THE FOSSIL FLORA OF THE GREY LIMESTONES OF VENETO, NORTHERN ITALY, AND ITS RELATIONSHIPS TO THE OTHER EUROPEAN FLORAS OF SIMILAR AGE

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ABSTRACT

The magnificent fossil flora of the Venetian Alps, in rocks of Jurassic age, includes a rich assemblage of bennettitalean, pteridosperm and conifer remains. Pteridophytes and the Caytoniales are also represented, but it is extremely doubtful that the Ginkgoales formed part of the flora. In this latter respect, the Italian flora is easily distinguished from the majority of other European floras of a similar age in which the Ginkgoales usually forms a conspicuous element.

It is also remarkable for the presence of *Phyllotheca*, a genus usually considered as confined to the former Gondwana continent. This unusual occurrence of a typically southern element on the modern European continent, north of the Mediterranean sea, considered together with certain geological data, is suggestive that the present location of the fossil flora may be different from that where it actually grew in Jurassic times.

INTRODUCTION

THE presence of a fossil flora in the Jurassic rocks of Northern Italy at a latitude of approximately 46°N has been known since 1764 when the first fragments of plants were discovered at Rotzo. Nevertheless, almost a century was to elapse before any serious study of the flora was to be undertaken. As a result of De Zigno's almost exclusive devotion to an investigation of the flora from 1852 until 1891, many new fossiliferous localities were discovered in the surrounding region and a fine collection of specimens was amassed. During this period De Zigno described and illustrated many of the plants in a series of publications which culminated in the two-volume *Flora fossilis formationis oolithicae* (1856-85). This work remained uncompleted at his death and the projected third volume was never published.

There was negligible attempt by De Zigno to examine the fossils microscopically, and hardly more by Grandori who introduced a revision of the Italian species described in the first volume of the *Flora fossilis* (GRANDORI, 1913). This was unfortunate, since many of the specimens still retain organic matter from which it is often possible to prepare good cuticle and to learn something about the microscopic structure of the plants. In the course of re-examination of De Zigno's specimens by modern methods I have been able to fill certain lacunae in our knowledge of the Grey Limestone plants. To date I have been able to clarify the systematic position of

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Geographical distribution of Jurassic floras in Europe and Greenland
(*the Spanish and Portuguese localities are omitted*)

Lower Jurassic:

1. Greenland (Scoresby Sound)
2. S. Sweden
3. Denmark (Bornholm)
4. Roumania (Anina)
5. England (Lyme Regis)
6. France (Normandy)
7. France (St. Honorine, Orne)
8. France (Lorraine)
9. France (Vendee, Deux Serves)
10. France (Lozère)
11. Italy (Veneto)
12. Hungary (Pécs)
13. S. W Germany (Wurttemberg)
14. N. W. Germany (Brunswick)
15. S. Poland (Grojec)

Middle Jurassic:

16. England (Yorkshire)
17. England (Stonesfield)
18. France (Mamers)
19. Sardinia
20. W. Ukraine (Kamenka)
21. Crimea

Upper Jurassic:

22. Scotland (Sutherland)
23. England (Portland)
24. France (Chateauroux, Indre)
25. France (Côte d'Or)
26. France (Dordogne)
27. France (Cirin, Orbagnoux, Ain)
28. Germany (Nussplingen, Solenhofen)

Fig. 1

Sphenozamites (WESLEY, 1958), and also to give the first descriptions and illustrations of the coniferous shoots which occur in the Italian flora (WESLEY, 1956). Further work, at present in progress, is producing some interesting results which it is hoped will be published before long.

The present survey of the flora and its relationships to other floras of similar age in Europe must inevitably be somewhat tentative, because much still remains to be done before all the species have been revised. Further investigations of the plant fossils will quite likely lead to some new interpretations and comparisons and some modification of the views presented here could follow. It should also be remembered that many of the determinations of species and their occurrences in a number of the other European floras date from the latter part of the last century. A badly needed reworking of these would doubtless lead to further modification and reassessment of views.

COMPOSITION OF THE FLORA

The whole aspect of the flora is certainly different from that as visualized by De Zigno, due, of course, to the later recognition of such extinct taxa as the Caytoniales, Bennettitales and pteridosperms. Thus many of the presumed ferns have been transferred to other groups with the result that the true ferns appear to have constituted a very minor element in the flora.

