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The sphenopsida of the south african upper permian

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2015-01-07
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TABLE 3 (Cont.)

Number	Length of Leaflets in mm.						Internode Length mm.	Stem Diam. mm.
	Leaflets Left			Leaflets Right				
	L	M	S	L	M	S		
N-MN1531	-	-	-	20,5	20,5	12,0	-	1,1
N-Mn1532	16,0	14,7	9,0	15,7	15,2	-	12,9	0,6
	-	-	-	-	16,5	-	13,6	-
N-Blw 71b	-	10,7	8,7	11,4	9,5	7,8	-	-
							12,8	2,0
	9,3	9,3	8,5	11,8	9,5	8,4		
							11,5	1,1
	-	8,7	7,7	8,8	7,5	7,8		
							9,7	1,6
N-Blw 70	8,8	-	-	-	-	-		
							7,2	0,7
	10,3	9,2	6,3	-	9,4	6,1		
							9,4	0,8
N-Blw 72a	10,3	9,6	6,4	-	-	-		1,4
N-Blw 73b	15,8	14,9	-	-	-	-	-	-
N-Blw 74b	19,0	18,9	-	-	-	-	19,2	-
N-Blw 75a	11,0	10,6	9,4	11,8	10,6	-	12,8	1,0
N-Blw 77a	20,4	17,3	8,3	-	17,2	8,9		
							12,3	0,4
	17,7	16,3	9,1	19,6	19,6	9,5		
							12,3	0,5
	18,7?	20,7	9,8	-	-	9,9		
							13,5	-
	-	21,9	-	22,0	17,1	11,3		
							15,2	1,0
	22,7	-	12,2	23,7	22,4	-		
							18,0	0,6
N-Esb 257	-	-	10,0	19,4	16,2	-		
							12,2	0,8
	-	-	11,9	25,5	22,0	-		
							15,6	? 0,8
	-	-	-	-	-	12,7		
							15,9 ?	? 0,8
N-Esb 253 a + b (L+R of a)	-	-	11,6	18,1	15,4	11,3	-	-

TABLE 3 (Cont.)

Number	Length of Leaflets in mm.						Internode Length mm.	Stem Diam. mm.
	Leaflets Left			Leaflets Right				
	L	M	S	L	M	S		
N-Kb 8a	3,7	3,5	-	-	-	-		
							4,4	?
	4,9	4,7	3,2	-	-	3,3		
							4,8	0,6 ?
	5,9	-	-	5,6	5,4	3,7		
							5,0	0,6
	6,4	5,4	4,1	5,9	5,9	3,9		
							6,5	0,6
	-	-	4,4	6,5	? 6,8	4,6		
N-Kb 8a	-	-	-	-	15,7	10,4	11,3	0,9
	-	16,6	-	17,8	13,8	9,5		
							12,0	?
	17,3	15,0	-	-	-	9,0		
							10,8	0,9
	18,0	15,2	10,2	-	14,5	-		
	-	22,0	-	-	-	+10,0		

L = Largest M = Medium (middle) S = Smallest

	Minimum	Mean	Maximum	n
Length Longest Leaflets (mm.)	3,7	(14,0)	25,5	51
Length Median Leaflets (mm.)	3,5	(13,3)	22,4	68
Length Smallest Leaflets (mm.)	3,2	(8,9)	14,0	70
Length Internode (mm.)	4,4	(12,3)	21,0	41
Stem Diameter (mm.)	0,4	(1,03)	2,0	37

Some of the broader stems with attached Sphenophyllum whorls are also two millimetres wide. Figure 32 has a stem fragment that is fairly broad (2,2 millimetre wide) with five ridges and four grooves, which is not at all like the recorded Sphenophyllum stems, and possibly belongs to Schizoneura or Raniganjia.

Although there are a fair number of specimens from many sites, there is no indication of the apex of a shoot being preserved, unless figure 6 with its very small leaflets is considered as coming from near the tip. It is more likely that edaphic, climatic or hormonal factors kept this particular specimen small.

