THE SPHENOPSIDA OF THE SOUTH AFRICAN UPPER PERMIAN

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I, the undersigned, herewith declare that this thesis 'The Sphenopsida of the South African Upper Permian', is my own work and has not been presented for a degree at any other University.

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ABSTRACT

Sphenopsid members of the extensive Upper Permian fossil plant collections are described. A short location guide with map and geological notes on the more important sites is given, and the relative importance (numerical and in terms of biomass) of the various species is discussed. Specimens of the following genera and species are described: Sphenophyllum speciosum, Phyllotheca cf.australis, P.cf.indica, P.cf.etheridgei, P.grossa, Raniganjia bengalensis, Schizoneura gondwanensis and Paracalamites australis. Three questionable Sphenopsid reproductive organs are described and a possible reason for the paucity of reproductive remains in Gondwana Sphenopsid fructifications is put forward.

The South African Sphenophyllum speciosum has a narrow connecting band at the base of the leaflets round the stem, possibly a regional variation. It is suggested that S.sino-coreanum be restricted to Cathaysia and S.speciosum to Gondwanaland.

Phyllotheca species are only referred to the already described species as they do show some different characteristics, but the morphological range of the described species is relatively unknown and may possibly accommodate these variations. The role of heterophylly is likewise incompletely understood, further clouding the Phyllotheca taxonomy.

Raniganjia bengalensis specimens are typical of the species, although the character of mucronate tips is not obvious. The use of the genus Umbellaphyllites in Gondwanaland does not appear justified.

Schizoneura gondwanensis is numerically the most rare in the present Sphenopsid collection but corresponds well to previously described specimens.

Paracalamites australis is considered a designation of convenience and as such the custom of erecting new species of Paracalamites for Gondwanaland is thought to be undesirable.

In conclusion the question of "mixed" floras, as well as certain ecological deductions are discussed.

To both my parents, who, throughout these years gave me both moral and financial support to enable me to complete this project.
My Mother initiated the spark of enthusiasm for things from antiquity and beyond, while my Father encouraged me and gave me good advice which I did not always have the wisdom to follow at the time when it was given.

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1 GENERAL INTRODUCTION

The classification of the class Sphenopsida of the *Sphenophyta* presents an anomalous situation. On the one hand, due to the definite characteristics of the articulated whorled fossil remains they are fairly easily referred to the group, and in most cases even the genera are recognized with superficial facility. On the other hand the controversies surrounding the specific classifications are many, some dating back almost to the beginning of a species' named existence in the nineteenth century. These controversies have not been resolved, due to various contributary causes, ranging from lack of collected or described material to isolated occurences of specimens. The arguments of the Gondwana versus Angara-Cathaysia floras having generic and even specific identity/non-identity of some fossil plants remain unsettled mainly due to the fragmentary nature of the vegetative remains and the almost complete lack of recognizable reproductive bodies.

The present work does not set out to finalize all aspects of these problems, but some of them will be resolved by the very nature of the work. It is the first comparative record of the Sphenopsida from the South African Beaufort series. Previous records are listed below:

Tate (1867), Seward (1904), Stem fragments *Phyllotheca*? *Schizoneura*? Hooker (1852), Feistmantel (1889), Seward (1908 b), *Schizoneura africana*, Fish River, Zeiller (1896) *Phyllotheca sp*. foliar fragment, Johannesburg. Etheridge (1902), Seward (1907), *Phyllotheca zeilleri*, Somkele and Umlalaas. Arber (1905), *Sphenophyllum*, Natal. Du Toit (1932), *Sphenophyllum*, *Phyllotheca* and *Schizoneura*, Bergville. Lacey et al (1975), *Sphenophyllum*, *Phyllotheca* and *Raniganjia*, Mooi River. Of these, only Arber (1905), Du Toit (1932) and Lacey et al (1975) are reports of specimens that are more than mere fragments, and hence taxonomically more reliable and useful. This thesis represents the putting on record several years of collecting and preparing of Lower Beaufort series fossils in South Africa from fourteen sites, three not having yielded any fossils of these groups.

As these fossil representatives of the Sphenopsid group tend to be the rarer elements of the *Glossopteris* flora probably more emphasis than deserved has in the past been placed on poorly preserved material which has the advantage of many specimens having been figured that would otherwise merely have been listed. A disadvantage, however, is that due to isolation of localities and the state of preservation of the material, new species were erected and placed into genera which probably already contained species that could adequately accommodate the new finds, had they been found in closer proximity and better preserved (see confusion over Phyllotheca australis and P.indica.)

The strange situation has arisen amongst Phyllotheca where, in most text books, northern hemispere examples are figured whereas the genus was instituted for a southern (Gondwana) form, and the Angara Phyllotheca are probably not referable to Phyllotheca at all (Meyen 1971).

