VII. *On Triassic Species of the Genera Zamites and Pterophyllum: Types of Fronds belonging to the Cycadophyta.* By E. A. NEWELL ARBER, M.A., F.L.S., F.G.S., Trinity College, Cambridge; University Demonstrator in Palæobotany.

(Plates 17-19.)

Read 20th June, 1907.

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INTRODUCTION.

IT is now a thoroughly established fact that the general aspect of the Mesozoic vegetation of the Rhætic, Jurassic, and Lower Cretaceous rocks differed entirely from that of the Palæozoic floras. In recent years our knowledge of the various representatives of plant life which succeeded one another during these two great epochs has been so greatly advanced that we are now in a position to inquire into the nature of the change from the older, Palæozoic, to the newer, Mesozoic, facies. Was it, on the whole, abrupt—a sudden transformation—or was it gradual and imperceptible? In the latter case we should expect to discover evidence of a well-marked transition flora, composed partly of old, partly of new types.

In this connection it is interesting to find that we can trace back the first incomings of several of the more important Mesozoic races to sediments of Palæozoic age. It seems clear that some at least of these groups, especially the Cycadophyta, which in Mesozoic times attained to the position of ruling or dominant races, did not spring into existence suddenly. The advent of the Cycadophyta is foreshadowed in both the Carboniferous

and Lower Permian rocks, and, to a greater extent, in the sediments lying between the Permian and Rhætic deposits. During Palæozoic times, however, other and older types of vegetation were dominant, while the Cycadophyta were as yet in the infancy of their development and formed a subsidiary group; a fact which is emphasised by their infrequent occurrence and lack of diversity.

Omitting from the list Gœppert's * *Cycadites taxodinus*, from the Lower Carboniferous (Culm) of Silesia, as founded on too imperfect evidence to be regarded as a satisfactory representative of the group, we find in the Upper Carboniferous of the Northern Hemisphere leaf-impressions of several members of the Cycadophyta, all which, however, are very rare as compared with other genera belonging to typical Palæozoic races. The fronds known as *Pterophyllum*, a large genus and one of the earliest to attain to the dominant phase in Mesozoic times, more especially in the Keuper and Rhætic periods, is known from the Westphalian division of the Coal Measures of France† and from the Upper Carboniferous and Permian of Germany‡.

The genus *Næggerathia*, a name now applied in a restricted sense, is exclusively Westphalian in age. The attribution of this genus to the Cycadophyta is, however, doubtful§. Other genera, such as *Zamites*|| and *Plagiozamites*¶, also appear on this horizon in the coalfield of Commeny, in France, and the latter also in beds of the same age in the Vosges. Zalessky** has recently shown that *Plagiozamites* is associated in Manchuria with a Stephanian flora. The genus *Sphenozamites*†† appears first in the Lower Permian near Autun, in France.

In the Permo-Carboniferous flora of India and the Southern Hemisphere (*Glossopteris* flora), a *Pterophyllum* of the subgroup *Anomozamites* is known, as well as a specimen doubtfully referred to the genus *Cycadites*‡‡.

Thus we see that a large number of the more important frond-genera of Cycadophyta are now known from the Palæozoic rocks, though others, such as *Podozamites*, *Otozamites*, and *Dioonites*, have so far not been found in formations older than the Mesozoic period.

In the present communication two very interesting fronds are discussed, one belonging to the genus *Zamites*, recorded now from both the Bunter and Keuper divisions of the Trias, and for the first time from British rocks; the other, provisionally referred to the genus *Pterophyllum*, from the Keuper rocks of Carinthia. Both these leaves have been previously described on several occasions, and, as we have seen, these genera have been already recognised from sediments of Palæozoic age. These particular species, however, have been the cause of much perplexity and confusion in the past. Both the fossils

* Gœppert (1866), p. 131, pl. 2. figs. 1-3.

† Zeiller & Renault (1888), p. 619, pl. 68. fig. 1; Renault & Zeiller (1886), p. 326.

‡ See Solms-Laubach (1891), p. 85.

§ See Solms-Laubach (1891), pp. 141 and 151.

|| Renault & Zeiller (1886), p. 327; Zeiller & Renault (1888), p. 614, pl. 67. fig. 7.

¶ Zeiller (1894), p. 174, pl. 8. figs. 1-5, pl. 9. fig. 1; Zeiller & Renault (1888), p. 615, pl. 67. fig. 8.

** Zalessky (1905), p. 401, text-figs. 13-15.

†† Renault (1881¹), (1881²), (1893), p. 327, pl. 81. fig. 1.

‡‡ Arber (1905), pp. 208-210.

have been regarded as Monocotyledonous leaf-impressions, and in the one case the same plant has been figured by different authors under totally distinct names, though almost invariably in the belief that its affinities lay with the same group. It will thus be found that the present consideration of *Zamites grandis* goes far to undermine the supposed evidence for the existence of Monocotyledons in the earlier Triassic epochs. It is also hoped that the present study will throw light on some of the earlier Mesozoic representatives of the Cycadophyta.

I would here express my thanks to my friend and pupil Mr. L. J. Wills, B.A., of King's College, Cambridge, who has made the important discovery of the first specimens of *Zamites grandis* from England*, for placing the material at my disposal for description.

I am greatly indebted to Professor Rothpletz, of Munich, for the loan of, and for permission to figure, the fine specimen of *Pterophyllum Bronni* described here, as well as for facilities for studying the collections in the Munich Museum.

I would also return my sincere thanks to Prof. Zeiller, of Paris; to Prof. Solms-Laubach and Prof. Benecke, of Strasburg; to Prof. E. Fraas and Dr. E. Schütze, of Stuttgart, and to Prof. Beckenkamp, of Würzburg, who have all most generously assisted me, either by allowing me free access to the collections under their care, or by other aids in connection with this and other studies of the comparatively little-known Triassic flora.

ZAMITES GRANDIS, nom. nov.

While the genus *Zamites* is known from the Palæozoic rocks, it has not hitherto been definitely recognised from the Trias, although it is a most abundant frond-type in the Rhætic, Jurassic, and Wealden formations. Only one fossil, and that, as we shall see (p. 115), of a very doubtful nature, has been recorded under this name from the Bunter of the Vosges. Renault and Zeiller† have called attention to the absence of any evidence of this type of frond in the Triassic rocks. On the contrary, as I hope to show here, Zamitean fronds have been frequently described and figured during the last 60 years, for rocks of this age in various parts of Europe, though under other names, and these Triassic fronds, which in my opinion should be included within this genus, possess certain peculiarities which have led most observers into error with regard to their real affinities.

