Revisiting the mid-Permian Agay flora of the Estérel basin (Provence, south-east France)

Iris Kuipers (3703584) MSc Thesis master Earth, Life and Climate, Utrecht University

Abstract

The conifer-dominated mid-Permian flora of Agay (Estérel Massif, Provence, south-east France) was first described by Visscher (1968). The present study revisits Visscher's publication by collating it with new material, arriving at a total count of 282 fossils. The analysis of these fossils yielded a similar species list in which the conifer *Ullmannia bronnii* is by far the most abundant. Other commonly found conifers are *Ullmannia frumentaria, Quadrocladus solmsii* and *Quadrocladus orobiformis*. The remaining 8% of the assemblage, contains the seed fern *Sphenopteris*, the holotype of the (putative) ginkgophyte *Esterella gracilis* and several fossils of uncertain affinity (inter alia the holotype of Sp. A Boersma and Visscher (1969)). This species composition shows similarities to the coniferous late Permian Zechstein flora. Combining the most recent paleomagnetic data and radiometric dating with information from other Permian basins in the Provence suggests a Wordian (mid-Permian) age for the Estérel flora.

Introduction

The formation of the supercontinent Pangea that started during the Carboniferous was almost complete at the end of the Permian (298.9 - 252.2 Ma) (Stanley, 2005). Due to the northward movement of Gondwana and its subsequent collision with Laurasia, the landscape of Pangea was very mountainous with extended dune deposits and evaporites in its continental interior developing under strong aridity caused by the great land-sea distance. The aridity on Pangea persisted and increased throughout its formation and existence. The warming by solar radiation and heat loss by longwave back radiation of Pangea's major land masses, located in the mid-latitudes, caused a very high seasonal contrast resulting in a strong monsoonal circulation in which winters became very cold and dry and summers became very warm and wet (Ruddiman 2001, Roscher and Schneider 2006). Due to this extreme land climate, ice sheets were unable to persist in high latitudes (Ruddiman, 2001). During the Permian the two seed plant groups that were already present in the early Carboniferous, the Cordaitales and pteridosperms, expanded and several new plant groups appeared (Willis and McElwain, 2014). Gymnosperms became the most dominant terrestrial plant group (Stanley, 2005) and (Late) Permian fossil assemblages are generally characterized by a dominance of drought resistant conifers (Kustatscher et al., 2014). Within the complex topography and extreme climatic diversity of the Pangean supercontinent, several floral provinces are recognized based on palaeobotanical evidence reconstructed from assemblages preserved in continental sedimentary systems (Lucas *et al.*, 2006).



Figure 1. Middle Permian biomes - the location of southern France is marked by a red circle (adapted from Willis and McElwain, 2014).

The fossil plant material studied in this thesis originates from Permian outcrops of the Agay basin, located in the Estérel massif (Provence, Southern France). Figure 1 shows the mid-Permian biomes where present-day Southern France, then located on the northern part of Pangea, was situated in the tropical summerwet biome. The most abundant fossil plant taxa found in this biome are the ginkgoales, conifers and some cordaites and seed ferns. The xerophytic traits of the plants found in this biome, indicating that the plants were adapted to limited water availability, indicate annual seasonality in this region. Comparing the climatic development in different European basins, Roscher and Schneider (2006) found that the maximum level of aridity was reached during the Roadian, Wordian and Early Captinian stages of the Middle Permian (Guadalupian) epoch. An overview of the general climatic trends throughout the Permian period is provided in figure 2.



Figure 2. General climate dynamics during the Permian period. The line thickness represents the strength of the changes. Adapted from Roscher and Schneider (2006).