One of the main problems which confronts the Sphenopsid taxonomist is the uncertain role played by heterophylly in the group. In the early years the possibility of heterophylly was not even mentioned (Feistmantel 1876 to Arber 1905), which led to the erection of new species, especially within the Phyllotheca range, for each variant form. Several of the early authors cautioned against the indiscriminate erection of new species, but most of them fell victim to doing so themselves, through "definite" differences on a few specimens found in relative isolation (e.g. McCoy 1847).

More recently Pant and Nautiyal (1967) suggested the grouping together of some Phyllotheca species with Raniganjia, all under one species (viz R.bengalensis), thus removing a wide latitude of heterophylly in Phyllotheca.

The paucity of preserved reproductive structures within the whole Gondwana Sphenopsid group complicates the situation further, the ultimate combining or separating of the genera and species being largely dependent on these hitherto elusive structures.

A further element of confusion entered the field of Sphenophyte taxonomy with the indiscriminate use of generic names in describing leafless stems. If they showed ribbing and clear division into internodes and nodes they were variously described as Schizoneura, Phyllotheca or calamite stems, without there being any clear indication as to which group these stems really represented. These arbitrarily classified fragments were then requoted in species lists till the false impression was gained that foliar samples are quite commonly represented in collections as no qualifying remarks are made in such lists, perpetuating the error and enlarging it. Genera are then quoted as occurring in areas, together with assemblages in which they do not occur, with possibly false ecological deductions being made from these lists.

Great stratigraphic importance was laid especially on Schizoneura by Feistmantel (1876 a, p.69) who tended to place the Indian Panchet and Damuda series in the Triassic due to the presence of this fossil, influenced by the belief that homotaxial floras indicated synchronous floras. Surange (1966 a, p.30) says that in India Schizoneura has a wide range both vertically and geographically being reported from the Barakar to the Triassic of the South Rewa Gondwana Basin. At the time of his writing (1876 a) Feistmantel had one fossil locality in the Panchet series in which Schizoneura was "the most important form" (p.67) (did he mean numerically or stratigraphically?). This type of comment is later used to give the impression that Schizoneura is abundant in the Gondwana deposits, and leads to statements such as ... "which is evidence to prove that Schizoneura, one of the most important members of the Glossopteris flora ..." (Kon'no 1960 p.163). Foliar remains of Schizoneura are certainly very easily recognizable elements of the Gondwana flora, but in no horizon as a whole is it numerically very abundant. Rigby (1969 b, p.7) does not figure Schizoneura in his "Gondwana scene" as it is not a common element of the Lower Gondwana flora, while all the other Lower Gondwana Sphenopsids are represented!

The Sphenopsids are thought to have had their origin in the Psilophyta, through the Hyeniales, which originated during the Lower Devonian, giving rise to the Sphenophyllales, and Calamitales in the Upper Devonian Period. The latter group gave rise to the Equisetales in the Upper Carboniferous (Smith 1955, p.154). He also mentions that the evolution of the equisetaceous series included the development of a sporophyte with leaves borne in transverse whorls along the stem and the evolution of the sporangiophore.

The Sphenophyta [illegible] into which group the Sphenopsida are placed, have the distinct [illegible]acteristics of alternation of generations with both the gametophyte and the sporophyte existing as independent plants at maturity (Smith, l.c.p.131). The sporophyte is differentiated into roots, stems and leaves and represents the usual fossil remains.

The Sphenopsida in the South African Daptocephalus zone (Kitching 1972) are represented by Sphenophyllum, Phyllotheca, Raniganjia, Schizoneura and Paracalamites in the present collection. In addition, the following fossils have been collected from localities noted in the thesis.

<u>Glossopteris</u> several species

<u>Sphenopteris</u> one species

<u>Noeggerathiopsis</u> one species

Scale leaves

Diverse seeds

Diverse fructifications

Wood

Insect wings

Bivalves

This total is far short of the eighteen different kinds of spores and pollens reported by Anderson (1975) for the <u>Daptocephalus</u> zone.

The Sphenopsids account for more than half of the reported foliar genera, thus achieving a greater significance when thus listed, than they are thought to have had numerically during the Beaufort times in the North Eastern Karroo Basin.

This thesis places on record the results of three years of collecting and preparing of specimens from the <u>Daptocephalus</u> zone. The aim is to give the reader a clear picture of the geographical distribution of the Sphenopsida in South Africa and their relative importance within that flora as a whole.

2 COLLECTION SITES AND GEOLOGICAL NOTES

During the years 1969-1971 material from the sites listed in Table 1 and shown on the map (figure 1) was excavated and the fossils prepared and placed into the Palaeobotanical collection of the Bernard Price Institute, University of the Witwatersrand, Johannesburg. The individual specimens have the respective site code and are numbered 1 - x in each case. The geological section of the more important sites is given in Figure 2 and they are marked + below.

2.1 The sites

<u>+ Bergville</u>

Immediately beyond the last house of the town on the road to Winterton, before the bridge over a sloot leading to the Tugela river is a track down to the river, with the site about half way down the slope, on the right.

