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ABSTRACT

Stem impressions of Lycopodiopsis (here taken to include Cyclodendron) are figured from the Permian of Western Australia, and the distribution of the genus is discussed. The stem impressions from the Permian of South Africa and Brazil hitherto recorded as "Sigillaria brardi" are considered to be older stems of Lycopodiopsis pedroanus. There are no satisfactory records of northern hemisphere lepidophytes in the Glossopteris flora of the southern hemisphere.

INTRODUCTION

N 1940 H. S. Rao re-investigated the anatomy of Renault's Brazilian genus Lycopodiopsis, confirming its distinction from Lepidodendron, and also discussed other records of Palaeozoic lycopods from the southern hemisphere. In 1947 Maack reviewed comprehensively the Brazilian distribution of L. derbyi, mainly on the basis of impression material ; he also decided that the South African Cyclodendron leslii (Seward) belonged to the same genus and might even be specifically identical with L. derbyi. The present note may be regarded as a pendent to these two papers, with the main conclusions of which I find myself in agreement. These conclusions can, I think, be carried further in emphasizing, firstly, the close relationship between several of the fragmentary lycopod remains which have been recorded from various parts of Gondwanaland, and secondly, the distinction which is now becoming clearer between the late Palaeozoic lycopods of Gondwanaland and those of the northern hemisphere.

Lycopodiopsis Renault (1890) was founded on material which showed both external features and internal anatomy, and both were figured. Therefore, although in much of the subsequent literature the anatomy has gained preponderant attention, there would be no ground for confining the generic name to material which exhibits internal structure alone. Petrified specimens are in fact so far known only from Brazil. In 1869 Carruthers had figured lepidodendroid twigs from Brazil as *Flemingites pedroanus* although "the one organ wanting in the specimens from Brazil is the cone on which to a considerable extent I founded the genus" (p. 152). The name *Flemingites* has long been accepted as a synonym of *Lepidostrobus* and is inapplicable to the southern hemisphere plants under discussion.

However, Lepidodendron pedroanum (Carr.), as it has been called since Zeiller so transferred it (1896), bears a close resemblance to some specimens of Lycopodiopsis derbyi. Typical leaf-scars of Lepidodendron are not in fact to be seen on the type specimens of "Flemingites" pedroanus in the British Museum (V. 230 a-h) as Carruthers himself pointed out, and this species is unquestionably congeneric with the impressions referred to Lycopodiopsis. The observed differences between Lycopodiopsis pedroanus and L. derbyi may well be due either to preservation or to differences in maturity of the various twig and stem fragments. It is perhaps significant that in Maack's floral lists the two names are never recorded together from one locality. Therefore, unless future work should disclose more reliable specific distinctions, it seems inevitable that Carruthers' specific name should have priority over Renault's. Lycopodiopsis pedroanus (Carr.) must, therefore, be adopted as the name of the plants hitherto described as Lycopodiopsis derbyi and Lepidodendron pedroanum. A fair range of figures of impression material from Brazil is given by Maack (1947) and Read (1941).

THE SUPPOSED "SIGILLARIA BRARDI" OF SOUTH AFRICA

In 1896 Seward recorded lepidodendroid stems, which he tentatively named *Lepidophloios*, from "a locality south of Johannesburg" (Vereeniging) in South Africa, associated with typical members of the Glossopteris flora. Subsequently he referred these stems to the species *Sigillaria brardi* Brongniart, apparently with the concurrence of both Kidston and Zeiller (SEWARD, 1897). Since then, many palaeobotanists have felt dubious about this identification, especially those who were familiar with the European S. brardi and who had seen some of the South African specimens in the British Museum.

Seward (1903, p. 87, PL. XI, FIGS. 4-6) described some small lycopodialian twigs, also from Vereeniging in the Transvaal, as *Bothrodendron leslii*, and in 1928 Kräusel, rightly regarding these (and some further specimens which he figured from South-west Africa) as distinct from *Bothrodendron*, instituted a new genus *Cyclodendron*. Twenty years earlier, however, David White (1908, p. 441) had said that he regarded the Transvaal *B. leslii* as referable to the Brazilian genus *Lycopodiopsis*. If, with Maack, we accept this, as I think we must, then *Cyclodendron* becomes a synonym of *Lycopodiopsis*.