The Genus ZAMITES, Brongniart, 1828.

- 1828. *Zamites*, Brongniart, Prodr. Hist. Végét. foss. p. 94.
- 1844. *Yuccites*, Schimper & Mougeot, Monogr. Plant. foss. Vosges, p. 42.
- 1870. *Macropterygium (pars)*, Schimper, Traité, vol. ii. p. 132.
- 1870. *Yuccites (pars)*, Schimper, *ibid.* p. 426.
- 1871. *Palæozamia*, Phillips, Geol. of Oxford, p. 169.
- 1873. *Yuccites (pars)*, Zigno, Fl. foss. Form. Oolith. vol. ii. p. 7.
- 1891. *Yuccites (pars)*, Saprota, Plantes Jurassiques, vol. iv. p. 69.

* Wills (1907).

† Renault & Zeiller (1886), p. 328.

1894. *Cordaites* (non Unger), Compter, Zeitschr. Naturwiss. Leipzig, vol. lxvii. p. 225.

1895. *Zamia*, Ward, 15th Ann. Rep. U.S. Geol. Surv. p. 350.

? 1903. *Næggerathiopsis* (non Feistmantel), Zeiller, Flor. foss. Gîtes Charb. Tonkin, p. 149.

It will be necessary to briefly consider the significance attached to this generic name, since the attribution of the fossils described here forms the main point of this communication.

In the past there has been some difference of opinion as to whether certain fronds should be included or excluded from the genus *Zamites*, and the sense in which this term has been used by several authors has often been extremely vague. Brongniart* originally referred to the recent genus *Zamia* a fossil frond from the Kimmeridgian of France, now known as *Zamites Feneonis*, Brongn., which together with the British Jurassic frond *Z. gigas*, Lindl. & Hutt.†, may perhaps be regarded as among the more typical members of the genus. The term *Zamites*, also first instituted by Brongniart, was, however, applied by him to a subdivision of the living genus *Zamia*, and the same author included several fossils under it. It is now generally agreed that such a use of the name of a still existent genus cannot be justified, and consequently the term *Zamites* has been raised to generic rank. It has also been found that Brongniart's original definition required emendation, and several attempts have been made by different authors to construct a satisfactory generic diagnosis by a modification of his scheme, so as to give it a more exact significance and to make it capable of wider application. An excellent sketch of these proposals has been given by Prof. Seward‡, and so the matter need not be referred to here at length.

The first really satisfactory diagnosis was that given by Schimper in 1870 in his 'Traité,' which may be quoted here *in extenso*, in view of the inclusion within this genus of the species described in this paper:—"Folia quoad formam et magnitudinem valde varia, nunc ex ovato-oblongo acuminata, nunc ex oblongo, nunc e lineali-oblongo acuminata, regulariter pinnata. Pinnæ plus minusve patentès nec rachi perpendiculariter insertæ, lanceolatae, lineali-lanceolatae, oblongæ, acuminatæ vel obtusæ, basi subito contracta plus minus distincte callosa rachis lateri anteriori adfixæ, solide coriaceæ, nervis sat distinctis strictis, inter se parallelis, ad folioli apicem cum hujus margine abruptis" §.

This diagnosis specifies several points to which I also attach importance, namely, the great variation in the size and form of the leaf exhibited by different species, the sudden nature of the contraction in the breadth of the pinna near its point of attachment, the presence of a more or less distinct basal callosity, and the strictly parallel and straight course of the nerves. Schimper further emphasises some of these peculiarities in the paragraph following the above extract in his book.

A more recent definition of Prof. Seward|| is as follows:—"Frond pinnate, pinnæ more or less obliquely inclined to the rachis and attached to the upper surface, apices

* Brongniart (1828), p. 94.

† Now referred to the genus *Williamsonia* of the group *Bennettitæ*.

‡ Seward (1895), pp. 75-78.

§ Schimper (1869), vol. ii. p. 151.

|| Seward (1895), p. 78.

acuminate and tapering or obtusely rounded, the base may be abruptly rounded and marked with a callosity near the point of attachment, or the pinnæ may be slightly and gradually narrowed towards the base, margins entire; veins parallel, but slightly divergent in the apical portion of each pinna."

This definition is of a somewhat wider nature than Schimper's, especially as regards the characters of the bases of the pinnæ. The author states, however, that "such a definition is perhaps suggestive of a genus with characters expressed in too general terms, and not sufficiently limited." Prof. Seward also lays great stress on the attachment of the pinnæ to the upper surface of the rachis, but even in species in which there is every reason to believe this is the case, it is a feature which is often very difficult to establish, and thus usually of slight value as a help towards a correct determination of the genus. Often when the rachis has been considerably flattened, and especially when the lower surface of the frond is viewed, the leaflets may appear to be attached laterally, though better specimens show that in reality such is not the case. In regard to the very species, *Zamites buchianus* (Ett.), to which Prof. Seward points as a fossil showing the true mode of attachment of the leaflets, there are many examples in the British Museum, and also in the Cambridge Museum, which would lead one to a false conclusion. Nathorst* has already instanced similar specimens from Japan. I am therefore not disposed to attach much importance to this character of the genus as an aid to its identification. As we shall see (p. 116) in the single instance in which the leaflets of the species of *Zamites*, described here, have been found attached to the rachis, the insertion appears to be lateral, although in reality it may have been dorsal.

On the whole, I consider Schimper's definition the most satisfactory as yet available. The fossils described here will be found to agree with it in detail.

The Species ZAMITES GRANDIS, *nom. nov.* (Pl. 17; Pl. 18. fig. 2; Pl. 19. figs. 1-3.)

1844. *Yuccites vogesiacus*, Schimper & Mougéot, Monogr. Plant. foss. Vosges, p. 42, pl. 21. figs. 1, 2.

1844. *Yuccites dubius*, Schimper & Mougéot, *ibid.* foot of pl. 21.

1865. *Pterophyllum giganteum*, Schenk, Flora Schwarz. Schiefer, Raibl, p. 18, pl. 2. fig. 2.