<u>Boschoek</u>

On the road between Dargle to Impendhle shortly after the Umgeni river there is a road to the left, to the Everglades Hotel. Continue for 9,3 km past the hotel, and on the left is the large road quarry excavated

TABLE 1.

SYNOPSIS OF LOCALITY DATA

Code	Locality	District	Farm Name	Latitude S	Longitude E
N-Bgv	Bergville	Bergville	Bergville opposite Farm Hongerspoort 1042	28° 43'	29° 22'
N-Bh	Boschoek	Mpendle	Bosch Berg 1025	29° 36'	30° 1'
N-Blw	Bulwer	Polela	Bulwer Town	29° 48'	29° 49'
N-Cd	* Cedara	Lions River	Waterfall 1015	29° 32'	30° 17'
N-EH	Estcourt Hospital	Estcourt	Estcourt Town	29° 1'	29° 53'
N-ESb	Estcourt Sheba's Breasts	Estcourt	Estcourt Town	29° 0'	29° 52'
N-EW	Estcourt Wagondrift Dam	Estcourt	Wagondrift 98	29° 2'	29° 49'
N-Gl	Glandisrock	Mpendle	Glandisrock 1805	29° 34'	29° 58'
N-In	Inhluzane	Mpendle	Welton 2108 (Furth 2038)	29° 32'	29° 57'
N-Kb	Kiesbeen	Harrismith	Kiesbeen 426	29° 16'	29° 23'
N-L	* Lidgetton	Lions River	Riet Vallei 1206	29° 26'	30° 7'
N-Lk	Loskop	Estcourt	Solferino 2127	28° 57'	29° 35'
N-LKF	Langekloof	Bergville	Langekloof 8281	28° 40'	29° 5'
N-ML	Moorleigh	Estcourt	Bergvliet 857	28° 59'	29° 43'
N-MN	Mooi River National Road	Mooi River	Langwacht 2168	29° 12'	29° 58'
N-MR	Mooi River Rosetta	Mooi River	Wellington 2212	29° 17'	29° 58'
N-RD	Rondedraai	Estcourt	Rondedraai 799	28° 17'	29° 55'
F-Ant	Antarctica	Mount Wisting	- Amundsen Glacier	± 86° 25'	±166°

Using the Topo-cadastral series 1: 250 000

* Probably Upper Ecca sites.