The material that is (re-)analyzed here, has been partly described by Visscher (1968) and is dated as Thuringian (270.6 - 251 Ma), which spans the mid- and late Permian. The aim of Visscher (1968) was to provide an age assessment based on paleobotany to constrain and support the paleomagnetic dating based on the remanesence of the Agay rocks for the doctoral thesis of Zijderveld, eventually published in 1975. The plant assemblage described by Visscher (1968) is mainly consisting of Ullmannia bronnii, U. frumentaria and Quadrocladus orobiformis and is therefore comparable to the Late Permian Zechstein assemblages from Germany (Durand, 2006). In 1969, Boersma and Visscher published an article describing two previously undescribed species, Esterella gracilis and Species A, that are present in the Agay fossil material. Since these two initial publications on this material, additional plant fossil material has been collected. Due to the many new insights in the field of paleobotany since the publication of these studies 50 years ago as well as the inclusion of the additional material, a revisited identification of the material and comparison of the assemblage to others could provide a better understanding of the conditions in the Estérel basin during the Permian. The aim of this thesis is to further constrain the age determination based on the most recent publications about the area and to obtain a quantitative analysis of the paleobotanical assemblage.

Geological setting and age of the Estérel basin



Figure 3. Location of the Estérel massif (after Durand, 2006).

The Estérel basin is one of the four Provence basins that lie along the Les Maures Massif (figure 3). The geology of the Estérel massif has originally been described in detail (Bordet, 1951), and an updated geological description and mapping has been provided by Zijderveld (1975). The use of the system created by Bordet, which assigns letters to each terrestrial sedimentary formation and volcanic unit, has been continued by Zijderveld (1975). The stratigraphic column modified by Vlag *et al.* (1997) (figure 4) includes these letters on the right side and shows that the Estérel massif comprises four basaltic and four rhyolitic formations that are interbedded by sedimentary units, which are divided into a lower and an upper group by an unconformity. However, the subdivision of the Estérel succession differs throughout the basin (Zijderveld, 1975).

The fossil plant material was collected in a small quarry and is assigned to the Gargalon Formation (layer **h** shown in yellow, figure 4) in the Upper Group in the Agay region. The Gargalon Formation consists firstly of unstratified conglomeratic rock containing rhyolite and basalt boulders, yellow tuff, and grey siltstone fragments, on top of which follows a thin layer of lacustrine gray flaggy arkoses and pelites with fossil material (Visscher, 1968). This is overlain by thick beds of a fine-grain pink arkose, a conglomerate with Amaranthine Rhyolite boulders and lastly by dark red purple arkoses. Layer **h** lies between light-pink arkose-like tuffs (R4t) and the D2 'Agay Basalts', which is most likely identical to the Gondin Basalt (Zijderveld, 1975). R4t represents the stratigraphic level of the R4 pyromeride which is a rhyolitic flow that is found in most of the basin's Upper Group, but is absent at this location. Formation **g** below the R4

Pyromeride also bears plant fossils; however, these are too poorly preserved to be identified (Zijderveld, 1975). Nonetheless, a palynological assemblage of formation **g** in rocks from the Le Muy quarry was obtained by Visscher (1968). The R4 pyromeride has been radiometrically dated using 39 Ar/ 40 Ar by Zheng *et al.* (1992) to before 264 ± 2 Ma. Vlag *et al.* (1997) resampled the Gargalon Formation in their verification of Zijderveld's paleomagnetic results (sample six is seen on the left in figure 5). They concluded that the virtual geomagnetic pole position of the formation indicates a Permian age but that the origin of the characteristic remanent magnetization (ChRM, the remanesence that is acquired at the time of deposition) of the Gargalon Formation is unclear. The ChRM could be instantaneously acquired but could also originate from a remagnetization shortly after deposition as the ChRM directions all lie close to the average Permian ChRM direction. Yet, the other results of Vlag *et al.* (1997) still indicate that the placement of the Permian succession of the Estérel rocks lies within the reversed Permo-Carboniferous/Kiaman superchron.



Figure 4. Stratigraphic column of the Estérel succession (adapted from Vlag et al. (1997)). The right side shows the labeling of the formations by Zijderveld (1975). The right side shows the radiometric ³⁹Ar/⁴⁰Ar ages (in Ma) from Zheng et al. (1992) and sample locations from Vlag et al. (1997). The Gargalon Formation is marked in yellow.