1870. *Yuccites vogesiacus*, Schimper, Traité, vol. ii. p. 427.

1870. *Macropterygium schenkii*, Schimper, *ibid.* p. 133.

1907. *Zamites vogesiacus*, Arber, in Wills, Geol. Mag. dec. 5, vol. iv. p. 32.

Localities.—The Bunter of the Vosges (Alsace), Germany; the Keuper of Bromsgrove (Worcestershire), England; the Lower Keuper of Raibl (Carinthia), Austria; and ? the Lower Keuper of Apolda (East Thuringia), Germany.

Diagnosis.—Frond pinnate. Pinnæ very large, most frequently detached, varying greatly in size, from 30-50 cm. in length and from 3-6.5 cm. or more at their greatest width, entire, lanceolate or somewhat linear-lanceolate; apex elongate, acuminate; base somewhat abruptly contracted, with a fairly well-marked callosity at the point of attachment, basal margin crescentic. Nerves strictly parallel, occasionally dichotomising, stout, close, numerous, not spreading nor diverging. Surface much puckered and pitted.

* Nathorst (1890), p. 46.

Description of the Specimens.

The lanceolate or linear-lanceolate pinna * figured on Pl. 17. fig. 1, reduced to half natural size, is almost complete, with the exception of a small portion of the apex, which is missing. It measures about 37.5 cm. in length, and 4.6 cm. across at its greatest width. At the base it narrows somewhat sharply to a breadth of 1.4 cm. The basal callosity is not very evident in the photograph. The general parallel course of the nervation can be made out fairly clearly in this specimen. The surface of the leaflet shows numerous puckerings, which are also evident on nearly all the examples of this frond.

An even larger pinna † is figured on Pl. 17. fig. 3, also reduced to half natural size. It is an almost complete leaflet, except that a small part of the base and a portion of the apex are wanting. It is the largest example obtained from Worcestershire. The complete pinna must have been nearly 50 cm. in length, and was about 6.7 cm. across at its greatest breadth. At the base it contracts to between 2-3 cm. in width. The lanceolate form of the leaflet is striking and the nervation is fairly clear.

Another specimen ‡, a basal portion of a pinna, is figured on Pl. 17. fig. 2, natural size, to show the nervation. It measures 23 cm. in length, and 5.5 cm. at its broadest part. The nerves appear to be stout and close, and are strictly parallel, with occasional dichotomy.

On the same specimen there is also another fragment of a pinna, 21 cm. long, in which the apex is quite complete. This is figured on Pl. 18. fig. 2 (natural size). The acuminate and elongate extremity of the pinna, ending quite acutely, is here well seen. The leaflet appears to be somewhat falcate in its upper portion, though this feature is not very evident in the present specimen owing to a slight distortion, due to the unevenness of the surface of the marl on which it rests. The curious puckered appearance of the surface of the leaflet, of frequent occurrence, is specially noticeable in this example.

The photograph on Pl. 19. fig. 1 shows the apical portion of an almost complete leaflet (natural size) §, which had become bent upon itself before incrustation took place. The entire pinna in the living state probably exceeded 40 cm. in length, with a maximum breadth of 5.5 cm. The apex is wanting. An excellent example || of an apical portion in which the actual tip of the leaflet is also missing is seen on Pl. 19. fig. 3 (natural size). It measures 14 cm. in length, and 5.5 cm. at greatest breadth. The falcate form of the apex is well shown.

The photograph on Pl. 19. fig. 2 (natural size) shows a basal fragment ¶, about 8 cm. in length, of a rather small leaflet. The thickening or callosity at the base is clearly seen. Another basal portion ** (Pl. 17. fig. 4), belonging to a still more slender pinna, shows the callosity, and also the contracted nature of the base of the leaflet, though the nervation is only very faintly marked.

* No. 24. British Triassic Plant Coll., Sedgwick Museum.

† No. 25. Ditto.

‡ No. 26. Ditto.

§ No. 22. Ditto.

|| No. 27. Ditto.

¶ No. 28. Ditto.

** No. 30. Ditto.

The whole of the above specimens were collected by Mr. L. J. Wills, B.A., from Mr. Griffin's North Quarry in the Keuper Marls at Rock Hill (Hill Top), one mile south-east of Bromsgrove, Worcestershire*, and were presented by him to the Sedgwick Museum, Cambridge.

Affinities of the Species.

The leaflets from the British Keuper Rocks, described above, are identical with certain fossils from the Bunter of the Vosges, figured by Schimper and Mougeot † in 1844, under the name *Yuccites vogesiacus* ‡. The type specimens are not to be found in the Strasburg University Museum, where I have sought for them in vain. There are, however, in that collection, a large number of other specimens, which there is every reason to believe are identical with the figured specimens, and also with the English examples discussed here. At the same time Schimper and Mougeot's figures do not give at all an accurate idea of these fossils, although there is very little doubt what they are intended to represent, when one compares the Strasburg material with them.

For reasons which will be discussed here, I have no hesitation in referring both the specimens from the Vosges, and the newly discovered, British representatives to the frond-genus *Zamites*. The specific name which would naturally be adopted for these fossils is *Zamites vogesiacus* (Schimper & Mougeot), but, by an unfortunate circumstance, this term is not available. For the same authors, in the same memoir, have also figured and described a totally different plant § under that name, the type of which is preserved at Strasburg, where I have examined it. Unfortunately it proves to be a very obscure impression of a Cycad-like frond, in sandstone, the genus of which is quite indeterminable. Despite Schimper and Mougeot's figures, the nervation is not visible, and the outlines of the pinnules are but feebly marked. The specimen, however, remains the type of *Z. vogesiacus*, Schimp. & Moug., and a new specific name must be adopted for the *Yuccites vogesiacus* of those authors, on its transference to the genus *Zamites* ||. I therefore propose the name *Z. grandis*, nom. nov., in allusion to the large size of the pinnæ of these fronds.

We may now turn to a discussion on the generic affinities of this and of other closely similar fossils; a subject of much confusion in the past, and the cause of considerable difficulty at the present.

Schimper and Mougeot ¶ regarded these fossils as simple leaves, with a parallel nervation, referable to the Monocotyledons, and therefore included them within the genus *Yuccites*, as members of the Liliaceæ. Zigno ** has also figured a Jurassic

* Wills (1907), p. 29.