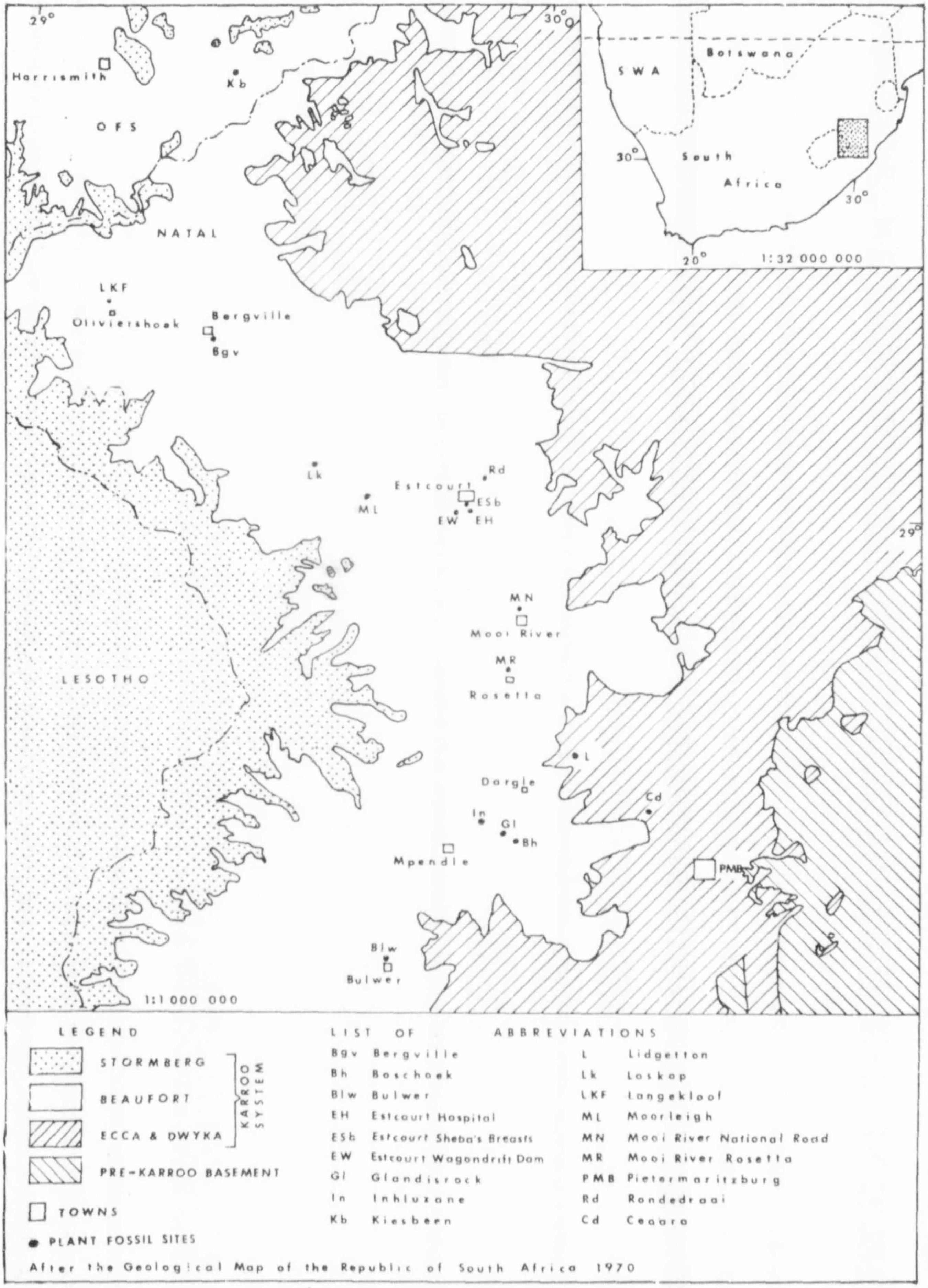


Figure 1 Map showing the location of collecting sites.

into the hill side.

Bulwer

Just before the road forks to Nottingham (Loteni) and Pietermaritzburg there is a small track to the left, which leads immediately to the large road quarry hidden from the road by a small hill and trees.

Cedara

From the N3 turn-off towards Cedara Station, continue past St.Joseph's Scholasticate turn-off, for a further three km., then turn left, continue as far as possible, then walk towards the Rietspruit river, where just above the waterfall, below a waterhole, the fossil horizon is exposed in the hillside.

Estcourt Hospital

In the subway under the main road to Mooi River between the Non-European and the White Hospital.

Estcourt Sheba's Breasts

The fossil site lies in the park along the Bushmans river in Estcourt, behind the War Memorial at Sheba's Breasts, up from the Weir.

Estcourt Wagondrift Dam

On the road to Moore Park, Berg en Vlei School, is the gate leading to the Wagondrift Dam club house. Immediately inside to the left of the gate is a small hill with the fossil layers.

Glandisrock (see Boschoek)

4,5 km past the Everglades Hotel is the farm Parkside; the site is just below a small waterfall in the stream near the house.

Inhluzane

On the road from Dargle to Mpendhle, 5 km beyond the Everglades Hotel turn-off looking downhill, some rapids are visible in the river. A short distance downstream is another small waterfall. The fossils are just above the waterfall below the sandstone layer.

+Kiesbeen

On the main road Johannesburg - Van Reenen, just before Swinburne is a dirt road to the left. Follow till on the farm Kiesbeen. Some distance past the house is a donga on the right hand side of the road, with the fossil layer exposed at water level, a few hundred metres away from the road.

Lidgetton

In Lidgetton from the old Johannesburg - Durban road turn left, after 2 km reach T-junction, turn left, and then right to "Bella vista". In the stream at the bottom of the property below a dam, where a small tributary

Figure 2. Key to the Geological Sections

a = 30 Cm. fine sandstone. Light olive gray 5Y 5/2 to dusky yellow 5Y 6/4.

b = 10 Cm. silt to very fine sand. Light olive gray 5Y 5/2 to dusky yellow 5Y 6/4.

c = 45 Cm. shale. Light olive gray 5Y 5/2 to olive gray 5Y 3/2 conchoidal fracturing. Mainly barren grading into fossiliferous band.

d = 30 Cm. very fine sand/shale. Olive gray 5Y 3/2 Phyllotheca band.

e = 70 Cm. silt/very fine sand. Olive gray 5Y 3/2 barren. Conchoidal fracturing.

f = 30 Cm. silt/very fine sand. Olive gray 5Y 3/2. Main fossiliferous layer. Glossopteris and wood.

g = ± 400 Cm. alluvium.

h = 115 Cm. silt. Mainly greenish gray 5GY 6/1 varying to medium dark gray N4.

i = 0-10 Cm. carbonaceous shale. Good plant fossil layer.

j = 2-10 Cm. coaly layer. Good pure coal with some plant impressions.

k = ? Cm. mudpellet conglomerate. Wet mudpellet purple olive 10Y 6/2. Matrix is also mud. Wet matrix greenish black 5GY 2/1.

l = 50 Cm. top soil.

m = 340 Cm. silt buff.

n = 60 Cm. silt buff on top to very carbonaceous – black at the bottom. The lower 20 cm. are densly packed with fossils. In the upper 40 cm. there are fossils, but sparser.

o = ? Cm. buff silt. Barren.

p = 140 Cm. fine sandstone. Dusky yellow 5Y 6/4.

q = 230 Cm. alternating bands of siltstone and fine sandstone. Light olive gray 5Y 5/2.

r = 105 Cm. siltstone. Light olive gray 5Y 5/2. Predominantly Glossopteris fossils.

s = 70 Cm. siltstone. Light olive gray 5Y 5/2. Sparsely fossiliferous.