Durand (2006) suggests that the age determination by Visscher (1968) of the Le Muy material should be changed to a Wordian age, which falls into the end of the Kiaman superchron. The Estérel basin can be compared to other Permian French basins by connecting the different volcanic flows and by the sparse biostratigraphical elements. The radiometric dating of the underlying pyromeride indicates that the R4 flow is at youngest of Capitanian age. Additionally, Durand states that the formation cannot be much younger than the Bau Rouge Member in the Toulon-Cuers basin, which has been assigned a Wordian age. Cassinis and Santi (2005) correlate the Gargalon Formation the to Pradineaux Formation that is found in the Bas-Argens basin. Chronostratigraphical data are somewhat conflicting when correlating the Provence basins and other studies: the Gargalon Formation is placed below an earliest Tatarian aged limestone layer (based on ostracod fossils) that lies above the Gondin basalt, but which is also located below formations featuring tetrapod footprints that are possibly Wordian (Durand, 2008). The Tatarian starts, like the Wordian, at 268.8 Ma, which would place the Gargalon Formation definitely within the Middle Permian and most likely into the Wordian. The updated identification of the plant fossils of the Gargalon Formation and subsequent comparison of the assemblage to that of other studies in this thesis might therefore aid the age determination.

Material and methods

The material, which is part of the paleobotanical collections of Utrecht University, consists of 131 rock samples. Most specimens were collected in the 1960's and some additional material was collected and added to the collection in the 1980's. The paleobotanical collections of the University of Münster also holds specimens from the same locality, but these are not included in this thesis. There are no publications about the material from the 1980's and the Münster material yet.

The rock samples contain 282 macrofossils which are mainly shoots, as well as several cones, scales and seeds. Visscher (1968) described saccate pollen grains in the fossiliferous Agay beds, which are not included in this analysis. The preservation of the fossils is sufficient to determine the genus and often the species of the fossils based on morphology but is too poor for cuticle analysis.

All specimens have been photographed with a Canon EOS1000D DSLR camera in natural light using an overhead tripod, resulting in 1054 digital images. The images have been digitally edited when necessary to improve the visibility of the fossils by enhancing the, often limited, contrast between the grey rocks and fossils and compensating for bad lighting, using the free and open-source GIMP software.

Results

The pie chart in figure 5 shows the groups that have been distinguished. The assemblage is dominated by the conifers *Ullmannia*, *Quadrocladus* and *Culmitzschia*, conifer cones, seeds and scales, and indet. conifers, together accounting for 90% of the total plant fossils. Ginkgophytes (putative) like *Esterella* and seed ferns such as *Sphenopteris* are also present.



Figure 5. Quantitative diagram of the floral composition of Agay.

As almost all plant remains are from conifers, the separate pie chart of figure 6 shows solely the distribution in the conifer assemblage. Roughly half of all conifers belong to the genus *Ullmannia*. The majority of the *Ullmannia* fossils could not be identified down to species level. Most of the fossils that could be identified are *Ullmannia bronnii*. Conversely, *U. frumentaria* is scarce in the assemblage and was not identified with a great degree of certainty.



Figure 6. Distribution of conifers in the floral assemblage of Agay.

Of the genus *Quadrocladus*, most specimens could be identified on species level. *Q. solmsii* was the most abundant species. *Q. orobiformis* is also present, however, its assignment is often highly uncertain.

All but two of the unidentified plant fossils are conifers, some of which are very small conifers (1-2 cm-long). One of the two unidentified plant fossils is shown in Plate 4, figure F.

Nine conifer cones of various sizes are found, one of which might belong to the conifer *Dolomitia* (Plate 5, top right). One of the cones is male, the gender of the rest is unknown.

Esterella is the only (putative) ginkgophyte genus found in the assemblage. Two specimens of *E. gracilis* are present, one of which is the holotype (specimen 3000) and one that is much smaller (specimen 3001, Plate 3).

Sphenopteris is the only seed fern genus present with two *S. kukukiana* fossils, one plant remain that is tentatively assigned to *S. valentinii* and one fossil that could not be further identified on species level (Plate 4).

One fossil of uncertain affinity, named Sp. A in Boersma and Visscher (1969), is housed in the collection of the Utrecht Botanical Gardens. Also of unknown affinity are the 10 bifurcated specimens present in the assemblage (Plate 4). These fossils measure between 0.5 and 4 cm and have rounded apices.