The view I now wish to put forward is that the somewhat Sigillaria-like specimens from Vereeniging are simply fragments of trunks or branches of the lycopod whose smaller branches or twigs were described as Bothrodendron (or Cyclodendron) leslii. Other authors have nearly, but not quite, reached the same conclusion. Thus Seward himself, in recording "Lepidodendron" pedroanum from Vereeniging (SEWARD & LESLIE, 1908, p.120), remarked, "A Lepidodendron of this type might be easily mistaken for Sigillaria brardi ", while Walton (1929, p. 66) suggested that a specimen which he described as cf. Cyclodendron leslii from Wankie, Rhodesia, might be "merely a condition of Sigillaria brardi". One has only to invert these statements in order to reach the probable truth, which is that the various fragments, referred to different genera, are simply different parts or states of one and the same type of plant. The slender basis for some of the attributions has been very much overlooked; thus in claiming Flemingites pedroanus as a Lepidodendron Zeiller remarked (1896, p. 607), "Quant aux cicatricules, elle sont presque toujours indiscernables; on aperçoit cependant assez fréquemment une dépression centrale [italics mine], correspondant au passage du faisceau foliaire ", and in material of the same species from South Africa Seward only detected "faint indications of the parichnos and leaf-trace scars, but the surface features have been partly obliterated " (SEWARD & LESLIE, 1908, p. 120). In 1897 (p. 330) Seward had commented on the

resemblance between a Vereeniging specimen, which he figured as ? Sigillaria sp., and "Lepidodendron" pedroanum from Brazil; in 1908 Seward and Leslie transferred it to the latter species. The drawings of supposed Sigillarian leaf-bases (SEWARD, 1897, p. 327) are not very convincing, and an inspection of the actual material suggests that if specimens are sufficiently badly preserved in a sufficiently coarse matrix, it will be possible to see here and there the markings which, by a stretch of the imagination, could be interpreted as Sigillarian or Lepidodendroid. Lycopodiopsis is distinguished (among other characters) by the absence of parichnos scars, and none of the South African material shows these scars unquestionably and consistently.

OTHER AFRICAN LYCOPOD RECORDS

Lycopodiopsis pedroanus has been recorded by Du Toit (1932, p. 398) under the name Cyclodendron leslii from Gondwana beds of Uganda. In addition to stem fragments he figures several specimens of lanciform leaves which closely resemble leaves to be seen in the original Brazilian material of L. pedroanus. He summarizes the distribution of the plant in Africa (p. 405) and remarks that it ranges "from the Middle Ecca (Union) up to the Lowest Beaufort Beds (Wankie) and is hence typically Lower Permian".

Cvclodendron mathieui Seward (1931) was described from beds believed to be Lower Permian at Kongolo in the Belgian Congo. The species was not diagnosed and Seward stated that his specimens " closely resemble and may be specifically identical with " C. leslii from South-west Africa, and though he thought that the original Bothrodendron *leslii* from Vereeniging might possibly be a distinct species, he agreed that the genus only superficially resembled Lepidodendron and Sigillaria and might be distinguished "by the absence of parichnos and a clearly defined pit marking the point of exit of a leaf trace ". He specifically says of C. mathieui : " none of the bosses in the scars afford any satisfactory evidence of the occurrence of a central pit and two lateral parichnos-pits such as one sees in Lepidodendron and Sigillaria". For the present I see no reason for separating the Congo specimens from Lycopodiopsis pedroanus.

Lepidodendron vereenigingense Seward & Leslie (1908, p. 119), if a Lepidodendron at all, which I very much doubt, is unlike any northern type. It may possibly be a poorly preserved state of *Lycopodiopsis*, but the evidence is inconclusive.

Arber (1905, p. 162) noted several "obscure lepidodendroids" in the British Museum (Natural History). Of these, the two specimens V. 7596 from Sengwe Coalfield, Rhodesia, are Lycopodiopsis pedroanus. V. 7594, which "rather recalls a Sigillaria", is just possibly inorganic, and if plant at all, is certainly not Sigillaria. Two decorticated stem casts from Vredefort, Orange River Colony, are scarcely determinable but could be Lycopodiopsis.

BRAZILIAN LYCOPOD RECORDS

Zeiller in 1896 (p. 612) described from Rio Grande do Sul specimens " dans lesquels il est impossible de ne pas reconnaître le Lepidophloios laricinus Sternberg ". A few lines later he dismissed as " sans importance pour la détermination " his observation that although one could discern here and there the scar left by the foliar bundle, it was impossible to distinguish the lateral and the ligular scars. The observation is in fact crucial, and Zeiller's Brazilian Lepidophloios is nothing but Lycopodiopsis pedroanus. The same doubtless applies to David White's Lepidophloios (1908, p. 455) although it was not figured. White also thought that "no doubt remains as to the unity of the South American type (of Sigillaria brardi) with the northern Sigillarian group " (p. 463), but he only figured one poor specimen which is singularly unconvincing. The specimen should be re-examined, but it would be very surprising if there were any real basis for his accompanying diagram of a leaf-base showing parichnos scars.