The specimens recovered from the various sites are all placed within Sphenophyllum speciosum. Even the specimen in figure 6 with its atypically small size is merely considered an aberrant form of the species for the time being, unless more specimens with consistently smaller whorls are found, possibly indicating a new species.

3.1.1.2 Discussion and Conclusion for Sphenophyllum speciosum

A morphological feature that tends to set the presently recorded specimens of Sphenophyllum speciosum apart from the previously recorded and figured specimens is that there is a distinct narrow band of tissue around the stem at the node from which the leaf whorls are subtended (see fig.27-30, 34-37 etc.). Arber (1905, p.37, fig.11) reported a single whorl from South Africa, and commented that the basal portions of the leaves seemed to be united into a short sheath.

Most descriptions both of the genus and the species mention that the leaflets are free to their base. It may be possible that the characteristic of a narrow band is very dependent on perfect preservation before it can be observed, which would explain why it is not noticed on all the specimens, even from the present collection. However, it may be a regional variation in the specimens attributable to the species, particularly as Arber already noticed it in the one fragment from South Africa he had for observation. Du Toit (1932) does not mention it nor show it in his figure. Unfortunately the detailed drawings of S.speciosum given by Feistmantel (1876 b, pl.15, fig.2a and repeated in 1880-81, pl.12A, fig.1a and fig.2a) do not show the attachment round the stem area clearly. The specimen figured by Feistmantel (1876 b, pl.15, fig.2) shows the central whorl with what might be interpreted as a band of connecting tissue, possibly recorded as such more in error than by the design, as there is no mention of such "sheath" in the text. The whorl

figured by Archangelsky (1960, pl.7, fig.3) shows a possible segment of the band between the two lowest leaflets.

The presence of such a connecting band between the leaflets as it joins the stem would explain why so many isolated complete whorls of S.speciosum are preserved, instead of only single leaflets as is so often the case in other species of the genus (see for example S.thonii from Hammanskraal).

The band would hold the leaflets together, even if the stem broke away from the whorl. Most specimens of the present collection show almost complete whorls, at least round the nodal area, which could be explained by the presence of such a band.

In most instances where a whorl is attached to a length of stem, the whorl is at the upper end of the internode. The internodal area tends to separate itself from just above the preceding node, there being no evidence of the separation following great strains or a crushed stem, the break appears to be more along the lines of an "abscission" layer. The intercalary meristem as described by Shabilion (1975) may account for such a zone of weakness leading to a clean separation of individual nodes due to preferential decomposition of the former intercalary meristematic region which is situated just above a node, or rather, at the base of the internode.

Amongst all the specimens of the present collection, and those figured previously as belonging to S.speciosum, there is no evidence of any branching. This may be indicative of long unbranched shoots. Another oddity is the absence of any recognizable growing points belonging to specimens of the species. The nearest recorded example is by Feistmantel (1876 b, pl.15, fig.1) where fairly large whorls are followed by successively smaller whorls, the final whorl diameter being slightly less than the length of the longest leaf of the basal whorl shown. In the central part of the shoot there is almost no difference in the size of successive whorls.

This lack of growing points may partly be due to the fact that a plant with long shoots would have relatively fewer growing points for the same area of vegetative growth than a plant with many short shoots. It is possibly also indicative of the plant having had determinate growth, so that once the shoot reached its determined number of nodes, even the final whorls of leaflets would grow and expand, and no evidence of an apical bud would then remain.