Species list

Ullmannia bronnii Göppert (Plate 1, figures A, B and D)

Ullmannia frumentaria (Schlotheim) Göppert (Plate 1, figures A and C)

Quadrocladus orobiformis (Schlotheim) Schweitzer (Plate 2, figure C; Plate 3, figures A and E)

Quadrocladus solmsii (Schlotheim et Nagelhard) Schweitzer (Plate 2, figures A, B, D, E and F; Plate 3, figure C)

Sphenopteris kukukiana Gotheim et Nagelhard (Plate 4, figure D)

Sphenopteris sp. (Plate 4, figure E)

?Culmitzschia florinii Ullrich

Esterella gracilis Boersma and Visscher 1969 (Plate 3, figure D)

Incertae sedis: Sp. A Boersma and Visscher 1969; forked specimens (Plate 4, figures A, B and C)

Discussion and comparison to other floras

The results confirm the main findings of the original Agay flora description (Visscher, 1968). The main difference is that some of the plant remains that were assigned to the genus *Ullmannia* have been re-identified, mostly as belonging to the genus *Quadrocladus*. *U. frumentaria* continues to be rare. Also, the specimens cf. *Pseudoctenis middrigensis* and *Pseudovoltzia* have been discarded from the assemblage. As there are no quantitative data available from Visscher (1968), since the focus of that study was on age assessment, a direct comparison is difficult to make. The labels belonging to the rock samples only contain the name(s) of either the most interesting or the largest fossil visible and rarely contain more than one identification. However, when counting the species on these labels, *U. bronnii* is far more abundant in the original research than the 43% found in this new assessment (figure 5).

Due to bad preservation, only the pollen species *Lueckisporites virkkiae* and *Nuskoisporites dulhuntyi* have been identified by Visscher (1968) from the many saccate pollen that were found. *Lueckisporites* is produced by Coniferalean cones, Voltziales and Majonicaceae and *Nuskoisporites* by Voltziales and Utrechtiaceae such as *Ortiseia visscheri*, *O. jonkeri* and *O. leonardii* (Marchetti *et al.*, 2015). *Lueckisporites virkkiae* is first seen in the Kazanian in Russia and can be found in assemblages dating up to the end of the Permian (Vázquez & Césari, 2017). Dominance of this species is characteristic for Lopingian British and west-European assemblages, reflecting the aridification during this time period (Stephenson, 2016). *Nuskoisporites dulhuntyi* specifically is produced by *Ortiseia*, but macro-remains are not found in the assemblage. It might be possible that some hard to identify fossils assigned to the genus *Quadrocladus* actually belong to the genus *Ortiseia* fossils might be present in the same formation, but in other parts of the basin.

Visscher et al. (1974) mention in a footnote that Esterella gracilis was also found in deposits from the Tatarian of the north of the Russian Platform by Molin & Koloda (1972). Lueckisporites virkkiae was, as in the Gratadis Fm. in Agay, also present in these deposits (Nilsson et al., 1996). E. gracilis was first found in the Agay assemblage and putatively assigned to the ginkgophytes by Bauer *et al.* (2013). Fossils of *E. gracilis* were later found in the Kupferschiefer (a Zechstein deposit) of Germany and Bauer et al. list five different specimens with measurements in their article. These measurements and the pictured specimens show a much wider petiole than that of the Agay specimens. Also, even though the width of the ultimate segments of the German specimens is narrower than the proximal segments, they seem to be less convex than in the Agay specimens. In the first place, Bauer et al. (2013) base their classification of Esterella as a ginkgophyte on the fact that Boersma and Visscher (1969) reported that Esterella is affiliated with ginkgophytes due to the dichotomous first two forks of the lamina. Secondly, they base their classification on morphological features. Though there is no mention of any affinity in Boersma and Visscher (1969) for Esterella (apart from algal affinity), a ginkgophyte association is suggested for Sp. A. Bauer et al. (2013) probably confused the information about Sp. A with that of *Esterella*, as they mention the \sim 45°