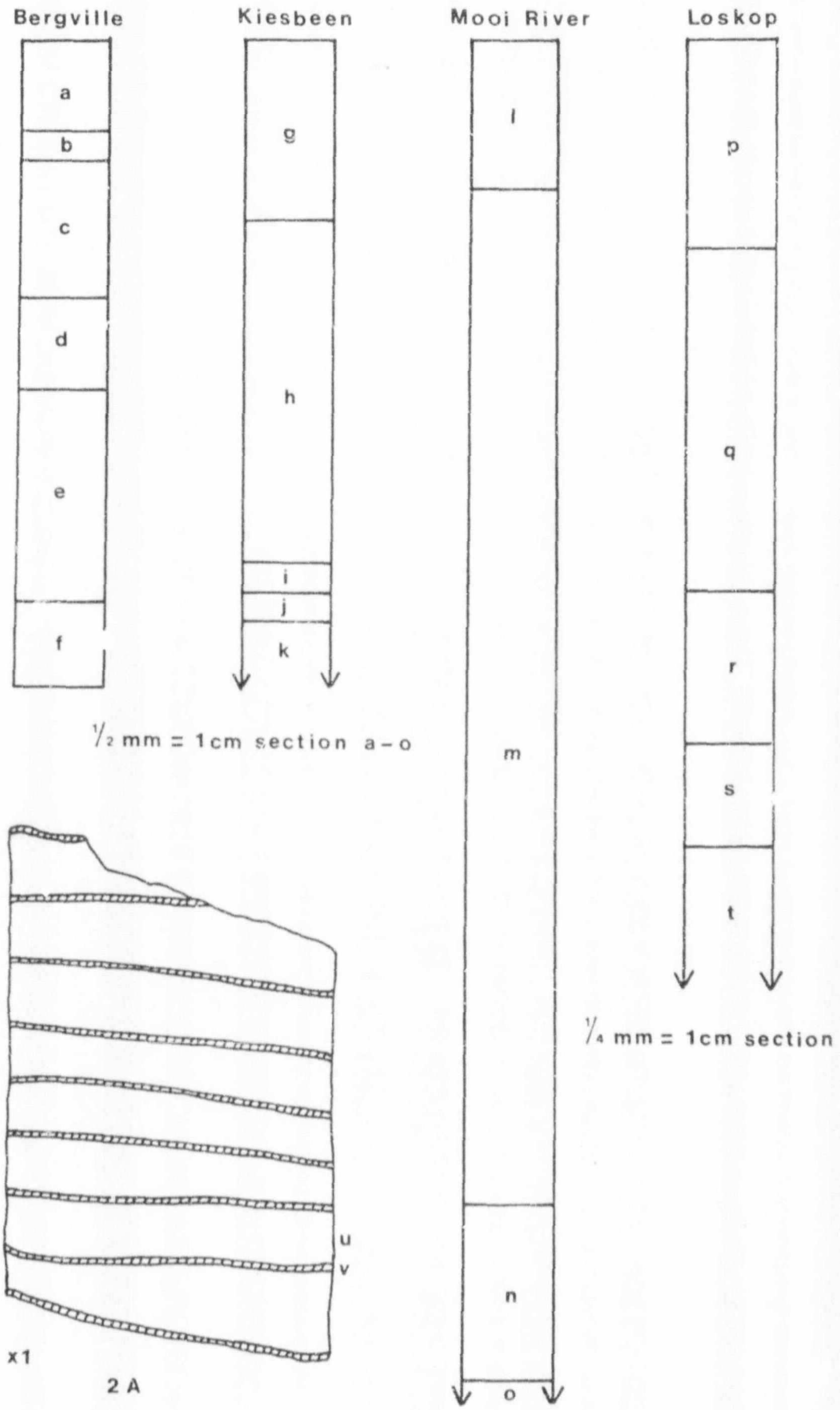
t = ? Cm. siltstone. Light olive gray 5Y 5/2 Glossopteris and Equisetaceous plant fossils.

u = Gray shale, barren	)	Shale from Loskop Quarry showing good seasonal leaf fall fossilization. Vertical accretion in very quiet conditions, no flooding.
v = Fossil layer	)	

The colour code is from the Rock Colour Chart (1963).

GEOLOGICAL SECTIONS

OF



from a pump house reaches the stream, lies the fossil horizon, below water level.

+ Loskop

On the provincial road from Estcourt to Bergville, just before the Courton bridge and the Sooilaer monument is a large roadside quarry to the left, exposing the fossil horizon.

Langekloof

On the way from Oliviershoek Pass to Bergville, to the right, is a road to the Royal National Park, curving round a school building. Just past the curve to the right is a track, follow a few hundred metres down a hill, where the fossil layer is exposed in a slight rise.

Moorleigh

On the dirt road from Estcourt to Bergville on the left past the 26 km stone is a bridge over a donga, continue up along the left hand arm of the donga, under the railway bridge, towards the "Nachtmuetze" hill. The site is under a sandstone ledge, in line with the Missionary Houses and the top of the hill, about 45 minutes walk from the road.