The probable extensive length of a Sphenophyllum speciosum shoot,

coupled to its slender though seemingly well reinforced and thus rigid stalk, raises the much asked question about the habit of the plant. That these stems were capable of maintaining a hold on other plants is doubtful as there is no evidence of specialized appendages which would be capable of establishing an anchorage on another structure. The lack of spiralling of the ridges on the stem, and the uniform, uniplaned orientation of the whorls does not support the idea of a liana-type strangling plant. The plant was probably procumbent, that is, trailing or lying flat and not rooting at the nodes as there is no evidence of adventitious roots having been formed below the whorl of leaves at a node, and surely some indication of such roots would occasionally be preserved if they had been present. There is an indication that there were several shoots arising from one root stock. Feistmantel (1881, pl.11A, figs.3,7,8) and figure 8 show two shoots lying in close proximity to each other, either roughly parallel or at an angle. Whether these shoots were subtended from one point or along a rhizome is not known. The presence of a rhizome is more likely, as is typical of Sphenopsids. Storch (1966, p.263) postulates that some Sphenophyllum grew in almost pure stands on the shore line of peat forming areas, or at least in damp places. These could then not have been dependent on other plants for support. He also mentions that not all Sphenophyllum species necessarily had the same habit or ecological requirements.

The idea of the plant having been a "low tree" (Rigby 1969 b) with leafy shoots attached to a trunk, does not seem likely. The suggestion of a main trunk subtending these fairly delicately leaved branches without intermediate branching being present would not be consistent with the regularly orientated leaf whorls and the leaf mosaic which is more indicative of a plant lying on a roughly horizontal surface.

From the apparently delicate nature of preserved shoots, Sphenophyllum speciosum probably grew in a fairly protected environment, perhaps open woodland, and thus possibly in relatively drier circumstances than Phyllotheca or Schizoneura which have not been found in close association with Sphenophyllum. It probably grew rapidly to its determined size under favourable conditions and under normal circumstances was a fairly rare element of the Daptocephalus/Glossopteris zone flora, although occurring at many different localities in Natal. S.speciosum appears to have had fairly wide ranges of tolerance to various climatic and edaphic factors as all the specimens, except one (fig.6), are amazingly uniform in size and general appearance. The one abnormally small specimen is regarded

as an aberrant form of S.specciosum, the other specimens being typical examples of the species.

Storch (1966, p.254) suggests that Zwickau in Germany appeared to have been an area of origin for Sphenophyllum as there was large variation in specific characters, as if they had not yet been "set". The uniformity of S.speciosum in South Africa could thus point to a well established species, removed from the centre of origin.

For the present study the generic name of Sphenophyllum is retained, not because this implies close association with the Euamerican forms of the genus, but the grounds on which S.speciosum would be removed from Sphenophyllum are not valid for other such species as S.thonii, which has been recorded without question from Wankie (Walton 1929, pl.C, fig.24; Teixeira 1947, pl.14, figs.1-4; Huard-Moine 1965, p.69; Lacey and Huard-Moine 1966, p.15). The last named also record S.cf.oblongifolium and S.cf.verticillatum from Wankie. These species do not show the trizygoid arrangement of anisophyllous leaves which appears to be among the main reasons for the separation. With other members of the Sphenophyllales present, sometimes in the same deposits (e.g.Wankie), there seems little point in removing one species into its own genus. By retaining the Gondwana Sphenophyllum species within the genus it would, however, be wise to remember that certain characters of the genus that have been established by anatomical and morphological study of Euamerican forms are not necessarily homologous in the Gondwana forms, although inclusion within the genus would imply such homology. It may be more dangerous to imply such false relationships as the unknown characters are then understood to be homologous and the final conclusion may thus be more confused than necessary. If one bears a possibly non-homology in mind, the generic name Sphenophyllum appears the most suitable for the present, until further investigations yield better information on morphological, anatomical and reproductive characters.

3.2 Order Equisetales

Family Phyllothecaceae

Genus Phyllotheca (Brongniart) 1828 Townrow 1955

Type species P.australis Brongniart 1828

Emended Diagnosis (Townrow 1955, p.39)

"Plants with main stems up to two centimetres in diameter, showing fine longitudinal ribs, only slightly lignified, nodes marked by transverse furrows. Main stems bearing branches, few or whorled, smaller than main

stems but otherwise similar, neither main stem nor branches bearing persistant leaves. Leafy shoots borne on main stems or branches, few or whorled, less than one centimetre in diameter, with fine longitudinal ribs, and hardly lignified. Leaves spreading, thin, flat, margins entire, single midrib (often indistinct), joined basally in a sheath seldom more than half as long as the leaves, showing commissural furrows. Commissural furrows not continued on to the leafy shoot. Midrib continued downwards as ribs on the leafy shoot.