White's Sigillaria australis (1908, p. 465) does not seem to me to be separable from the other Brazilian stems. The single specimen on which the species was founded has all the appearance of a Lycopodiopsis, and one cannot help doubting the diagrams of leafbase impressions on Pl. VI, Figs. 11 a-d. White himself said that this specimen "does not appear closely related to any species of Sigillaria in the northern Permo-Carboniferous flora".

White (1908, p. 447) recorded *Lepidodendron pedroanum* in addition to the other supposed species of lycopods just mentioned, but his discussion of the material supports

the view that although not in fact distinct from each other, they were distinct from the northern genera to which they had been referred. Thus, White saw (or thought he saw) parichnos scars in one specimen only, which was not figured because " unfortunately in the effort to clear away the encrusting charcoal residue from the bolster impressions of this specimen, in order to illustrate it, nearly the whole mould was accidentally effaced " (p. 449, footnote). This seems to imply that the supposed parichnos scars were only seen on the coaly matter covering the leaf-bases, and that when the coaly matter was removed, the scars were no longer visible; White imagined that he had accidentally destroyed them, and because he had accepted the generic reference to Lepidodendron, it did not occur to him that the scars had never been there at all.

The specimens figured by Lundquist (1919) as *Sigillaria brardi* and *Sigillaria* sp. are characteristic examples of *Lycopodiopsis*.

Subsequent authors in Brazil, although often quoting Zeiller's and White's names in lists, have tended to figure the smaller stems, as well as decorticated fragments of larger stems, as *Lycopodiopsis derbyi*, and stems showing better-defined leaf-bases as *Lepidodendron pedroanum*. However, no new evidence has been brought forward in support of the reference to *Lepidodendron*.

Sigillaria? muralis White (1908, p. 467), founded on a single fragment of secondary wood, and Sigillaria sp. (WHITH, 1908, p. 471), referring to megaspores alone, are valueless as records of northern lycopods in Gondwanaland. The same applies to leafimpressions referred to Sigillaria by various authors.

THE ARGENTINE

The possible occurrence of L. pedroanus in Argentina requires further investigation. The combination Lepidodendron pedroanum was actually first used by Szajnocha (1891, p. 207) for some specimens, then believed to be of Lower Carboniferous age, from Retamito in the province of San Juan. Zeiller (1896, p. 408) considered these to be distinct from the L. pedroanum of Brazil. This record, however, is probably the basis for the statement sometimes made that Lycopodiopsis pedroanus has been found in pre-Gondwana beds. According to Frenguelli (1944) a re-examination of the Retamito beds suggests a lower Stephanian and not a Culm age. Frenguelli discusses the problem at length, without coming to any very definite conclusion, although he too suggests (p. 251) that more than one type of plant has been included in *L. pedroanum*.

The supposed record of Lepidodendron sternbergii from Gondwana beds in the Argentine apparently originated with Bodenbender (1896) who merely gave the name in a list in a table, with no figure, description, nor locality, and no mention in the text. Apparently it was to have been described by Kurtz, but I can find it only in a rather unfortunate posthumous publication (KURTZ, 1921) where on Pl. XIV, Fig. P is a drawing of a worn or decorticated lepidodendroid named L. sternbergii var. aculeatum, of which Jongmans in the Fossilium Catalogus remarks that it is "vollständig wertlos". Other lycopods are figured in this publication which suggest that Lycopodiopsis pedroanus may occur in the Argentine, but the work (for which Kurtz himself was not responsible) contains so many errors as to be completely unreliable.