+ Mooi River National Road

On the N3 freeway between Mooiriver and Estcourt, in the first road cutting after Grantleigh stream lies the site, now inaccessible, and grassed over.

Mooi River Rosetta

The collection site is on the road to Rosetta from Mooi River, just past the overhead railway bridge, on the right hand side, some two metres up from the road, on a ledge.

Rondedraai

On a dirt road to Weenen turning to the left shortly before Estcourt coming from Johannesburg, lies the farm Rondedraai. The farm road leading to the house has a small embankment on the right hand side, which is fossiliferous.

2.2 Notes and comments on the sites

Most of the fossiliferous rocks are fine silt-stone to shale. At Estcourt Sheba's Breasts there is a massive dolorite intrusion nearby which has baked the shale. The Kiesbeen and Mooi River Rosetta localities are in a black carbonaceous shale whilst Bulwer, Mooi River National Road, Moorleigh, Inhluzane, Estcourt Wagondrift dam and Boschoek are all on a pale yellow weathering rock, with slightly more carbonaceous bands at irregular intervals. The other sites have light to dark olive gray coloured rock. Most sites have well laminated layers; Bergville shows a fair degree of conchoidal fracturing. Some degree of "varving" is present at most sites, with Loskop showing the most regular pattern of barren gray shale interleaved with narrow fossiliferous layers (Figure 2 A) in some parts of the deposit. This type of vertical accretion reflects very quiet conditions with no flooding (Turner 1974 pers.comm.). The Bulwer, Inhluzane and Mooi River National Road sites have sparsely preserved vegetable remains while most of the other sites have a great deal of crowding of the "autumnal leaf fall" type. Only Bergville shows a clear distinction between a lower Glossopteris layer and an upper Phyllotheca layer (see geological section for Bergville, Figure 2) possibly denoting the silting up of an open stretch of water with subsequent colonisation by Phyllotheca species.

2.3 The distribution and frequency of Sphenopsid remains

Below is a list (Table 2) of the sites, and the Sphenopsid remains found at each one of them. The total number of collected specimens is given, as well as the number of specimens for each of the presently described species. The relative percentage is shown, but this figure is not meant to represent the actual frequency at which these fossils are found; it being as well to remember that most of these genera are the rarer elements of the flora and as such have been very selectively collected. Their relative abundance thus reflects a much higner percentage value than is thought possible. With this error kept in mind the figures are regarded as useful in indicating the relative rarity of the plant remains.

The figures revealed in Table 2 are interesting especially if the fact of the selective collecting is taken into consideration. The percentage figures are all much too high as not only were the Sphenopsid remains retained in most instances even if they were poor specimens, but, for every Glossopteris leaf retained many were discarded, both in laboratory preparation and already in the field.

In these calculations there is a great degree of inaccuracy introduced by the fact that the percentages are worked out on the number of hand specimens and not on the number of plant organs represented on these specimens. This error leads to the percentages given for the various rare species again being too high.

Another difficulty with this type of calculation is that detached plant organs such as leaves, stems, fertile parts and scale leaves are

TABLE 2

DISTRIBUTION AND FREQUENCY OF SPHENOPSID REMAINS FROM THE VARIOUS COLLECTING SITES

Genera and Species / Sites	Total Number of Specimens	*Sphenophyllum speciosum*	*Phyllotheca cf. australis*	*Phyllotheca cf. indica*	*Phyllotheca cf. etheridgei*	*Phyllotheca grossa*	*Raniganjia bengalensis*	*Schizoneura gondwanensis*	*Paracalamites australis*	% of Flora belonging to the Sphenopsida at a particular site
Bergville	559			149 / 26,7			2 / 0,4		78 / 14,0	40,9
Boschoek	51									0
Bulwer	508	7 / 1,4		2 / 0,4			1 / 0,2			2,0
Cedara	304						12 / 3,9		1 / 0,3	4,2
Estcourt Hospital	59									0
Estcourt Sheba's Breasts	409	2 / 0,5					4 / 1,0	2 / 0,5	25 / 6,1	8,1
Estcourt Wagondrift Dam	87		8 / 9,1		2 / 2,3				2 / 2,3	13,8