angle of the insertion to the axis, which is measured on Sp. A., as one of the morphological features suggesting that *E. gracilis* belongs to the ginkgophyte order. Their misinterpretation of the data might also have been induced by the first association of *E. gracilis* with the ginkgophytes by Remy and Remy (1977), who published a photo of *E. gracilis* and called it *Trichopitys* (al. *Esterella*) *gracilis* instead. They also based their classification of *E. gracilis* into the genus *Trichopitys* on its dichotomous branching. Also, Visscher (pers. comm.) suggests that the large size of the leaves of *E. gracilis* might be a reason to reconsider the association of *E. gracilis* with the ginkgophytes.

The forked specimens of unknown affinity that were found (Plate 4, figures A, B and C), were identified as Sphenobaiera sp. in Visscher (1968). However, according to Bauer et al. (2013), the name Spenobaiera should only be used if the leaves are deeply dissected and wedge-shaped with a dichotomous venation and if a distinct petiole is not present. Venation is not visible on our fossils, which might be due to preservation and/or image quality, but as the specimens are all fragmentary it is unsure whether a petiole was present or not. Therefore, the determination as Sphenobaiera cannot be conclusively made. Lausberg and Kerp (2000) have found a very large amount of forked plant parts in a Lower Permian German flora, which are of roughly the same size and shape as those found in this assemblage. Six of the forked plants have a rounded base and pointed endings and are assigned to Gomphostrobus bifidus. These characteristics are not found on the forked plant remains from Agay. The rest of the fragments from Lausberg and Kerp (2000) are presumably leaves, but no affinity is assigned to these leaves. Other findings of similar fossils suggest affinities to Carpentieria marocana, Baiera sp. and *Ginkqophyllum* (Lausberg and Kerp, 2000). Due to the uncertainty of these assignments and the difference in appearance of the fossils within the Agay assemblage, the classification of Sphenobaiera sp. is changed to incertae sedis.

A first comparison of the Agay flora can be made with the macroflora from the Toulon-Cuers basin, which is another Provence basin. This Wordian flora, thought to be slightly older than the Agay flora, comes from the Bau Rouge Member of the Les Salettes Formation and is dominated by U. frumentaria (Durand, 2006). Other species recognized are U. bronnii, Pseudovoltzia liebeana, Lesleya (al. Taeniopteris) eckardtii, «Sphenopteris» dichotoma and Odontopteris osmundaeformis (Cassinis et al., 2003). Higher up in the section, a coniferophyte wood fragment was found that was linked to Ullmannia. These macro- and microfloral asssemblages are comparable to those of the North-Italian Tregiovo Fm. (Durand, 2008). The fossil-bearing part of the Tregiovo Formation is radiometrically dated to middle Kungurian age (Early Permian) (Forte et Even though conifers including Hermitia, Feysia, Quadrocladus al., 2018a,b). and Dolomitia are also the most abundant group in the different assemblages of this formation, albeit in varying percentages, they differ from the French assemblages: Ullmannia, for example, is absent in these assemblages as a macrofossil (Forte et al., 2018a,b; Marchetti et al., 2015). Other taxa found in the diverse macrofossil assemblages sphenophytes (Annularia), ginkgophytes (Sphenobaiera), pteridosperms are (Peltaspermum), taeniopterids and sphenopterids (Forte et al., 2018b). However, miospores have been found that were produced by U. bronnii and U. frumentaria

(Marchetti *et al.*, 2015). Moreover, Remy and Remy (1977) have in fact found *U. frumentaria* at different locations in the Tregiovo horizon. The Tregiovo flora seems, despite its similarities to the Toulon-Couers assemblage, not very comparable to the Agay flora.

Another Italian flora is found in the Bletterbach Gorge, also located in the Northern regions. This flora is of Lopingian (Late Permian) age and, unlike other European Lopingian floras and other Permian floras from Italy, dominated by ginkgophytes rather than conifers (Kustatscher *et al.*, 2017). Thus, this flora is again not comparable to the Agay assemblage.