The Filicales are represented by relatively few specimens which are for the most part fragmentary and not securely identified. The generic determinations which have been made suggest that only five families occurred. *Gleichenites elegans* Zigno unfortunately is non-fertile so that its attribution to the Gleicheniaceae is by no means certain. However, its appearance and mode of branching is very typical of the family and I have little reason to doubt the correctness of the identification. One small piece of *Dictyophyllum* (originally called *Camptopteris jurassica* Goepp.) indicates the presence of the Dipteridaceae, as does possibly *Protorhipis asarifolia* Zigno. Nothing is known of the soral or sporangial characters of *Protorhipis*, but its entire, orbicular lamina is quite distinct from the divided forms which are usually called *Hausmannia* and referred to this family. The Dicksoniaceae is thought to be represented by the *Coniopteris*-like *Hymenophyllites leckenbyi* Zigno [known elsewhere as *Sphenopteris leckenbyi* (Zigno) Halle]. Its somewhat wedge-shaped pinnules, as well as the strongly anadromic first order of branching of the frond, set it apart from the most closely similar species, *Coniopteris simplex* (L. &. H.) Harris (formerly known as *Tympanophora racemosa* L. & H.). Fragments of *Phlebopteris polypodioides* Brongn. and specimens of *Laccopteris rotzoana* Zigno, the latter more correctly assigned to *Matonidium*, point to the occurrence of the Matoniaceae. The specimens called *Marzaria paroliniana* Zigno are clearly parts of fern fronds and belong to the *Phlebopteris-Matonidium* complex. There is absolutely no evidence whatsoever, for regarding *M. paroliniana* as a detached whorl of equisetalean leaves, even though Harris (1961) has found that the generic name was misused for some Yorkshire specimens now referred to *Annulariopsis simpsoni* (Phillips) Harris.

Two reasonably well defined species of *Equisetites* are also present representing another group of pteridophytic plants. *E. bunburyanus* Zigno, in general, is a slender form, while the other, larger form with many leaf teeth (*E. veronensis* Zigno), recalls the well known *Equisetum columnare* Brongn., but appears to be quite distinct from it. A quite unexpected articulate plant, *Phyllotheca brongniartiana* Zigno, also occurs.

Another less common group in the flora is the Caytoniales. De Zigno assigned his specimens of *Sagenopteris* to four species, but these were reduced to two by Grandori — *S. nilssoniana* (Brongn.) Ward and *Pseudosagenopteris angustifolia* (Zigno) Grandori. The larger of these two, *S. nilssoniana* (syn: S. *rhoifolia* Presl), originally called *S. goeppertiana* by De Zigno and which name has been retained by Vakhrameev (1964), typically has four leaflets and is much like the Yorkshire *S. colpodes* Harris (HARRIS, 1964) but differs in having broader leaflets with very obtuse apices. It is not known yet whether there are any cuticle characters by which it may be further distinguished. The smaller form characteristically has five leaflets, but sometimes four, which caused Grandori to adopt the combination *Pseudosagenopteris angustifolia*. While the presence of a fifth leaflet may be nothing more than an abnormality of a typical *Sagenopteris*, where four

leaflets are a generic character, it seems useful for the moment to continue to use this distinction. The species is very much like the small forms of *Sagenopteris phillipsi* (Brongn.) Presl, but the cuticle characters of the Italian form still remain unknown.

An interesting point is the almost certain absence of any representative of the Ginkgoales. Grandori considered that two of the specimens may be referable to this group, but a preliminary examination leads me to believe that insufficient evidence is to hand. *Cyclopteris minor* Zigno, which De Zigno regarded as a fern, is a small specimen that is not securely identified with *Gingkoites*, even though the fan-shaped, entire and petiolate, lamina shows dichotomous venation. There is no trace of the lamina having been bilobed. Nor does the dichotomously forked *Trevisania furcellata* Zigno (renamed *Trichopitys lindleyana* Schimp. by De Zigno in an unpublished MS of later date) appear to be a slender gingkophyte of the *Baiera*-type for there is evidence of some sort of articulation (remarked upon by De Zigno) which is suggestive of its having been a branching shoot system rather than a much divided leaf.