Bulwer	[illegible]	[illegible] / 1,4		[illegible] / 0,4			[illegible] / 0,2			2,0
Cedara	304						12 / 3,9		1 / 0,3	4,2
Estcourt Hospital	59									0
Estcourt Sheba's Breasts	409	2 / 0,5					4 / 1,0	2 / 0,5	25 / 6,1	8,1
Estcourt Wagondrift Dam	87		8 / 9,1		2 / 2,3				2 / 2,3	13,8
Glandisrock	157								19 / 12,1	12,1
Inhluzane	420						1 / 0,2	6 / 1,4	1 / 0,2	1,9
Kiesbeen	245	2 / 8,1								8,1
Lidgetton	513								114 / 22,2	22,2
Loskop	506	16 / 3,1			82 / 16,2	11 / 2,2			43 / 8,5	30,0
Langekloof	128								12 / 9,4	9,4
Moorleigh	41								11 / 26,8	26,8
Mooi River National Road	1553	5 / 0,3		3 / 0,2			1 / 0,06	1 / 0,06		0,6
Mooi River Rosetta	68								6 / 8,8	8,8
Rondedraai I & II	348									0
<u>TOTAL</u> :	5956	0,5	0,1	2,6	1,4	0,2	0,4	0,2	5,2	10,6
Corrected Total without <u>Paracalamites australis</u> :	5644	0,6	0,1	2,7	1,5	0,2	0,4	0,2		5,7 %

Explanation of Figures :

Number of Specimens
% of collection from that site

taken to represent a unit, and these units are then added to produce percentages for the different groups of plants. This means that for one original plant several different organs may be counted individually as they are now not known to belong together. The final calculations are thus far from accurate, one *Glossopteris* tree, shedding hundreds of leaves and scale leaves, fertile organs and parts of branches, has a greater chance of contributing several specimens to a collection than a plant that has only a few leaves. The percentage obtained by adding the collected units may possibly begin to approach a realistic level for the biomass percentage of the various species, but even then, the figure is at best regarded with caution and is used, not as an accurate numerical representation of a species within a flora, but rather as a relative indication of that species' importance in the flora, keeping in mind all the inaccuracies that may influence the final calculations, right from the hazards of fossilization to biased collecting.

This bias in preferential collecting of the rarer elements of the flora undoubtedly affects the final figures in table two. To what extent a particular site is affected must again vary, and the relative reliability of the figures from sites with few specimens collected is also reduced.

The rarity of the Sphenopsids is forcibly demonstrated by the fact that they probably constitute less than 5,7 per cent of the whole flora. This corrected figure is used instead of the 10,6 per cent as also shown in table two, as *Paracalamites australis* specimens are taken as stems of some of the foliar genera, and can thus not be counted a second time.

Considering that in the floristic list given some pages previously, the Sphenopsids account for more than fifty per cent of the listed foliar genera and that numerically they constitute less than 5,7 per cent of the collected flora shows that they are indeed very rare elements of the South African *Daptocephalus* zone flora.

2.4 The Daptocephalus zone

The Upper Permian Lower Beaufort beds referred to the *Daptocephalus* zone (Kitching 1972) include all the sediments between the sandstones that normally overlie the *Cistecephalus* band and the base of the *Lystrosaurus* zone (Kitching 1977, p.19). In the Natal area where most of the fossil plant sites occur, the Ecca series is overlain by much attenuated *Daptocephalus* zone strata with a maximum thickness of about

120 metres consisting

> of very dark bluish-gray and light green-gray mudstones and shales interbedded with cream coloured, medium- to coarse-grained lenticular sandstone beds. Thick feldspathic grits with small quartz pebbles and occasional inclusions of granitic rock and mudstone are not uncommon. ... on both lithological and palaeontological evidence it seems possible that the major northern facies change represented in the north and north-eastern Orange Free State could be extended into northern Natal (Kitching l.c.).

The Daptocephalus zone deposits in the North-Eastern parts of the Karroo basin were probably laid down in relatively hot and wet conditions, lenticular sandstone deposits being formed in flood plains dissected by water courses (Kitching 1977 pers.comm.). The vegetation remains found in the fossil deposits are thought to have been preserved in shallow bays of a lake and to represent the plant assemblages growing along water courses and lakes. Most of the remains appear to be preserved roughly in situ and not to have been carried by currents for any great distance.

Hobday (in press) classifies the Beaufort group as a lacustrine basin with the Northern and Eastern basin margins (into which area the sites under discussion fall) being areas of "persistent energy fluvial influx" and the prevalent sedimentary patterns in some respects resemble the Ecca deltaics.

Rust (1975, p.548) suggested that

> the environment was mainly lacustrine marshy and fluviatile. The climate was evidently not favourable for luxuriant plant growth because only some insignificant coal seams developed towards the extreme north-east in the Beaufort Basin.

Compared to most other listed floras, the Daptocephalus assemblage does not appear to have been a very varied one, perhaps indicating relatively harsh climatic conditions, either drier and/or colder as the Glossopteris leaves of the Beaufort are small, narrow leaves.

3 SYSTEMATIC PALAEOBOTANY

The classification according to Boureau (1964) is followed in the ensuing section, with the exception that the genus Paracalamites is placed after the foliar genera, namely Sphenophyllum, Phyllotheca, Raniganjia and Schizoneura, as Paracalamites is a form-genus, representing the stems of a variety of Sphenopsid genera.

The Sphenophyta have a single class, the Sphenopsida, which has several orders incorporated in it, of which only the Sphenophyllales and Equisetales are represented in the South African Lower Permian. Apart from Sphenophyllum all the other genera are included in the Equisetales. Following Boureau's (l.c.) order, the Sphenophyllales will be dealt with first.