Cuticle (only known in two species) showing elongated epidermal cells and stomata of an Equisetalean sort.

Cone (only known in four species) large, up to seven centimetres long, axis up to seven millimetre in diameter, consisting of distant alternate whorls of sterile bracts and sporangiophores. Bracts either like foliage leaves or modified, at least seven millimetres long, numerous. Sporangiophores twice branched (P.australis) or possibly branched in the stem cortex (P.deliquescens, P.uluguruana). Sporangia either few on small sporangiophore heads (P.australis) or many on large solid sporangiophore heads (P.deliquescens, P.uluguruana). Spores unknown".

Brongniart (1828b p.151) described some specimens from the coal mines on the Hawkesbury River, near to Port Jackson N.S.W., as Phyllotheca australis, distinguishing them from the superficially similar species of Equisetum and Equisetites by the occurence of long free leaflets that spread out from the top of this sheath, whereas both Equisetum and Equisetites have short tooth-like projections that remain closely appressed to the stem. Brongniart described the new specimens as having

> simple, straight, articulated stems, surrounded at regular intervals by a tight fitting sheath, terminated by long linear leaflets, which are erect, or more often spread out, and even reflexed; they are narrow linear, without a distinct venation, at least twice as long as the sheath. The sheaths have faint longitudinal furrows, which disappear towards the base and seem to correspond to the spacing of the leaves. The stem in the portion that separates the sheaths, appears to be smooth, but on larger, probably older, stems; there are regular striae as in Calamites.

Townrow (1955, p.39) limits the size of Phyllotheca stems to twenty millimetre diameter, as the stems are only slightly lignified. There is some degree of branching, occasionally whorled, but usually more random. Townrow (l.c.) says that neither the main stem nor branches bore persistent leaves.

The original description was fairly loose and no figures were published. M'Coy (1847, p.153) makes it plain that there was some

confusion as to the nature of the sheaths and leaves as Lindley and Hutton (1831-37) claimed that the leaves arose immediately from the stem and had within them a closely fitting sheath round the stem. M'Coy (l.c.) found some further specimens confirming the position of the leaflets on the edge of the sheath. He instituted two new species, P.ramosa and P.hookeri on the grounds of the stems being branched and the sheath being large and sac-like. He was the first to figure Phyllotheca.

M'Coy (l.c., p.154) pointed out that the branch origin in the axil of the sheath on or above the node, completely removes Phyllotheca from Equisetum where the branches arise below the node, outside the sheath. (M'Coy favoured an inclusion in the Casuarina.) Dana (1849, p.719) already proposed the inclusion of P.ramosa and P.hooke[illegible]h P.australis as do many other authors (see Table 4).

Bunbury (1861, p.335) instituted a new species. P.indica material from Nagpur, India, which he defined as having lax, bell-shaped sheaths, and although he himself admitted a close similarity and possible identity with P.australis, the slight differences and geographic distance made him propose a new species. There has been a great deal of controversy about the validity of P.indica or its inclusion with P.australis. Seward (1898, p.288) synonymized the two and since then various authors accept or reject this synonymy (see Table 4). A difficulty in classifying the Phyllotheca remains is that they are often fragmentary and poorly preserved.

Zeiller (1902, p.30) instituted P.griesbachi for one hand specimen from India showing three stems with sheaths fused for about ten millimetre tightly fitting the stem at the base, and rapidly spreading into a horizontal disc bearing thirty to forty long leaflets. It appears to be a rare species, but its validity has not been contested.