One major element of the flora comprises a number of thick-leaved fronds assigned to the genera *Cycadopteris* and *Dichopteris*. Both types have thick cuticles, especially *Cycadopteris*, and for this reason it is suggested that they belonged to the pteridosperms and were not ferns as De Zigno considered them. Numerous isolated seeds, up to an inch in length occur, and there is a possibility that some of them may have come from the plants which bore the fronds called *Cycadopteris* and *Dichopteris*. This is pure assumption, however, since there is no organic connection. I have evidence of the presence of genuine cycads in the flora and these seeds could equally have been produced by such plants.

Specimens of *Dichopteris*, often of large size and as much as a yard in length, are typified by a single, dichotomous fork of the main rachis. The lamina is pinnately divided with the pinnae deeply pinnatifid or even divided into discrete pinnules, so that the frond may be described as truly bipinnate. In many ways *Dichopteris* approximates to both *Pachypteris* and *Thinnfeldia*, but it differs in the forking of the main rachis. Many authors in the past have fused *Dichopteris* with these two Mesozoic genera, but I believe there is adequate reason for maintaining it as a separate taxon. De Zigno described five species, but Grandori reduced these to a single group, *D. visianica* Zigno. I believe that neither was quite right and that two species may be defined. Finally it may be mentioned that *Dichopteris* shares with *Dicroidium* the common feature of a forked rachis.

Cycadopteris is also a problematical genus, it having been retained as distinct from *Lomatopteris*, *Odontopteris*, *Kirchneria* and *Thinnfeldia* by some authors, but merged with one or more of these genera by others. In my opinion it should retain its rank as a distinct genus, even though it has much in common with *Lomatopteris*. Again I cannot quite agree with De Zigno, who defined four species, or Grandori, who reduced these to one under a different name [*Lomatopteris jurensis* (Kurr) Schimp.]. I think that two species can be defined, *C. brauniana* Zigno and *C. heterophylla* Zigno.

The most interesting feature of the Veneto flora is the abundance of bennettitalean remains, especially fronds belonging to the genera *Otozamites*, *Sphenozamites* and *Ptilophyllum* and possibly also *Zamites*. The extreme limits of these genera are not particularly clear and intergradations occur which often make their separation difficult. Nevertheless, the species are usually well defined. It is certain that *Otozamites* was the commonest representative with the largest number of specimens and species. There are at least eight or nine good species and possibly more. Special interest pertains to *O. bunburyanus* Zigno and *O. feistmantelii* Zigno which have long been considered as occurring in other more northerly floras. Current work, as yet unpublished, clearly shows that forms from elsewhere with closely similar gross morphology belong to different species and that true *O. bunburyanus* and *O. feistmantelii* were probably confined to Veneto. Another characteristic species, not recorded from elsewhere, is *O. massalongianus* Zigno.

The genus *Sphenozamites* is represented by two species of which one, *S. rossii* Zigno, is unique amongst the Bennettitales in having spinous dentate margins to the more basal pinnae.

Ptilophyllum is also represented by at least two species, one large and called *P. grandifolium* Zigno, the other smaller,

differing from previously described species, and called *P. triangulare* Wesley in MS.

Some *Pterophyllum*-like fronds have been found, but their taxonomic position awaits investigation. *Anomozamites* is not represented at all. Typical ovulate organs of the Bennettitales have yet to be discovered, but there are several 'male inflorescences' which can be assigned to the genus *Weltrichia*.

It is possible that some cycadophytes of uncertain affinity were present since some large taeniopteroid fronds, as well as some peculiar once-pinnate fronds called *Pterophyllum platyrachis* Zigno (though not a true *Pterophyllum* in any sense), have been found. There is also the peculiar entire, strap-shaped frond, *Yuccites schimperianus* Zigno, of which the relationships are unknown.

Conifers also occur with great frequency and are represented chiefly by *Brachyphyllum* (five species) and *Pagiophyllum* (seven species). There are also some shoots of *Elatocladus*-type and a peculiar form called *Dactylethrophyllum peristictum* Wesley. None of these leafy shoots bears reproductive structures so that their real taxonomic position within the Coniferae remains unknown. Nevertheless, I can state that genuine *Stachyotaxus* and araucarian cone-scales, not yet described, are present.

Summarizing the composition of the flora as a whole then we see that it is dominated by a variety of Bennettitales, with small-leaved conifers and plants with large, coriaceous leaves forming other major elements. Very much less strongly represented are the Caytoniales and the pteridophytes, while the evidence for the presence of gingkophytes is very debatable. In addition, there are two unusual genera, *Phyllotheca* and *Yuccites*.

