.

Arthaber, G. von 1903. Die alpine Trias des Mediterran-Gebietes. *In*: F. Frech (ed.), *Lethaea geognostica. Handbuch der Erdgeschichte*, 223–472. Verlag der E. Schweizerbart'schen Verlagsbuchhandlung, Stuttgart.

Ash, S.R., Litwin, R.J., and Traverse, A. 1982.The Upper Triassic fern *Phlebopteris smithii* (Daugherty) Arnold and its spores. *Palynology* 6: 203–219.

Barone-Nugent, E.D., McLoughlin, S., and Drinnan, A.N. 2003. New species of *Rochipteris* from the Upper Triassic of Australia. *Review of Palaeobotany and Palynology* 123: 273–287.

Blanckenhorn, M. 1886. Die fossile Flora des Buntsandsteins und des Muschelkalks der Umgegend von Commern. *Palaeontographica* 32: 117–153.

Bock, W. 1969. The American Triassic Flora and Global Distribution. *Geological Center Research Series* 3: 1–357.

Boureau, E. and Doubinger, J. 1975. *Traité de paléobotanique, IV/ 2: Pteridophylla (première partie)*. 772 pp. Masson Ed., Paris.

Broglio-Loriga, C., Fugagnoli, A., Van Konijnenburg-van Cittert, J.H.A., Kustatscher, E., Posenato, R., and Wachtler, M. 2002. The Anisian Macroflora from the Northern Dolomites (Kühwiesenkopf/Monte Pra della Vacca, Braies): a first report. *Rivista Italiana di Paleontologia e Stratigrafia* 108: 381–389.

Brongniart, A. 1828a. *Histoire des végétaux fossiles, ou, Recherches botaniques et géologiques sur les végétaux renfermés dans les diverses couches du globe. Vol. 1*. 488 pp. D'Ocagne, Paris.

Brongniart, A. 1828b. *Prodrome d'une histoire des végétaux fossiles*. 223 pp. Levrault éd., Strasbourg.

Calanchi, N., Lucchini, F., and Rossi, P.L. 1977. M. Agnello: un apparato vulcanico a condotto centrale nelle Dolomiti. *Minerologica Petrografica Acta* 21: 221–229.

Calanchi, N., Lucchini, F., and Rossi, P.L. 1978. The Volcanic Rocks from the Mount Agnello Area (Fiemme Valley, Italy): A contribution to the knowledge of the Mid-Triassic magmatism of the Southern Alps. *Tschermaks mineralogische und petrographische Mitteilungen* 25: 131–143.

Calligaris, R. 1982–1983. *Resti vegetali in terreni ladinico della Val di Braies*. 6 pp. Tesina in paleobotanica, University Trieste, Trieste.

Calligaris, R. 1986. Geologia della Val di Braies e segnalazione di nuovo località fossilifere a vegetali nel Ladinico superiore. *Atti Museo Civico di Storia Naturale* 24: 1–64.

Collinson, M.E. 1996. "What use are fossil ferns?"—20 years on: with a review of the fossil history of extant pteridophyte families and genera. *In*: J.M. Camus, M. Gibby, and R.J. Johns (eds.), *Pteridology in Perspective*, 349–394, Royal Botanic Gardens, Kew.

Corsin, P. and Waterlot, M. 1979. Palaeobiogeography of the Dipteridaceae and Matoniaceae of the Mesozoic. *Proceedings of the Fourth International Gondwana Symposium. Hindustan Publishing Corporation (India), Delhi* 1: 51–70.

Fliche, P. 1910. Flore fossile du Trias en Lorraine et Franche-Compté avec des Considérations finales par M.R. Zeiller. *Bulletin de la Société des sciences de Nancy* 11: 222–286.

Frenguelli, J. 1942. Contribuciones al conocimiento de la Flora del Gondwana superior en la Argentina. *Notas del Museo de La Plata* 51: 341–353.

Frentzen, K. 1922. Die Keuperflora Badens. *Verhandlungen des Naturwissenschaftlichen Verein Karlsruhe* 28: 1–78.

Gianolla, P. 1993. *Le successioni stratigrafiche ladinico–carniche nel Sudalpino orientale*. 199 pp. Unpublished Ph.D. thesis, Padova University, Padova.

Gothan, W. 1937. Über eine Buntsandsteinflorula von Üdingen bei Düren (Rheinland). *Jahrbuch der Preussischen Geologischen Landesanstalt* 58: 352–360.

Grauvogel-Stamm, L. 1978. La flore du Grès à *Voltzia* (Buntsandstein supérieur) des Vosges du Nord (France). *Sciences Géologiques, Mémoires* 50: 1–225.

Harris, T.M. 1961. *The Yorkshire Jurassic Flora 1. Thallophyta–Pteridophyta*. 212 pp. British Museum (Natural History), London.

Hoernes, R. 1912. Zur Geologie von Predazzo. *Sitzungsberichte der königlichen Akademie der Wissenschaft* 121: 3–31.