† Schimper & Mougeot (1844), p. 42, pl. 21.

‡ The stem figured by Schimper and Mougeot (1844), p. 43, pl. 29. fig. 4, and attributed to this plant, belongs, in all probability, to the Conifer *Voltzia*: see Blanckenhorn (1886), p. 135, and Schütze (1901), p. 245.

§ Schimper & Mougeot (1844), p. 34, pl. 18. fig. 1.

|| When I compiled the list of plant-remains given in Mr. Wills's paper (1907), p. 32, I unfortunately overlooked the fact that Schimper and Mougeot specific name could not be applied to these specimens.

¶ Schimper & Mougeot (1844), p. 42; Schimper (1869), vol. ii. p. 426.

** Zigno (1873), p. 7, pl. 26. figs. 1-4.

plant from Italy, which he refers to this same genus, under the name *Yuccites Schimperianus*, Zigno, which is almost certainly *generically* identical with the Triassic fossils discussed here. Again the *Yuccites burgundiacus* of Saporta*, from the Bathonian of France, is of like affinity, though the *Y. angustior* of the same author†, from the Bunter of the Vosges, is, judging by its reticulate nervation, quite distinct generically. Saporta‡ referred the genus *Yuccites* to his group of Proangiosperms.

The plant figured by Compter§, from the Lower Keuper of East Thuringia, under the name *Cordaitea keuperianus*, sp. n., agrees very closely in shape with the specimens described here. It is possible that it may even be specifically identical with the British fossils, though it appears to be rather smaller, and, not having seen the specimen, I have hesitated to unite them.

Velenovský|| has figured some leaves, which he termed *Krannera mirabilis*, from the Cretaceous of Bohemia, which bear a very close resemblance to the specimens under discussion here. That author, however, suspected that these leaves were attached directly to stems of a curious, cone-like form, with which they were associated. The matter thus remains in doubt, with a distinct possibility that the leaves assigned to *Krannera* may eventually prove to be of a similar nature to *Zamites grandis*.

My interpretation of these fossils is an entirely different one. I believe them to be simply the detached pinnæ of a large frond of the Zamitean type, with long leaflets. It is true that in many of the typical members of the genus *Zamites*, such as *Z. (Williamsonia) gigas* (Lindl. & Hutt.) from the Lower Oolite, *Z. Feneonis*, Brongn., from the Kimmeridgian, or *Z. buchianus* (Ett.) from the Wealden, the pinnæ are only of moderate length, and are almost invariably still attached to the rachis, and thus the frond, even if fragmentary, is complete in this respect. But in the case of a frond with very long and large pinnæ, the latter would naturally be more liable to have become detached from the rachis during the process of preservation.

The form and nervation of these detached pinnæ agree exactly with those of the better known species mentioned above, in which the leaflets are by comparison short. They show the same sudden contraction in width, near the point of insertion, and a basal callosity; in fact all the characters included in Schimper's definition, already discussed.

It is true, however, that, neither in the case of the English specimens, nor the examples from the Vosges, has a frond been found with the pinnules attached to the rachis. But continuity between these organs is certainly to be seen in the case of a frond from the Keuper of Raibl, in Austria, named by Schenk¶ *Pterophyllum giganteum*. Schenk's type is preserved in the Geological Museum of the University of Würzburg, where I have had the pleasure of seeing it. Schenk, in his description, pointed out the

* Saporta (1891), p. 79, pl. 236. figs. 1, 1 a.

‡ Saporta (1891), p. 69.

|| Velenovský (1885), p. 1, pl. 1. figs. 1, 4, 5, 6, 7.

† Saporta (1891), p. 74, pl. 234. fig. 1.

§ Compter (1894), p. 225, pl. 4. fig. 9.

¶ Schenk (1865), pp. 18, 19, pl. 2. fig. 2.

obvious similarity of this frond to that of the recent Cycads, especially *Ceratozamia*. He also compared it with *Pterophyllum Bronni*, Schenk (see p. 120), and referred it to the same genus. The special interest of this specimen lies in the fact that the pinnæ are attached, apparently laterally, to a broad rachis. Since the pinnæ are all in continuity, it is impossible to say whether a callosity occurs at the base of each. The general shape of the leaflets, bearing in mind, as Schenk has pointed out, that the apical portions are wanting, as well as the characters of the nervation, lead me to regard it as identical with, or scarcely distinguishable from, *Zamites grandis*.

Although in Schenk's specimen the leaflets are apparently attached laterally, it by no means follows that such was really the case in the living state. I have already commented (p. 113) on the difficulties of ascertaining the exact manner of attachment in many specimens of Zamitean fronds. I see no reason to regard this leaf as being other than a pinnate frond, though Schimper * placed it in a new genus *Macropterygium*, as a new species *M. Schenkii*.

If my view of the nature and attribution of Schenk's fossil is correct, then the case in favour of the interpretation, here adopted, of the leaflets of *Zamites grandis*, from England and the Vosges, is greatly strengthened.

Further evidence may be found in a common fossil from the Stonesfield Slate of England, *Zamites megaphyllum* (Phillips), which has recently been redescribed by Prof. Seward †. This is a leaflet very closely allied to *Zamites grandis*, but apparently specifically distinct, for the apex is more elongately acuminate and the pinnæ are more nearly linear in form. The pinnæ, as a rule, also occur detached, and may be more than 30 cm. long. The Cycadean affinity of the frond was, however, early recognised in this case, for one of Phillips's ‡ type specimens (recently refigured by Seward §) shows the leaflets apparently in continuity with the rachis; though here again the precise manner of attachment is not very evident. I am in agreement with Prof. Seward who says "on the whole I incline to the opinion that the numerous Monocotyledon-like leaves from Stonesfield are the pinnæ of a Cycadean frond" ||.

Solms-Laubach ¶ has also called attention to the fact that, in some fronds of *Zamites*, the pinnules frequently become isolated from the rachis, and in this condition may have been liable to misidentification.

Lastly, in this connection, it may be pointed out that Cycad-like fronds with very long pinnæ have been referred to other genera, in which the leaflets are, in the majority of cases, only of moderate length. The Rhætic fossil *Podozamites distans*, Presl, var. *longifolia*, Schenk **, is a good example. A detached leaflet of such a frond would be just as liable to misidentification as one of the pinnæ of *Zamites grandis*.