AGE AND ENVIRONMENT OF THE FLORA

The remarkable composition of the flora may be nothing more than a reflection of an incomplete record resulting from the particular conditions under which preservation has occurred, but equally it may be attributed to its being of an age not represented among the plant bearing rocks of neighbouring regions.

The age of the flora is generally considered on geological grounds to be Upper Domerian (Upper Middle Lias), and in this respect is rather unusual since most of the other European Jurassic floras flourished either during the early part of the Lias or much later during the Bajocian s.s. and Bathonian and Upper Jurassic time. The Italian flora is thus younger than the well known *Thaumatoperis*-flora of Greenland, S.W. Germany, Scania and certain parts of France, and older than the famous Inferior Oolite flora of Yorkshire, the Middle Jurassic flora of Sardinia, and the Upper Jurassic floras of Cirin (France) and Nussplingen and other places in Germany. The only floras of approximately the same age are those of Bornholm, and Grojec in Poland.

Petrographic evidence from the limestones in which the plant remains are preserved points to an environment like that of the seas around the Bahamas at the present day, where finely crystalline aragonite is being precipitated from ocean waters in areas of shallow water bordered by mangroves. The size and mostly good preservation of the specimens suggests that little drifting of the organs had occurred after falling from their parent plants, and that sedimentation had been taking place in localities away from tidal waters, in calm water free from wave action and surface disturbances which would have damaged large, entire or pinnatifid leaves. The absence of water-worn fragments suggests that the flora was almost autochthonous and that it is preserved very near where it grew.

The paucity of ferns and the relatively scrappy nature of their remains could be due to the failure of their delicate leaves to be preserved in marine sediments. Tough-leaved plants would tend to suffer much less from immersion in sea-water and consequently their remains would tend to predominate in the preserved record of the flora. However, since optimum conditions appear to have prevailed for the preservation of the plant remains and the flora was most likely autochthonous in origin, we may assume that the composition of the flora was not so very different from the record preserved in the rocks and that it represents the vegetation of a particular type of habitat in which a number of the members were growing under the influence of saline waters. We may visualize a brackish swamp with thick-leaved plants growing near the shoreline. Quite near and probably on higher ground were the conifers, while further away from the influence of brackish water were the ferns, probably only in small numbers.

Of course, it may be argued that the predominance of coriaceous types, some of them showing xeromorphic characters, indicates a relatively arid climate, an idea which gains significance in the light of the almost certain absence of a gingkophytic element. Yet undoubted fern remains do occur which surely suggests that conditions of reasonable humidity existed.

RELATIONSHIPS TO OTHER EUROPEAN FLORAS

A glance at the accompanying map will show that the nearest located early Jurassic floras to that of Veneto are those of S. W. Germany (Wurttemberg), S. Poland (Grojec), E. France (Lorraine) and S. France (Lozère), all of which are separated from Northern Italy by the alpine arc. It is with these floras that immediate comparisons must be made for the equally near floras of central E. France (Côte d'or and Ain) and those of Germany (Nussplingen and Solenhofen) are of much younger Upper Jurassic age. The only geographically near Middle Jurassic flora is that of Sardinia.

The German, French and Polish floras clearly belong to the first half of the Lias, but whether they are exactly coaeval is not quite certain. The differences which exist suggest that the French and Polish floras might be slightly younger than that of Germany. The German flora is of Lower Liassic age and can be clearly identified with the well-known *Thaumatopteris*-flora of Greenland and elsewhere in N. W. Europe, even though it contains species which occur outside the zone in other parts of Europe and Greenland (HARRIS, 1937). The Grojec flora lacks the large *Thinnfeldia* element which is so prominent in both Germany and France. By reason of the fact that it contains good *Thaumatopteris* zone-fossils like *Thaumatopteris* itself, *Phlebopteris angustiloba* (Presl) Hirmer & Hörhammer, *Phl. muensteri* (Schenk) Hirmer & Hörhammer, *Pterophyllum subaequale* Hartz and *Otozamites obtusus* L. & H., side by side with oolitic genera such as *Pachypteris*, *Brachyphyllum* and *Marskea*, the Grojec flora must be considered as of slightly younger age, probably Middle Lias (REYMANOWNA, 1963). The French flora is also probably slightly younger than the German flora for, though they are very much alike, it lacks some of the more delicate leaved types and there is an increase in such characteristic genera of the Oolite as *Otozamites* and *Brachyphyllum*.