Furthermore, a Thuringian flora was found on the Balearic Islands, which is the only known Upper Permian flora from the Iberian Peninsula. In this assemblage, conifer species *Pseudovoltzia liebeana, Teaniopteris sp., Ullmannia sp.* were found as well as seeds and a male cone. The palynological assemblage found with this megaflora matches that of other Thuringian microfloral assemblages from the Balearic Islands and other Western European locations (Bercovici *et al., 2009*). This small assemblage contains species known from the Zechstein flora, which is the most notable Lopingian flora.

The deposition of the Zechstein sequence, which includes the aforementioned Kupferschiefer deposit, was caused by transgressions and regressions of the Zechstein Sea, and this sequence can be found in basins in Germany and the United Kingdom. The floral assemblages of this sequence are characterized by a dominance of conifers and by its low species diversity (Schweitzer, 1986). Ullmannia is present in all Zechstein floras, but there is a stratigraphical and geographical variation in the abundance of U. frumentaria, the most common Upper Permian conifer, and U. bronnii (Schweitzer, 1986). Pseudovoltzia is the next most commonly found conifer, and other common conifers are Quadrocladus solmsii and Q. orobiformis, which are found in Middle Germany and the Rhineland, and *Culmitzschia florinii* (possibly *Ortiseia*). The seed fern *Callipteris martinsi* is present in virtually all Zechstein floras, as well as the ginkgophyte Sphenobaiera digitata. Neocalamites mansfeldicus, a sphenophyte, can be found in Germany as well as in the United Kingdom. Different species of the seed fern genus Sphenopteris are also always present in the Zechstein assemblages. Visscher (1968) likened the Agay flora to the Zechstein flora, stating that all important species except for Pseudovoltzia liebeana are present. With the dominance of conifers in the assemblage, especially Ullmannia, the presence of Quadrocladus and Sphenopteris and its low diversity, this still seems to be the best comparison. Besides the absence of Pseudovoltzia, the most notable difference is the absence of the xerophytic seed fern Callipteris.

Like *Callipteris*, conifers are mainly xerophytes. Schweitzer (1986) recognized two plant associations that reflect the Upper Permian climate: the *Neocalamites*-Sphenopterid association, reflecting more humid conditions, and the *Callipteris*-conifer association, which is indicative of dryer conditions. It is most probable to assign the Agay flora to this last category due to the large number of conifers and the low abundance of *Sphenopteris* in the assemblage. Also, Forte *et al.* (2018a) reported drought-adapted

Sphenopteris species from the Tregiovo Fm., so the presence of *Sphenopteris* in the Agay assemblage in itself does not have to reflect a higher (local) water availability. Furthermore, conifers are not only linked to moisture limited environments, but are also indicators of climates with increased seasonality (Marchetti *et al.*, 2015). In the Tregiovo assemblages for example, not only conifers, but also hygrophytes such as sphenophytes, ferns and seed ferns are present, which require water for reproduction. Combined with the presence of conifers, this points to climatic seasonality (Marchetti *et al.*, 2015). The two Tregiovo assemblages from Forte *et al.* (2018b), one of which is showing a distribution of plant groups similar to the Agay assemblage, are called xerophytic despite the presence of hygrophytes in one of the assemblages. They are thus linked to a possible aridification of the Tregiovo Basin during the Cisuralian. The Agay assemblage might thus also be called xerophytic.

Conclusions

Whilst the 'Thuringian' age determination in Visscher (1968) is still correct, its meaning is confusing according to Durand (2006), and the age determination might therefore be further narrowed down to a Wordian age, which is supported by the more recent paleomagnetic data. Comparison with the other Provence basins and other European macrofloral assemblages still confirms the analogy of the Agay flora to that of the Zechstein, even though the Zechstein floras are Lopingian and *Quadrocladus* seems more abundant in Agay than in the classical Zechstein assemblages as described by Schweitzer (1986). The Agay flora features drought-adapted species and thus reflects the aridification that reached its maximum during the mid-Permian.