Arber (1905, p.26) instituted the species P.etheridgei for specimens from Australia described as Phyllotheca sp. by Etheridge jun. (1895). These are fairly distinct, having a large peltate, almost horizontal, disc with relatively short free leaflets. P.sahnii erected by Saksena (1952) from India is fairly similar. Pant and Nautiyal (1967, p.61) are in favour of including P.sahnii with Raniganjia bengalensis and P.etheridgei as R.etheridgei.

Etheridge (1902, p.72) instituted P.zeilleri for specimens from Zululand. The sheath was described as shallow-collar-like, and the leaflets up to seventyfive millimetres long. Du Toit (1932) united

P.zeilleri with P.australis, and Townrow (1955, p.50) commented that it was probably fairly similar to P.indica. Boureau (1964) does not list it, while Arber (1905, p.29) compared it to P. deliquescens.

One lone specimen from near Prince Albert (Cape Province), South Africa, was described by Seward (1908 b) as P.whaitsi, and given as having been found in the Uitenhage series, (Upper Jurassic to Lower Cretaceous) although Kitching (1976, pers.comm.) thinks it was more likely from Dwyka deposits. Both horizons are not typically Phyllotheca-bearing and in Harland et al (1967, p.227), the species is referred to as the last occurence of the genus. The specimen is refigured here (Figure 43), because a second whorl, not shown in the original is clearly visible on the edge of another cleavage plane, but whether or not the individual leaflets do unite at the base is difficult to decide. The lower whorl is incomplete at the point where the upper whorl shows an apparent leaf gap, thus it cannot be ascertained whether this gap is of diagnostic value or not. Without a very clear sheath and an asymmetrical arrangement of the leaves the specimens might be more accurately classified with the Annularia-like plants (e.g. A.pseudostellata Potonié) rather than Phyllotheca. Its systematic position is regarded as somewhat uncertain.

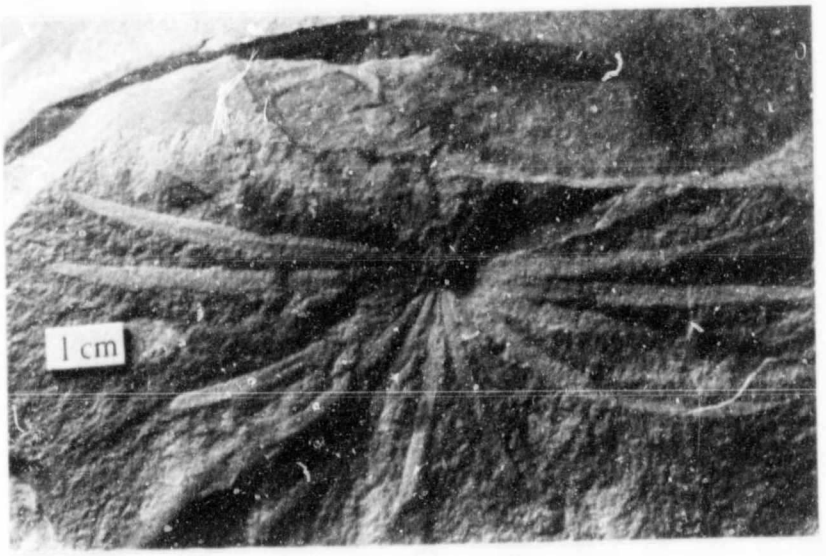


Figure 43 The specimen of P.whaitsi. There is a second whorl (top) that is not shown in the original figure.

White (1908, p.427) insituted P.muelleriana from Brazil, mentioning its similarity to P.australis. Kurtz (1921) figured but did not describe (work published posthumously) P.leptophyllum from Argentina. Townrow (1955, p.50) retains this species, as even in large leafy shoots the leaves do not spread. Boureau (1964) does not list it.

Surange and Kulkarni (1968, p.95) erected P.ampla as a species having long free leaflets and stout stems. They also erected P.angusta only on epidermal characters, which appears to be a premature practice at this stage, very little being known about the epidermal structure of the genus as a whole.