An analysis of the Italian flora reveals a combination of early Liassic elements such as *Sagenopteris nilssoniana*, *Stachyotaxus* and possibly *Phlebopteris angustiloba*, together with a diversity and abundance of the oolitic genera *Otozamites* and *Brachyphyllum*. Lingering on from much earlier time is *Yuccites*, while *Phyllotheca* is not recorded elsewhere in Europe. The complete absence of *Thaumatopteris*, but a combination of early Liassic and oolitic elements, the latter predominating, suggests that the Italian flora is of slightly younger age still than the French and Polish floras. This is in accord with its placement at the top of the Middle Lias on purely geological evidence.

A comparison of the generic and specific composition of the flora with those of Germany, France and Poland reveals very few similarities. The nearest approach is to the French flora, where shared genera are *Yuccites*, *Otozamites*, *Cycadospadix*, *Cycadeospermum*, *Brachyphyllum*, *Pagiophyllum* and *Equisetites*. These genera do not occur in the German flora, though *Otozamites* does make its appearance in the Upper Lias of Wurttemberg together with *Pagiophyllum*. Apart from *Otozamites* and *Brachyphyllum*, they do not occur in the Polish flora either. The Italian flora shares *Phlebopteris* and *Sagenopteris* with the German and Polish floras and *Stachyotaxus* (absent from Germany) with the Polish, the three genera not being represented in the French flora. It differs from all three trans-alpine floras in lacking *Clathopteris*, *Ctenopteris*, *Thinnfeldia*, *Thaumatopteris* and *Cladophlebis* which are common to all of them. It further agrees with the French flora in lacking some of the German and Polish common genera such as *Neocalamites*, *Marattiopsis*, *Nilssonia* and *Ctenis* as well as certain strong coniferous and gingkophytic elements.

In fact the distinctiveness of the Italian flora is quite remarkable, for not only are there these dissimilarities, with such genera as *Ctenis*, *Anomozamites*, *Nilssonia*, *Cladophlebis*, *Todites* and the gingkophytes completely omitted, but there are also present such forms as *Gleichenites*, *Dichopteris*, *Cycadopteris*, *Cycadospadix*, *Sphenozamites*, *Dactylethrophyllum*, *Yuccites* and *Phyllotheca*, all of which impart an aspect to the flora which is quite unlike that of any other in Europe.

The flora of Sardinia, quite clearly of Middle Jurassic age, is also different in aspect from the Veneto flora, though the presence of *Yuccites* and *Sagenopteris* points to a remote relationship.

What the antecedents of the Veneto flora were, or to what new vegetation it gave rise are questions which remain unanswered. A small Triassic florule from the Continental Ladinic stage has been found in the nearby Val Gardena (LEONARDI & PAN, 1953), as well as an even earlier Permian one (LEONARDI, 1948). The Ladinic florule comprises *Yuccites*, two species of *Pagiophyllum*, *Cycadospadix* and a *Voltzia*-like leafy shoot. *Yuccites*, *Cycadospadix* and *Pagiophyllum* are common to the Veneto and French Lorraine early Jurassic and the Sardinian Middle Jurassic floras, and it may that a connection through some early distribution centre in the Mediterranean region can be inferred. The Veneto centre soon became effectively isolated by some barrier from the French region, thus leading to the development of a flora peculiar in its composition and differing in many ways from other floras of much the same age. It is a fact that the present location of the fossiliferous strata is in the Dinaric fold system of the alpine arc, and that these strata are generally considered to have been derived from the folding of deposits that were originally accumulated in areas bordering the southern shores of the Tethyan Mediterranean. The intervening body of water would have been a very effective barrier between the developing floras of the Lias. The idea of the flora inhabiting an area on the southern shores of the ancient Mediterranean becomes more plausible when the presence of *Phyllotheca* is considered. This genus is not recorded in floras elsewhere in Europe, and in general is confined to the former Gondwana region whose northern borders formed the southern coastlines of Tethys. Highly provoking is the recent hypothesis, based on palaeomagnetic data, that the Veneto region occupied a point somewhere in the eastern part of the modern Mediterranean during Jurassic time (RUTTEN, 1964). Such ideas could indeed account for the many peculiarities of the Veneto flora, but very much stronger evidence is awaited before they can be accepted.

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