Jung, W., Selmeier, A., Schaarschmidt, F., Velitzelos, E., and Dernbach, U. 1995. *Versteinerte Wälder*. 188 pp. Ed. D'Oro, Heppenheim.

Kustatscher, E. 2004. *Macroflore terrestri del Triassico Medio delle Dolomiti e loro inquadramento biocronostratigrafico e paleoclimatico mediante palinmorfi*. 220 pp. Unpublished Ph.D. thesis, University of Ferrara, Ferrara.

Kustatscher, E. and Van Konijnenburg-van Cittert, J.H.A. 2005. The Ladinian flora (Middle Triassic) of the Dolomites. Palaeoenvironmental reconstructions and palaeoclimatic considerations. *Geo.Alp* 2: 31–51.

Kustatscher, E. and Van Konijnenburg-van Cittert, J.H.A. 2010. Seed ferns and Cycadophytes from the Triassic Flora of Thale (Germany). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 258: 195–217.

Kustatscher, E. and Van Konijnenburg-van Cittert, J.H.A. 2011. Ferns from the Triassic Flora of Thale (Germany). *Neues Jahrbuch der Geologie und Paläontologie Abhandlungen* 261: 209–248.

Kustatscher, E., Wachtler, M., and Van Konijnenburg-van Cittert, J.H.A. 2004. A number of additional and revised taxa from the Ladinian flora of the Dolomites, Northern Italy. *Geo.Alp* 1: 57–69.

Leonardi, P. 1953. Flora continentale Ladinica delle Dolomiti. *Memorie dell'Istituto di Geologia e Mineralogia dell'Università* 18: 1–20.

Leonardi, P. 1968. *Le Dolomiti. Geologia dei monti tra Isarco e Piave*. 1019 pp. Manfrini Ed., Rovereto.

Lucchini, F., Rossi, P.L., and Simboli, G. 1982. Il magmatismo triassico dell'area di Predazzo. *In:* A. Castellarin and G.B. Vai (eds.), *Guida alla Geologia del Sudalpino centro-orientale*, 221–229. Società Geologica Italiana, Guide Geologiche Regionali, Roma.

Millay, M.A. and Taylor, T.N. 1990. New fern stems from the Triassic of Antarctica. *Review of Palaeobotany and Palynology* 62: 41–64.

Mojsisovics, E. 1879. *Die Dolomit–Riffe von Südtirol und Venetien: Beiträge zur Bildungsgeschichte der Alpen*. 551 pp. A. Hölder Verlag, Wien.

Mutschlechner, G. 1932. Geologie der St. Vigiler Dolomiten. *Jahrbuch der Geologischen Bundesanstalt* 82: 163–273.

Nathorst, A.G. 1906. Über *Dictyophyllum* und *Camptopteris spiralis*. *Kungligar Svenska Vetenskapsakademiens Handlingar* 41 (5): 5–24.

Nathorst, A.G. 1907. Über *Thaumatopteris schenkii* Nath. *Kungligar Svenska Vetenskapsakademiens Handlingar* 42 (3): 5–9.

Ogilvie Gordon, M.M. 1927. Das Grödner-, Fassa- und Enneberggebiet in den Südtiroler Dolomiten. *Abhandlungen der Geologischen Bundesanstalt* 24 (2): 1–376.

Ogilvie Gordon, M.M. 1934. Geologie von Cortina d'Ampezzo und Cadore. *Jahrbuch der Geologischen Bundesanstalt* 84: 60–215.

Potonié, H. 1899. *Lehrbuch der Pflanzenpalaeontologie. mit besonderer Rücksicht auf die Bedürfnisse des Geologen*. 402 pp. Dümmler Vertragsbuchhandlung, Berlin.

Pott, C. and McLoughlin, S. 2011. The Rhaetian flora of Rögla, Northern Scania, Sweden. *Palaeontology* 2011: 1–27.

Preto, N., Kustatscher, E., and Wignall, P.B. 2010. Triassic climates—state of the art and perspectives. *Palaeogeography, Palaeoclimatology, Palaeoecology* 291 (1–2): 1–10.

Rühle von Lilienstern, H. 1931a. Nachtrag zu meiner Arbeit über *Chiropteris* Kurr. *Paläontologische Zeitschrift* 13 (5): 230–232.

Rühle von Lilienstern, H. 1931b. Über *Chiropteris* Kurr. *Paläontologische Zeitschrift* 13: 254–274.

Schenk, A. 1864. Beiträge zur Flora des Keupers und der rhätischen Formation. *Berichte der naturforschenden Gesellschaft zu Bamberg* 7: 51–142.

Schimper, W.P. 1869. *Traité de Paléontologie végétale ou la flore du*

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

monde primitif dans ses rapports avec les formations géologiques et la flore du monde actuel I. 738 pp. J.B. Baillère et Fils éd., Paris.