M'Coy (1847) figured the first record of a sporangiate specimen of P.australis. The internodes are scarcely as long as they are wide "the sheaths are the exact length of the internode, and fringed on the upper margin with a dense little whorl, of (I think two-celled) anthers." (p.155)

Townrow (1955) described beautifully preserved fertile material of P.australis where he describes the nodes of normal shoots as slightly longer than wide. There are about thirty bracts per whorl each one only ten millimetre long by 0,25 to 0,5 millimetre wide, forming an arching sheath over the sporangiophores of which there are about six per whorl, twice branched, with few reflexed sporangia at their end.

Gothan (1927) described P.uluguruana from Tanzania: the overall preservation was not very good, but two Phyllotheca-like leaf whorls are visible, which appear to have many sporangia between them. This structure apparently is comparable to P.deliquescens as described by Schmalhausen (1879). Høeg and Bose (1960, p.30) mention and figure fertile material from the Belgian Congo (Zaire). They compare it with P.australis as figured by Townrow (1955) although it bares more similarity with P.uluguruana (Gothan 1927) by having what appear to be normal fertile leaf whorls with sporangiate areas in between, rather than modified bracts as described by Townrow (l.c.) for P.australis.

Surange (1966 a, p.47) suggested that the cone was probably terminal on a stem that had leafy shoots below. The specimen figured (pl.2, fig.2) by Høeg and Bose (l.c.) clearly shows the continuation of the foliar shoot beyond the top-most sporangial cluster. The spores are unknown.

Meyen (1971, p.25) proposed that the Gondwana and Angara Phyllotheca would best be placed in separate families based on fertile shoots,

Gondwanostachyaceae (type genus Gondwanostachys S.Meyen) and Tschernoviaceae (type genus Tschernovia S.Meyen). The genus Phyllotheca would be regarded as a form genus of vegetative parts and would not be included in any family. Meyen (l.c.,p.11) proposes the discontinuation of using P.deliquescens as the type material is lost and the illustrations thereof are too diagrammatic to show any details.

Townrow (1955, p.44) describes the roots of Phyllotheca as dichotomous (at least in the type species P.australis) swelling just before a dichotomy; the exact number of roots (? arising from a rhizome ?) is not known but probably about eight. Unlike the other genera belonging to the Gondwana Sphenopsids, Phyllotheca has some fertile remains preserved. These help to separate the Southern and Angara forms, but the taxonomy of the vegetative parts remains somewhat vague, although it would appear that most authors now accept at least the three species P.australis, P.indica and P.griesbachi for the Gondwana province. (Surange 1966 a; Pant and Kidwai 1968). The taxonomic position of P.etheridgei and P.sahnii is not clear.

Table 4 is a chronological record of the figured references (and a few unfigured references) to Gondwana Phyllotheca. The scant taxonomic information supplied by the early authors is likewise tabulated, as well as any comments they made about the genus. In the foregoing section only references recording new species of Phyllotheca were considered, the remainder of the literature review being presented in tabular form.

Summary

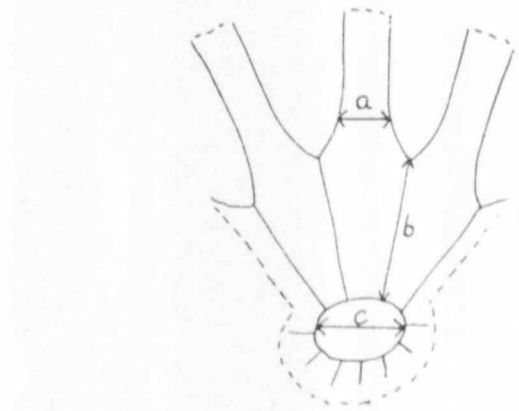
Phyllotheca differs from the superficially similar species of Equisetum and Equisetites by having long free leaflets that spread out from the top of the sheath, whereas the other two genera have short tooth-like projections that remain closely adpressed to the stem. The foliar shoots are simple articulated stems that have tight fitting sheaths arising at the node. The sheath spreads out into a disc with the uninerved free leaflets radiating out from the edge. Many species have been proposed through the years, most being described from poorly preserved material. These species were then later synonymized with earlier species, with the result that P.australis, P.indica and P.griesbachi are generally recognized as the Gondwana Phyllotheca species. The taxonomic position of P.etheridgei and P.sahnii is not clear. Meyen (1971) proposed two different families for the Gondwana and Angara Phyllotheca, based on fertile shoots, which show basic differences, while the foliar, sterile