Acknowledgements

I would like to thank prof. dr. F. Wagner-Cremer for her support, guidance and patience during the process of writing this thesis and for not letting me give up. I would also like to thank prof. dr. J.H.A. van Konijnenburg-van Cittert for her invaluable help with the determination of the fossils, providing literature, answering my questions and giving feedback, prof. dr. H. Visscher for his advice and his help with the determination of the fossils, dr. J. van der Burgh for retrieving the material and his help and time during the photographing thereof and prof. dr. H. Kerp for providing me with the topic and a literature list. And, last but not least, many thanks go to my family and friends for their encouragement and understanding.

References

Bauer, K., Kustatscher, E., & Krings, M. (2013). The ginkgophytes from the German Kupferschiefer (Permian), with considerations on the taxonomic history and use of Baiera and Sphenobaiera. *Bulletin of Geosciences*, 88(3), 539-556.

Bercovici, A., Diez, J. B., Broutin, J., Bourquin, S., Linol, B., Villanueva-Amadoz, U., ... & Durand, M. (2009). A palaeoenvironmental analysis of Permian sediments in Minorca (Balearic Islands, Spain) with new palynological and megafloral data. *Review of Palaeobotany and Palynology*, *158*(1-2), 14-28.

Boersma, M., & Visscher, H. (1969). On two Late Permian plants from southern France. *Mededelingen Rijks Geologische Dienst, Nieuwe Serie*, 20, 57-63.

Bordet, P. (1951). Etude géologique et pétrographique de l'Estérel. Impr. nationale.

Cassinis, G., Durand, M., & Ronchi, A. (2003). Permian-Triassic continental sequences of Northwest Sardinia and South Provence: stratigraphic correlations and palaeogeographical implications. *Bollettino della Società Geologica Italiana*, 2(119), e129.

Cassinis, G., & Santi, G. (2005). Permian tetrapod footprint assemblages from Southern Europe and their stratigraphic implications. *The Nonmarine Permian. New Mexico Museum of Natural History and Science Bulletin*, 30, 26-38.

Durand, M. (2006). The problem of the transition from the Permian to the Triassic Series in southeastern France: comparison with other Peritethyan regions. *Geological Society, London, Special Publications, 26*5(1), 281-296.

Durand, M. (2008). Permian to Triassic continental successions in southern Provence (France); an overview. *Bollettino della Società geologica italiana*, 127(3), 697-716.

Forte, G., Kustatscher, E., van Konijnenburg-van Cittert, J. H., & Kerp, H. (2018a). Sphenopterid diversity in the Kungurian of Tregiovo (Trento, NE-Italy). *Review of Palaeobotany and Palynology*, 252, 64-76.

Forte, G., Kustatscher, E., Roghi, G., & Preto, N. (2018b). The Permian (Kungurian, Cisuralian) palaeoenvironment and palaeoclimate of the Tregiovo Basin, Italy: Palaeobotanical, palynological and geochemical investigations. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 495, 186-204.

Kustatscher, E., Bauer, K., Butzmann, R., Fischer, T. C., Meller, B., van Konijnenburg-van Cittert, J. H., & Kerp, H. (2014). Sphenophytes, pteridosperms and possible cycads from the Wuchiapingian (Lopingian, Permian) of Bletterbach (Dolomites, northern Italy). *Review of Palaeobotany and Palynology*, 208, 65-82.

Kustatscher, E., van Konijnenburg-van Cittert, J. H., Looy, C. V., Labandeira, C. C., Wappler, T., Butzmann, R., ... & Visscher, H. (2018). The Lopingian (late Permian) flora from the Bletterbach Gorge in the Dolomites, Northern Italy: a review. *Geo. Alp*, *14*, 39-61.

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

Lucas, S. G., Schneider, J. W., & Cassinis, G. (2006). Non-marine Permian biostratigraphy and biochronology: an introduction. *Geological Society, London, Special Publications, 265*(1), 1-14.

Marchetti, L., Forte, G., Bernardi, M., Wappler, T., Hartkopf-Fröder, C., Krainer, K., & Kustatscher, E. (2015). Reconstruction of a late Cisuralian (Early Permian) floodplain lake environment: palaeontology and sedimentology of the Tregiovo Basin (Trentino-Alto Adige, Northern Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology, 44*0, 180-200.