Schimper, W.P. and Mougeot, A. 1844. *Monographie des Plantes fossiles du Grès Bigarré de la Chaine des Vosges*. 83 pp. G. Engelmann Ed., Leipzig.

Schimper, W.P. and Schenk, A. 1879. *In*: K.A. Zittel (ed.), *Handbuch der Palaeontologie, Teil II. Palaeophytologie. Lief. 1*, 1–152. Oldenbourg, Leipzig.

Schweitzer, H.-J., Van Konijnenburg-van Cittert, J.H.A., and Van der Burgh, J. 1997. The Rhaeto-Liassic flora of Iran and Afghanistan. 10. Bryophyta, Lycophyta, Sphenophyta, Pterophyta—Eusporangiatae and Protosporangiatae. *Palaeontographica B* 243: 103–192.

Schweitzer, H.-J., Schweitzer, U., Kirchner, M., Van Konijnenburg-van Cittert, J.H.A., Van der Burgh, J., and Ashraf, R.A. 2009. The Rhaeto-Liassic flora of Iran and Afghanistan. 14. Pterophyta—Leptosporangiatae. *Palaeontographica B* 279: 1–108.

Stockar, R. and Kustatscher, E. 2010. The Ladinian Macroflora from the Cassina beds (Monte San Giorgio, Switzerland): a first report. *Rivista Italiana di Paleontologia e Stratigrafia* 116: 161–176.

Taylor, T.N., Taylor, E.L., and Krings, M. 2009. *Palaeobotany–The Biology and Evolution of plants*. 1230 pp. Elsevier, Amsterdam.

Tidwell, W.D. and Ash, S.R. 1994. A review of selected Triassic to Early Cretaceous Ferns. *Journal of Plant Research* 107: 417–442.

Todesco, R., Wachtler, M., Kustatscher E., and Avanzini, M. 2008. Preliminary report on a new vertebrate track and flora site from Piz da Peres (Anisian–Illyrian): Olanger Dolomites, Northern Italy. *Geo.Alp* 5: 121–137.

Van Konijnenburg-van Cittert, J.H.A. 1993. A review of the Matoniaceae based on in situ spores. *Review of Palaeobotany and Palynology* 78: 235–267.

Van Konijnenburg-van Cittert, J.H.A. 2002. Ecology of some Late Triassic to Early Cretaceous ferns in Eurasia. *Review of Palaeobotany and Palynology* 119: 113–124.

Van Konijnenburg-van Cittert, J.H.A., Kustatscher, E., and Wachtler, M. 2006. Pteridophytes from the Anisian locality Kühwiesenkopf (Dolomites, Northern Italy). *Palaeontology* 49: 943–968.

Vardabasso, S. 1930. *Carta geologica del territorio eruttivo di Predazzo e Monzoni nelle Dolomiti di Fiemme e Fassa*. Scala 1:25.000. R. Scuola d'Ingegneria, Padova.

Viel, G. 1979a. Litostratigrafia ladinica: una revisione. Ricostruzione paleogeografica e paleostrutturale dell'area dolomitico-cadorina (Alpi Meridionali) parte I. *Rivista Italiana di Paleontologia e Stratigrafia* 85: 85–125.

Viel, G. 1979b. Litostratigrafia ladinica: una revisione. Ricostruzione paleogeografica e paleostrutturale dell'area dolomitico-cadorina (Alpi Meridionali) parte II. *Rivista Italiana di Paleontologia e Stratigrafia* 85: 297–352.

Wachtler, M. and Van Konijnenburg-van Cittert, J.H.A. 2000. The fossil flora of the Wengen Formation (Ladinian) in the Dolomites (Italy). *Beiträge zur Paläontologie* 25: 105–141.

Wagner, W.H. Jr. 1979. Reticulate veins in the systematics of modern ferns. *Taxon* 28: 87–95.

Webb, T.A. 1982. Triassic species of *Dictyophyllum* from eastern Australia. *Alcheringa* 6: 79–91.

Weber, R. 2008. *Phlebopteris* (Matoniaceae) en el Triasico y Jurasico de Mexico. *In*: R. Weber (ed.), Plantas triásicas y jurásicas de México. *Universidad Nacional Autónoma de México, Instituto de Geología, Boletín* 115: 85–115.

Wissmann, H.L. and Münster, G. Graf von 1841. *Beiträge zur Geognosie und Petrefactenkunde des südöstlichen Tirol's vorzüglich der Schichten von St. Cassian*. 152 pp. Buchner'sche Buchhandlung, Bayreuth.

Zeiller, R. 1900. *Éléments de Paléobotanique*. 116 pp. Georges Carré et C. Naud, Paris.

Zhang, W., Chang, C.-C., and Zheng, S.L. 1980. Phylum Pteridophyta, phylum Spermatophyta and subphylum Gymnospermae. *In*: X{?} (ed.) *Palaeontological Atlas of Northeast China. II. Mesozoic and Cenozoic Volume*, 221–308. Shenyang Institute of Geology and Mineral resources, Beijing.

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use