We may therefore conclude, viewing the whole of this evidence, that there are strong reasons to be adduced in support of the interpretation of the Keuper fossils maintained here.

* Schimper (1869), vol. ii. p. 132.

† Seward (1904), p. 110, pl. 10. figs. 4-5, pl. 12. figs. 1, 3-5, and text-fig. 11.

‡ Phillips (1871), p. 169, diag. 30. fig. 6.

§ Seward (1904), p. 114, text-fig. 11.

|| Seward (1904), p. 111.

¶ Solms-Laubach (1891), p. 88.

** Schenk (1867), p. 162, pl. 37. fig. 1.

There are, however, several other genera with which these leaflets, and especially imperfect, detached fragments of the pinnæ, are liable to be confused, and these may be briefly noticed.

Næggerathia, Sternberg.—This genus is now restricted to certain leaves, known only from the Westphalian rocks of Bohemia, of which *N. foliosa*, Sternb., is the typical species. Its affinities are wholly uncertain. The only specimens of *Zamites grandis*, which might be confounded with it, are short basal fragments of the leaflets, which are easily distinguished by the callosity at the point of attachment, and by the sudden contraction in width at the proximal extremity.

*Cordaite*s, Unger (including *Rhoptozamites*, Schmalhausen).—Some imperfect fragments of the leaflets of *Zamites grandis* recall rather vividly certain leaves of *Cordaite*s, but when complete pinnæ are available they are easily recognised by the basal characters, and also by the fact that they are the leaflets of a pinnate frond, and not leaves spirally arranged on a shoot.

Næggerathiopsis, Feistmantel.—In the case of this imperfectly-known member of the *Glossopteris* flora, probably closely allied to, if not identical with, *Cordaite*s, where the manner of attachment of the leaves is as yet undetermined, the detached pinnæ of *Zamites grandis* are with difficulty distinguished, and then chiefly by their basal characters. It is possible that the fossils from the Rhætic rocks of Tonkin, referred to *N. Hislopi* by Zeiller*, may be fragments of leaflets of a Cycad-like frond with long pinnæ, but the matter must remain doubtful for the present. One of Zeiller's figures, however, shows a distinct basal callosity.

Podozamites, Bronn.—The species of this genus with long leaflets are easily distinguishable from *Z. grandis*, by the fact that the pinnæ are much more narrowly contracted at the base, and the veins less numerous and less crowded. The manner of arrangement of the leaflets on the axis or rachis is also a distinctive feature.

It has been seen that, on the interpretation of the Triassic fossils discussed here, there are good reasons for regarding as portions of ~~Zamitean~~ fronds with very long pinnæ several other, previously described examples (see pp. 115–116) from rocks of various ages, hitherto assigned to such genera as *Yuccites* and *Cordaite*s, some of which have been attributed with confidence to the class Monocotyledons. The list could be considerably extended. The fossils figured by Heer, and more recently by Leuthardt†, from the Keuper of Neue Welt, near Basle (Switzerland), under the name *Bambusium Imhoffi*, Heer, of which I have seen an example in the Basle Museum, are almost certainly pinnæ of a Zamitean frond, and may even be identical with, or closely related to, *Zamites grandis*. This again, in the opinion of Dr. Leuthardt in his recent memoir, is an example of a Triassic Monocotyledon.

It is possible that some of the leaves now assigned to the genus *Phœnicopsis*, Heer, more especially *P. elongatus* (Morris)‡ from the Rhætic of New South Wales and

* Zeiller (1902), p. 149, pl. 40. figs. 1–6, ? 7–8.

† Leuthardt (1903), pt. 1, p. 6, pl. 1. figs. 1–3.

‡ Seward (1903), p. 67, pl. 9. figs. 1, 9, 10.

S. Africa, may have been the long detached pinnæ of fronds similar in type to, but distinct from, *Zamites grandis*, though the evidence in this case is not so strong.

In collections of the Rhætic flora of Theta, near Bayreuth, in Bavaria, one sometimes notices such a leaf as that figured on Pl. 18. fig. 3 ($\frac{3}{4}$ nat. size). They are of considerable length, 19 cm. in the figured example*, and of linear form, with a fine, rather faint, parallel nervation. For some time past I had been puzzled as to the generic identity of this fossil, which apparently was not described by Schenk† in his Monograph of this flora, nor by any subsequent author. When, however, the English material of *Zamites grandis* came into my hands, I realised that, in all probability, this specimen was another example of a detached leaflet of a species of *Zamites* with very long, narrow pinnæ. It is interesting to find that the surface of the leaflet of this Rhætic fossil shows numerous small pittings or puckerings, recalling those which occur on the specimens from the English Keuper.

It may be also pointed out that several species of Cycad-like fronds, with very long pinnæ, have been already referred to the genus *Zamites*. In addition to *Z. megaphyllum* (Phillips), the following are cases in point:—*Z. africana* (Tate)‡, *Z. Milleri*, Zigno§, and possibly *Z. Renevieri*, Heer||. The frond recently figured by Ward¶ as *Zamia Washingtoniana* is probably another example.

PTEROPHYLLUM BRONNI, Schenk.

The genus *Pterophyllum*, like the genus *Zamites*, is known from the Palæozoic rocks, but, unlike the latter, it is already known to be a very abundant and typical type of frond in the Keuper rocks of Europe, and also in the Rhætic. The study of the Zamitean fronds from the English Keuper naturally led to a comparison with the Austrian fossil, first described by Bronn as *Næggerathia vogesiaca*. The loan from the Munich Museum of the excellent example figured here, for which I am greatly indebted to Prof. Rothpletz, has extended our knowledge of this very interesting fossil, and has given an opportunity for the publication of more accurate figures than those of Bronn, which appeared nearly fifty years ago.

The Genus PTEROPHYLLUM, Brongniart, 1825.

(Ann. Sci. Nat. sér. i. vol. iv. p. 211.)

This generic name was originally proposed by Brongniart for two Swedish fossils, which are now transferred to another genus. In 1828, however, the same author** gave the following diagnosis of the genus, and included under it such typical species as

* No. 294, Foreign Plant Coll., Sedgwick Museum. A specimen in the British Museum (Nat. Hist.), No. 15,049, is 25 cm. in length.