Molin, V. A. & Koloda, N. A. (1972). Verkhnepermiskie sporouo-py'tsevye kompleksy severa Russkoi platformy. [Upper Permian spore and pollen complexes in the northern Russian platform]. *Akad. Nauk SSSR, "Nauka", Leningrad.* 76 pp.

Nilsson, I., Mangerud, G., & Mørk, A. (1996). Permian stratigraphy of the Svalis Dome, southwestern Barents Sea. *Norsk Geologisk Tidsskrift*, *76*(3), 127-146.

Remy, W., & Remy, R. (1977). Die Floren des Erdaltertums.-468 pp. Essen (Glückauf).

Roscher, M., & Schneider, J. W. (2006). Permo-Carboniferous climate: Early Pennsylvanian to Late Permian climate development of central Europe in a regional and global context. *Geological Society, London, Special Publications, 265*(1), 95-136.

Ruddiman, W. F. (2001). Earth's Climate: past and future. Macmillan.

Schweitzer, H. J. (1986). The land flora of the English and German Zechstein sequences. *Geological Society, London, Special Publications*, *22*(1), 31-54.

Stanley, S. M. (2005). Earth system history. Macmillan.

Stephenson, M. H. (2018). Permian palynostratigraphy: a global overview. *Geological Society, London, Special Publications, 45*0(1), 321-347.

Vázquez, M. S., & Césari, S. N. (2017). The Permian palynological Lueckisporites-Weylandites Biozone in the San Rafael Block and its correlation in Western Gondwana. *Journal of South American Earth Sciences*, *76*, 165-181.

Visscher, H. (1968). On the Thuringian age of the upper Palaeozoic sedimentary and volcanic deposits of the Estérel (southern France). *Review of Palaeobotany and Palynology*, 6(1), 71-83.

Visscher, H., Slater-Offerhaus, M. G. H., & Wong, T. E. (1974). Palynological assemblages from "Saxonian" deposits of the Saar-Nahe Basin (Germany) and the Dôme de Barrot (France)—an approach to chronostratigraphy. *Review of Palaeobotany and Palynology*, *17*(1-2), 39-56.

Vlag, P., Vandamme, D., Rochette, P., & Spinelli, C. (1997). Paleomagnetism of the Estérel rocks: a revisit 22 years after the thesis of Hans Zijderveld. *Geologie en Mijnbouw*, *76*(1-2), 21-33.

Willis, K., & McElwain, J. (2014). The evolution of plants. Oxford University Press.

Zijderveld, J. D. A. (1975). Paleomagnetism of the Estérel Rocks (Doctoral dissertation).

Zheng, J. S., Mermet, J. F., Toutin-Morin, N., Hanes, J., Gondolo, A., Morin, R., & Féraud, G. (1992). Datation 40Ar-39Ar du magmatisme et de filons minéralisés permiens en Provence orientale (France). *Geodinamica Acta*, *5*(3), 203-215.

Plates

<u>Plate 1</u> A 2562 left: Ullmannia bronnii, right: Q. orobiformis? B 2570 U. bronnii C 2571 U. ?frumentaria D 4549 U. bronnii + indet. conifer E 4543 Ullmannia sp. F 4598 Ullmannia sp.

<u>Plate 2</u> A 2569, B 2647, D 16589B, F 2564A Quadrocladus solmsii C 2650 ?Q. orobiformis E 4567 cf. Q. solmsii

<u>Plate 3</u>

A 2566 ?Quadrocladus orobiformis
B 4574 indet. conifer
C 2559 cf. Q. solmsii
D 3001 Esterella gracilis
E 4576 Q. orobiformis

<u>Plate 4</u>

A 4585/1, B 4585/2, C 4585/3 Indet. forked plant fossils D 2558 Sphenopteris kukukiana E 4583 Sphenopteris (?valentinii) F no id. indet.

<u>Plate 5</u> A 4584, C 4580, D 2649, E 4581 cones B 2950 Dolomitia sp.

<u>Plate 6</u> A 2651 male cone B 2568/2, C 2568/3, D 4573 E 2568/1 seeds and scales F 4894 small indet. conifer

























Plate 6