TABLE 4. A chronological record of the figured references to Gondwana Phy

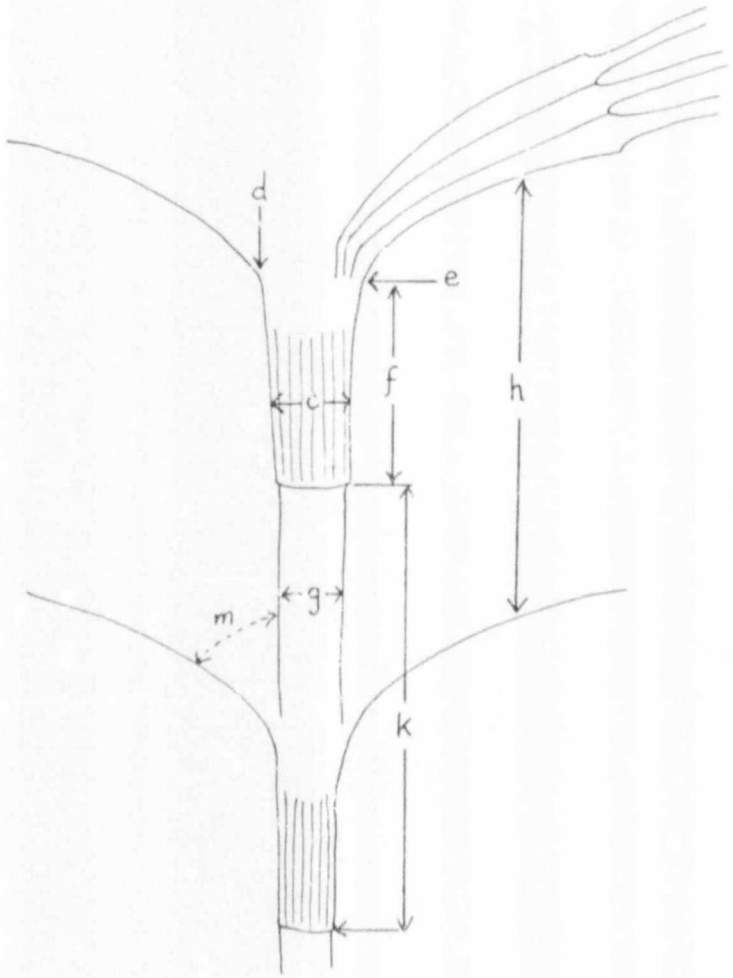
Date	Author	Page and Fig. Reference	Species	No. of Free Leaflets	Length Free Leaflets	Nature of Fr Leaflets
1828b	Brongniart	p. 151	Phyllotheca australis Bgt.		More than 2 x she th	linear, t
1847	M'Coy	p.151-157 pl.11	P.australis		2 x sheath	
	do	p.156 pl.11 fig.2-3	P.ramosa M'Coy		2-3 x sheath	thin, flat
	do	p.157 pl.11 fig.4-7	P.hookeri M'Coy		2 x sheath	thick, nar
1849	Dana	p.719 pl.13 fig.1-4	P.australis		about 30mm	lower le spread, dr
	do	pl.14 fig.1	P.australis	16	about 12mm	upper near erect
1861	Bunbury	p.335 pl.10 fig.7-8	P.indica Bunbury	numer-ous	nearly 2 x sheath	erect t recurved
1878	Feistmantel	p.83 pl.6 fig. 3 pl.17 fig. 1-2	P.australis	21,23		linear, c back
1880-81	do	p.67 pl.12A fig.3-9	P.indica	numer-ous	longer than sheath	erect to reflexed
1883	Tenison-Woods	p.73	P.australis			
1890	Feistmantel	p.79 pl.14 fig.2-4	P.australis			
1895	Etheridge	p.149 pl.16 fig. 4,5	Phyllotheca sp.	at least 20		sharp poi curve obl outwards
	do	pl.17 fig.1-5, 7-9, pl.18 fig 3	Phyllotheca sp.	about 30		tooth-li
1896	Zeiller	p.372 pl.18 fig.5	Phyllotheca sp.			filiform
1902a	Arber	p.4 and 14				
1902	Zeiller	p.30 pl.7 fig.1	P.griesbachi Zeiller	30-40	20-25mm	linear, a ate tips