3.1 SPHENOPHYTA

Class SPHENOPSIDA

Order Sphenophyllales

Family Sphenophyllaceae

Genus Sphenophyllum (Brongniart)* Storch 1966

Type species: Sphenophyllum emarginatum Brongniart

1820-25 Rotularia Sternberg

1822 Sphenophyllites Brongniart

1828a Sphenophyllum Brongniart

Diagnosis (Storch 1966, p.268)

> Krautig, wohlriechend lebende, laengsgerippte und quergegliederte Pflanzen von mehr als ein Meter Laenge und teilweise reicher Verzweigung; wobei von einem Nodium ein, zwei oder drei Aeste abgehen, die aus dem Protoxylem entspringen und den Stengel oberhalb der an den Nodien angehefteten Blattwirbel verlassen. Die Sprossstaerke schwankt zwischen weniger als ein und 15 Millimeter, Internodien laengsgerippt und zwei bis 80 Millimeter lang. Die wenig zahlreichen Rippen meist nicht alternierend, daher auch die Blaetter superponiert, Indernodien manchmal mit Trichomen oder Stacheln besetzt. Laengsgliederung durch Form des Primaerxylems (dreifluegelig!) bedingt. Zahl der Blaetter meist ein Vielfaches von drei, schwankt von sechs bis achtzehn (?) pro Wirbel. Blaetter einfach linealisch, gabelig verzweigt oder zerschlitzt und ungeteilt oder geteilt keilfoermig bis eifoermig, von gleich starken, dichotom gegabelten Gefaessen durchzogen. Einige Arten sind heterophyll, an den Achsen niederer Ordnung dann die einfachen oder stark zerteilten Blaetter. Andere Arten mit "Trizygia"-Beblaetterung. Blaetter waehrend der stratigraphischen Verbreitung an Spreite und Groesse zunehmend ....

The genus Sphenophyllum made its debut included under the family Marsileaceae (Brongniart 1828b, p.66-68) which probably influenced successive generations of palaeobotanists to regard it as an aquatic plant. He described thus (p.68):

> simple stem, articulated, verticillate leaves, six to twelve in number, free to their base, cuneform, entire or emarginate, or even bifid, with lobes more or less deeply lacinate, almost dichotomous. Fructifications unknown.

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*Vogellehner (1967, p.138) suggests that the name of the genus should be attributed to Brongniart as a nomen conservandum, Zeiller (1888, p.708) researched the matter and found that Koenig (1825) published only part of his "Icones fossilium sectiles", (p.1-4, pl.1-9) the remainder being handed out to colleagues, that is, never published.

About sixty species are included under Sphenophyllum (Storch 1966, p.243). They are typically plants with slender articulated stems, tumid at the nodes and the ribbing of the internodes is continuous through the nodes. Zeiller (1879, p.29) states that branches arise in isolation at the nodes between the insertion of two contiguous leaflets. The leaves form verticils at the node and are present in multiples of three; successive whorls are superposed. The leaflets are sessile and free from one another at the point of attachment, that is, not fused into a sheath. Some species are heterophyllous. The venation is typically dichotomous, one or two veins usually entering the base of the leaflet. Sporne (1962, p.98) and Good (1973, p.929) say that one basal vascular bundle is supplied to the leaflets, which then dichotomizes several times, sometimes already in the cortex. A single vein reaches the tips in forms with a dentate margin. Seward (1898, p.390) states that the adventitious roots are rarely found, and their surface is not ridged and grooved as is the foliar stem. The fructifications are usually cones on the terminal ends of foliar shoots or short side branches and they are probably all homosporous (Storch 1966, p.269). (But see Thoday 1908 and Arnold 1944.)

The systematic position of the Sphenophyllales is still somewhat doubtful. Seward (1898, p.389) said they could not legitimately be included in any of the other groups of vascular cryptogams. They may have points of contact with various living plants but are an isolated type. They are included within the Sphenopsids showing jointed, longitudinally ridged stems, with whorls of superimposed leaves at each node.

Feistmantel (1876 b, p.343) already queried the inclusion of the genus under the Marsileaceae (placed there by Brongniart 1828 b) on the grounds that the Marsileaceae have only one whorl of leaves at the end of a stalk, while Sphenophyllum has a verticil at each node. Tension-Woods (1883, p.76) reported on McCoy's (1847, p.146) idea of Vertebraria being a Sphenophyllum with such short internodes that the whorls of leaves are brought into contact with one another, probably a freshwater plant. The fact that some Sphenophyllum species have a heterophyllous condition with finely divided leaves lower down the stem and more entire leaves higher up, led several authors to believe the aquatic environment theory. The plants are generally accepted as being trailing, creeping plants (Plumstead 1969, p.48, Seward 1898, p.392). Storch (1966, p.268) mentions lengths of more than one metre for a stem. One species, S.spinulosum Yabe and Oishi has a spiny stem which may have enabled it to be a true climber.