† Schenk (1867).

‡ Seward (1903), p. 25, pl. 5. fig. 5.

§ Zigno (1873), vol. ii. p. 40, pl. 30. fig. 6; Miller (1872), p. 432, text-fig. 136.

|| Heer (1865), p. 144, text-fig. 95; Saporta (1875), vol. ii. p. 112, pl. 93. fig. 2.

¶ Ward (1905), p. 503, pl. 111. fig. 1.

** Brongniart (1828), p. 95.

P. Jægeri and *P. longifolium* from the Keuper rocks :—" Feuilles pinnées, à pinnules d'une largeur à peu près égale, s'insérant sur le pétiole par toute la largeur de leur base, tronquées au sommet ; nervures fines, égales, simples, peu marquées, toutes parallèles."

Schimper* restricted the genus to leaves with strictly linear leaflets, an emendation which has since been generally accepted. The recent definition of *Pterophyllum* given by Prof. Zeiller† may be quoted as an accurate analysis of the chief characters of the fossils usually included under this name :—

" Frondes simplement pinnées ; folioles linéaires, plus ou moins longues par rapport à leur largeur, tantôt tronquées, tantôt arrondies, plus rarement effilées en pointe à leur sommet, attachées au rachis par toute leur largeur, quelquefois même non peu élargies à leur base ; parcourues par des nervures simples ou dichotomes, parallèles entre elles."

It will be seen that the species described here as *Pterophyllum Bronni*, Schenk, does not agree in certain important respects with this definition of the genus. A discussion of this question may, however, be reserved until a description of the specimen has been given.

The Species PTEROPHYLLUM BRONNI, Schenk, 1865.

(Plate 18. fig. 1 ; Plate 19. fig. 4.)

1858. *Næggerathia vogesiaca* (non Schimp. et Moug.), Bronn, Beitr. trias. Fauna & Flora Raibl, p. 129, pl. 6. figs. 1-4.

1865. *Pterophyllum Bronnii*, Schenk, Flora Schwarz. Schiefer, Raibl, p. 18.

1870. *Macropterygium Bronnii*, Schimper, Traité Pal. Végét. vol. ii. p. 132.

Locality.—Keuper of Raibl, Carinthia, Austria.

Diagnosis.—Frond large, pinnate. Rachis stout, from 1-1.5 cm. in breadth, faintly striated longitudinally. Pinnæ large, entire, spreading ; varying slightly in size and shape, on an average 15 cm. or more in length, and 5 cm. or more across at their greatest width, a little below the apex ; cuneate or more or less oblanceolate. Margin entire ; apex truncated, usually somewhat unsymmetrical ; lateral angles rounded. Base not markedly contracted. Nerves fine, very numerous, close, parallel, straight, terminating at the broad apex, and not bending outwards towards the margin.

Description of the Specimen.

The fine specimen in the Munich Museum (figured on Pl. 18. fig. 1, reduced to two-thirds natural size) shows a small fragment of the rachis and portions of five pinnæ, all probably belonging to the same frond. The uppermost leaflet is almost complete (Pl. 19. fig. 4). It measures 16.2 cm. in length, and 5.3 cm. across at its greatest breadth. The apex appears to be slightly emarginate ; but this is very possibly due to some accident in the preservation, for it does not appear to be the case in the other pinnæ, in all of which the distal extremities are quite intact. At the base, the pinna is imperfect and obscure, and it cannot be ascertained with certainty whether it is still

* Schimper (1869), vol. ii. p. 133.

† Zeiller (1903), p. 174.

attached to the fragment of the rachis seen below (*cf.* Pl. 19. fig. 4). The nervation is not very distinct neither in this nor any of the other leaflets, though the course of the veins is quite clear. The dichotomy of the veins at the base, and occasionally throughout the lamina, cannot be clearly made out, though there is good reason to suppose that it occurs. There is a possibility that this leaflet may have been the terminal pinna of the frond, but this again is a point which cannot be satisfactorily decided. In the photograph on Plate 19. fig. 4 it is shown natural size.

The next highest pinna on the right-hand side is shorter, the length being 4.4 cm., and its greatest breadth about 4 cm. At the base it appears to be distinctly narrowed near the point of attachment, but its width here may well have been somewhat greater in the living state. It is, in all probability, still attached to the rachis (*cf.* Pl. 19. fig. 4).

The next lowest leaflet is almost certainly attached for a distance of about 1.2 cm., though a part of the base is missing (*cf.* Pl. 19. fig. 4). It is 13.8 cm. long and 5.4 cm. across at its broadest part. There is no trace of any callosity at the base in either this instance or that of the pinna next above. The unsymmetrical nature of the apex is clearly seen.

The two lower pinnæ, each about 5 cm. broad at their widest part, are imperfect, but show the apical characters very well.

The photograph on Plate 19. fig. 4 shows a portion of the same specimen slightly below natural size. In addition to the terminal pinna, the rachis (*r.*), with two pinnæ still attached, is clearly seen.

Affinities of the Species.

The generic attribution of this fossil raises a difficult question, and one on which there has already been some difference of opinion. Bronn *, in his original description published in 1858, regarded it as the same plant as Schimper and Mougeot's *Yuccites vogesiacus*, here described under the name *Zamites grandis*, *nom. nov.*, though he admitted that at first sight it appears to be very different. There can be no question that the Raibl plant is not specifically identical with the specimens from the Bunter of the Vosges and the Keuper of England, as all authorities are agreed, but the problem remains as to whether it is *generically* distinct, and, if so, the genus in which it should be placed.

Attention may here be called to one or two points in connection with Bronn's figures. In the first place, as Schenk † has already pointed out, the leaflets are quite simple and entire, and not lobed as Bronn's specimens indicated; an appearance no doubt due to bad preservation. Although one of the examples figured by that author ‡ shows a rachis with several, rather distant, leaflets attached, Bronn inclined to the opinion that, on the whole, it represented a shoot, bearing leaves arranged as in *Næggerathia*. Schimper § compared it with *Podozamites*, and instituted a new genus *Macropterygium* for its reception.

* Bronn (1858), p. 129.

‡ Bronn (1858), pl. 6. fig. 1.

† Schenk (1865), p. 18.