LYCOPODIOPSIS IN AUSTRALIA

In 1890 Foord (p. 102, PL. IV, FIGS. 4, 4a, 5) recorded some lycopod fragments from the Kimberley district of Western Australia which Kidston thought might be Lepidodendron and Stigmaria. Though not well preserved, it is probable that these are all examples of Lycopodiopsis, especially in view of some later discoveries by A. Wade (1937) who found in the Permian Lower Ferruginous series of the West Kimberley district numerous lepidodendroid fragments rather poorly preserved in coarse matrices, all of which I identified at the time as Cyclodendron sp., and which I now regard as referable to Lycopodiopsis pedroanus. Some of these, now in the Geological Department of the British Museum, are figured on Pl. 1, and it will be seen that they resemble closely specimens figured by Maack and others from Brazil. Wade also listed "Bothrodendron cf." and "Lepidodendron cf.", but I do not know on what authority, and I imagine that these names are likely to refer to the Lycopodiopsis; out of some forty or more specimens submitted to me, I saw none which could not be attributed to this genus. So far as I know, all of them were from the Lower Ferruginous series, and they were associated with Glossopteris sp., Vertebraria sp., Noeggerathiopsis hislopi, and Samaropsis milleri.

I have figured Samaropsis milleri on Pl. 1, Fig. 5, as it is rather uncommon. The specimen is an ovate-cordate seed, about 3×2.5 cm., agreeing very closely indeed with specimens figured by Feistmantel from the Karharbari beds of India as Carpolithes *milleri*. Seward subsequently showed that traces of a surrounding wing or testa were sometimes preserved, and transferred the species to Samaropsis. The present specimen is not sufficiently well preserved to show the wing clearly, though there is a possible trace of it at one point. S. milleri is very similar indeed to S. leslii Seward from the Ecca beds of Vereeniging in South Africa, where Lycopodiopsis is also a characteristic member of the flora. It also resembles the rather smaller S. dawsoni (Shirley) from the Lower Bowen series of Queensland. Walkom has recorded S. *milleri* from Upper Kuttung (Lower Carboniferous) beds of the Werrie basin, New South Wales, but his specimen is much smaller and not so markedly cordate ; it is in any case too imperfect to be identified with a Permian species, and since no other plants are known to be common to the two formations in Australia the identification seems improbable.

Raggatt and Fletcher (1937) and Teichert (1941, 1947) record Lepidodendron and Bothrodendron from Western Australia. The former remark (p. 164) : " Dr. Wade's work in the Kimberley Basin of Western Australia shows that Lepidodendron and Bothrodendron both occur above the Nura-Nura limestone, the age of which is undoubtedly Permian." Teichert also speaks of *Bothrodendron* in the Irwin river district. Discussions of the age of "Gondwana" beds here and elsewhere might be considerably clarified if authors could get away from the easy acceptance of northern plant genera like Lepidodendron, Bothrodendron and Sigillaria, often regarded as typically Carboniferous, when the specimens on which the records are based are either doubtful lepidophytes which are difficult to determine with accuracy, or are demonstrably of the southern Lycopodiopsis type. It seems likely that all the lepidodendroids mentioned but not figured nor described by Wade, Raggatt and Fletcher, and Teichert are referable to the Lycopodiopsis which I have here, provisionally at any rate, included in L. pedroanus.

SUMMARY

Lycopodiopsis pedroanus (Carruthers) is an arborescent lycopod widely spread in the southern hemisphere Glossopteris flora. It has been found in Brazil, in Central and South Africa, and in Western Australia.

The material at present available is too fragmentary and often too poorly preserved for the establishment of satisfactory species, and Lycopodiopsis pedroanus is, therefore, taken to include : Lycopodiopsis derbyi, Lepidodendron pedroanum, Sigillaria brardi and Lepidophloios laricinus from Brazil; Cyclodendron (or Bothrodendron) leslii, C. mathieui, Sigillaria brardi, and Lepidodendron pedroanum from Africa; and Cyclodendron sp. from Australia. Probably Sigillaria australis from Brazil is also synonymous.

A review of the lycopods in the Glossopteris flora suggests that not only is there no species which is common to the northern flora, but that there is no satisfactory evidence of the existence in the southern hemisphere at this period even of any northern This would genus. further strengthen suggestion that the lycopods Sahni's of the Glossopteris flora evolved from pre-Gondwana lycopods of the southern hemisphere.

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EXPLANATION OF PLATE 1

The specimens are all from the Permian (Lower Ferruginous Series), nr. Mt. Smith, Poole Range, West Kimberley, W. Australia, and are in the Geological Department, British Museum (Nat. Hist.). 1. Lycopodiopsis pedroanus (Carr.). Nat. size. V. 25712. 2. L. pedroanus (Carr.). Nat. size. V. 25713.

3. L. pedroanus (Carr.). Nat. size. V. 25719.

4. L. pedroanus (Carr.). Nat. size. V. 25716.

5. Samaropsis milleri (Feistm.). Nat. size. V. 25721.

PLATE 1





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