§ Schimper (1869), vol. ii. p. 132.

Though the matter can hardly be said to be finally proved at present, there appears to be a very strong probability that the leaf of this species was really a pinnate frond, and that, like *Zamites grandis*, the large leaflets frequently became detached from the rachis, as in the case of several of Bronn's figured examples. The arrangement of the leaflets in the specimen figured here (Pl. 18. fig. 1), although the fossil is admittedly imperfect, in conjunction with the frond described by Bronn, in which the pinnæ are still attached to the rachis, will hardly permit of any other conclusion, though the question cannot be finally settled until more complete specimens have been obtained.

In this view of the Raibl specimen, I am in agreement with Schenk *, who in 1865 decided that its affinities lay in the direction of the *Cycadophyta*, and corrected Bronn's specific determination. Schenk further concluded provisionally that the fossil most nearly approaches the genus *Pterophyllum*, and adopted the new name *P. Bronni*, which is that provisionally made use of here. There are only two other fossils with which I am acquainted which at all resemble this plant. One of these is the *Sphenozamites Rogersianus* of Fontaine †, from the Triassic rocks of the Richmond coalfield in Virginia, U.S.A. Fontaine's figures do not, however, agree very well with the Austrian specimen, though Stur ‡ has gone so far as to say that both are specifically identical. Yet as regards generic affinity, the two plants are obviously closely related. In the size and shape of the leaflets, the American specimens show a striking agreement with Bronn's species, especially as regards the apex. The basal characters are, however, different, judging by Fontaine's figures, which show pinnæ attached only by a small portion of the base, the upper and lower basal angles of which are rounded. In the specimen described here the pinnæ are strictly wedge-shaped, and apparently attached by their entire base. The nervation also differs. In the Austrian specimen, no trace of transverse striæ between the nerves can be detected, and the veins pursue a more parallel course direct to the apex, and do not radiate as in the figure of the American plant. This frond, however, as a whole, supports the conclusion as to the pinnate nature of the leaf described here.

The other species, *Sphenozamites tener* of Compter §, from the Keuper of Thüringia, is considerably smaller than the Raibl specimen, and does not appear to be very closely related. The first specimens figured were fragmentary, and consisted for the most part of detached pinnæ. In these the shape is rhomboidal rather than cuneate, and the nervation appears to approximate more closely to that of the genus *Sphenozamites*. Compter also figures the cells of the epidermis of the leaflets, which he points out are of the Cycadean type. A further specimen, figured by the same author in 1894, has several fragments of pinnæ united to the rachis. On the whole it shows obvious points of agreement with the figures of *S. Rogersianus* given by Fontaine, though it is no doubt a smaller plant specifically distinct.

* Schenk (1865), p. 18.

† Fontaine (1883), p. 80, pl. 43. fig. 1, pl. 44. figs. 1 & 2, pl. 45. figs. 1 & 2.

‡ Stur (1888), p. 210.

§ Compter (1883), p. 12, pl. 1, and text-figs. 10-17, and Compter (1894), p. 222, pl. 4. fig. 3.

The question as to the genus, to which the frond described here should be referred, is a difficult one, and the following genera may now be considered in this connection.

Sphenozamites.—It does not appear to me to be possible to attribute the Raibl fossil to this genus, as at present defined. The name *Sphenozamites* was proposed by Brongniart, in 1849, to include fronds of the *Otozamites*-type, which were not auriculate at the base, and possessed a radiating nervation. In the specimens referred to *Sphenozamites* and figured by Zigno *, Renault †, Seward ‡, and others, the spreading nature of the nervation is clearly seen, and the shape of the pinnules more closely approximates to the rhomboidal than to the cuneate form. The margin in some species is also toothed.

It might, perhaps, be possible to extend the diagnosis of this genus so as to include the Raibl species, but at the present time such an attempt would hardly seem advisable.

Zamites.—The specimen discussed here appears to be quite distinct from the fossils attributed to this frond-genus, both as regards the shape of the pinnæ, and in respect to the nervation. As compared with *Zamites grandis*, the nerves are sometimes finer and closer, and there is no evidence of a callosity at the base of the leaflet. Zeiller § has, however, recently described a frond from the Rhætic of Tonkin under the name *Zamites truncatus*, Zeiller, in which the shape and nervation of the leaflets offer some points of comparison with the present specimen, but the pinnæ are much smaller, and the agreement is not a close one.

Pterophyllum.—It is admitted that this plant differs from typical members of this genus in a marked degree, especially as regards the size and shape of the pinnæ. Yet it appears to me to be more closely allied to *Pterophyllum* than to any other frond-genus with which I am acquainted. In some of the typical species of *Pterophyllum* from the Triassic rocks, especially *P. longifolium*, Brongn. ||, the leaflets are sometimes contracted at the base and broadest at the apex, thus approximating in some slight degree towards the cuneate form, though they are on a much smaller scale than in *P. Bronni*. If we were to imagine such a frond magnified several times and the wedge-like shape of the pinnæ further accentuated, we should arrive at a leaf which would correspond fairly closely with the latter species both in form and nervation.

On the whole we may conclude that the Raibl fossil agrees with the diagnoses of this genus given by Brongniart, Zeiller, and others, with the chief exception that the pinnæ are broadly wedge-shaped in form and not linear. It would thus seem preferable to adopt Schenk's provisional reference of this plant to the genus *Pterophyllum*, than to make use of Schimper's term *Macropterygium*.

It remains to be pointed out that detached pinnæ of this frond, especially when fragmentary, are liable to be mistaken for the leaves of *Cordaites* and other genera in which the nervation is closely similar, but which are simple leaves, spirally arranged

* Zigno (1873), vol. ii. p. 105, pls. 39 & 40.

† Renault (1893), p. 327, pl. 81. fig. 1.

‡ Seward (1904), p. 119, pl. 11. fig. 4, and text-fig. 12 on p. 120.

§ Zeiller (1902), p. 166, pl. 43. figs. 3-6.

|| Cf. Leuthardt (1903), pt. i. p. 16, pls. 7-10.

on branches. They also strongly resemble detached leaflets of the Upper Carboniferous genus *Neggerathia* *, whose affinities remain wholly doubtful.

GENERAL CONCLUSIONS.

The two fossils described here belong to a flora as yet comparatively little known. Both are derived from approximately the same horizon, the Keuper; the one from England, the other from Carinthia. Among the known fossil plants of Cycadophycean affinity they may be considered as exceptional instances of megaphylly. Yet as regards mere size they are in no way remarkable when compared with the fronds of many species of living Cycads.

The specimens discussed here under the name *Zamites grandis*, nom. nov., illustrate the difficulties which arise as a corollary of the fragmentary preservation of such large fronds. In nearly every case the pinnæ have become detached, and usually the leaflets themselves are incomplete. Such impressions are often extremely difficult to determine. It has been shown here that the long Monocotyledon-like leaves, often nearly 50 cm. in length, which have recently been discovered in the Keuper rocks of Bromsgrove, are in reality the large detached pinnæ of a Cycadophycean frond belonging to the form-genus *Zamites*. This conclusion has thrown light on a considerable number of similar Mesozoic fossils, previously described under the names *Yucoites*, *Cordaite*s, *Bambusium*, &c., and regarded as evidence of the existence of Monocotyledons, Proangiospermeæ, Cordaitales, or other groups in the earlier Mesozoic rocks.

The fronds of *Zamites grandis* are practically the first well-preserved plant-remains which have ever been described from the British Trias, excluding the Rhætic. Only a few obscure impressions, chiefly of cones and *Equisetaceous* stems, have hitherto been recorded, and even these have proved to be of rare occurrence †. They also fill a gap in our knowledge of the vertical distribution of this genus, for *Zamites*, although known from the Palæozoic rocks, has not hitherto been recognised beyond doubt from Mesozoic sediments of earlier age than the Rhætic. Incidentally the recognition of this species from England tends to emphasise the close affinity of the fossil plants from the various Triassic deposits of Europe, for it is now known from the Bunter of the Vosges, the Lower Keuper of Carinthia, and possibly also from the same horizon in Thuringia.

The other species described here, *Pterophyllum Bronni*, Schenk, is a very rare type of frond, known only from the earlier Triassic rocks of the Continent, and possibly also from beds of the same age in the United States. Apart from its large size, it is especially interesting on account of the difficulty of including it within the limits of any of the recognised frond-genera of Cycadophyta. It is by no means a typical example of a *Pterophyllum*, though it appears to be on the whole more closely allied to that genus than to any other.

* See Solms-Laubach (1891), pp. 141 and 151.

† In addition to the specimens described here, Mr. Wills has obtained several other well-preserved plant-remains from the same locality in the Keuper of Bromsgrove, which he has also presented to the Sedgwick Museum, Cambridge, and is describing.

In some respects it may be regarded as combining characters common to several Mesozoic Cycad-like fronds, for one can easily see how smaller leaves, such as those of *Sphenozamites*, or of other species of *Pterophyllum*, or even some Zamitean fronds, could be derived from it. On the other hand, if the *individual leaflets* of the pinnate frond are alone considered, they show a very remarkable similarity to the *leaves* of the Palæozoic genera *Cordaitea* and *Næggerathiopsis*.

It is, perhaps, hardly necessary to add that it is impossible to correlate either of these fronds with those of living genera of Cycads. Wieland has recently pointed out that great variations in the size and form of the leaves are found within a single genus of these plants. He says "the pinnules of the *Zamia* present many gradations, from linear forms quite as narrow and long as pine needles to elliptical or somewhat spatulate, thick, and fleshy forms like those of *Z. furfuracea*, which strongly recall the blades of certain species of *Cordaitea*"*. Further, we know that several species of the Mesozoic *Zamites* have proved to be the foliage, not of Cycads, but of a very distinct race, the Bennettiteæ.

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* Wieland (1906), p. 191.

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EXPLANATION OF THE PLATES.

(All the photographs are by Mr. Tams, Cambridge.)

PLATE 17.

- Fig. 1.** *Zamites grandis*, nom. nov. An almost complete pinna, in which, however, a small portion of the apex is wanting. From the Keuper of Mr. Griffin's North Quarry, Rock Hill, near Bromsgrove (Worcestershire). No. 24, British Triassic Plant Coll., Sedgwick Museum, Cambridge. Half nat. size.
- Fig. 2.** *Zamites grandis*. A basal portion of a pinna, showing the nervation. From the same locality. No. 26 in the same collection. Nat. size.
- Fig. 3.** *Zamites grandis*. A large incomplete pinna. From the same locality. No. 25 in the same collection. Half nat. size.
- Fig. 4.** *Zamites grandis*. A basal portion of a slender pinna, showing the callosity at the point of attachment. From the same locality. No. 30 in the same collection. Nat. size.

PLATE 18.

- Fig. 1.** *Pterophyllum Bronni*, Schenk. Five pinnæ, all probably belonging to the same frond, and a small fragment of the rachis. From the Lower Keuper of Raibl, in Carinthia. From the specimen in the Munich Museum. Two-thirds nat. size.
- Fig. 2.** *Zamites grandis*. Apical portion of a pinna. From the same locality as the specimens figured on Plate 17. No. 26, British Triassic Plant Coll., Sedgwick Museum, Cambridge. Nat. size.
- Fig. 3.** *Zamites* sp. Portion of a pinna. From the Rhætic of Phantaisie, near Bayreuth, Bavaria. No. 294, Foreign Plant Coll., Sedgwick Museum, Cambridge. Three-fourths nat. size.

PLATE 19.

- Fig. 1.** *Zamites grandis*. Apical portion of a pinna, bent upon itself. From the same locality as the specimens figured on Plate 17. No. 22, British Triassic Plant Coll., Sedgwick Museum, Cambridge. Nat. size.
- Fig. 2.** *Zamites grandis*. Basal portion of a slender pinna, showing the callosity at the base. From the same locality. No. 28 in the same collection. Nat. size.
- Fig. 3.** *Zamites grandis*. Apical portion of a pinna. From the same locality. No. 27 in the same collection. Nat. size.
- Fig. 4.** *Pterophyllum Bronni*, Schenk. Three pinnæ, probably still attached to the rachis (r.). The nervation is clearly seen. From the Lower Keuper of Raibl, Carinthia. From the specimen in the Munich Museum. Slightly below nat. size.

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W. TAMS, photo.

London Stereoscopic Co. imp.

ZAMITES GRANDIS, SP. NOVA.

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