s to Gondwana Phyllotheca.

h ets	Nature of Free Leeflets	∅ Disc	Length Sheath	Nature of Sheath	Comment on Mid-rib or Commissures	Country or Horizon	Comments
then heath	linear, thin			tightly fitting	M indistinct	Hawkesbury River NSW	simple stems
eath							fertile specimen
x th	thin, flattened			coarsly striated	M fine, indistinct	Mulubimba NSW	branched stems
eath	thick, narrow		whole internode	¼" long (Arber 1901) loose sac-like	M strong prominent	NSW	stem simple, ridged up to 2"
t t	lower leaflets spread, drooping upper nearly erect		half internode	much wider than stem		NSW	he synonymises P.ramosa and P.hookeri with P.australis
ly eath	erect to recurved		nearly whole internode	funnel or bell-shaped. Zeiller (1902) says tight against stem all the way.	M distinct	Nagpur Central India	stems strongly and coarsely furrowed. May be P.australis
	linear, curved back					NSW	
r n	erect to reflexed					Nagpur Central India	also erected r.robusta now Stellotheca robusta
							P.hookeri is luxuriant growth of cf.P.australis
							P.hookeri and P.ramosa are P.australis
	sharp pointed, curve obliquely outwards					NSW	P.hookeri?
	tooth-like	1¼"	¼"		M and C present	NSW	
	filiform			open sheath		Francis, Johannesburg. RSA	Arber (1905) thinks new species. Perhaps P.indica but sheath more open.
						NSW	synonymizes P.ramosa and P.hookeri with P.australis
5mm	linear, acuminate tips	15-20 mm	2-3mm	tight around stem at base, spreads to horizontal disc	M clear	S.Rewa, India	



A



Б

Figure 44 A and B are schematic drawings of a Phyllotheca to show the various measurable dimensions.

shoots from both provinces are indistinguishable at present and would be included in the form-genus Phyllotheca.

3.2.1 Note on method of measuring Phyllotheca

Measurements given in tables 6 to 8.
Length of the free leaflets; in almost all instances the full length of the leaflet is not preserved, as the tip and an uncertain distance of leaflet are usually missing. The measurement given merely records the length of the longest preserved leaflet.
Figure 44, A and B are schematic drawings of a Phyllotheca to show the various measurements made.

The width of the base of the free leaflet is measured across (a), before the sudden widening to form the united disc.
The width of the united disc is indicated by (b), being from a point marked by the commissural line on the outer edge to where the disc takes a sharp turn at the top of the sheath. (d) This point is difficult to mark exactly, depending on the angle of preservation and the form of the sheath opening, if broadly cup-like it is more difficult to measure, and the measurements are not absolutely reproducable. The length of the closely adpressed sheath is likewise difficult to measure exactly for precisely the same reasons, a gradual widening of the sheath opening to meet the disc being the most difficult type of sheath/disc to measure, (e) shows the top end of the sheath as used for measurements, (f) shows length measurement of the sheath, (c) shows the stem diameter recorded in brackets, (g) shows actual stem diameter, (h) and (k) were both used to give an indication of internode length, depending on which was clearer, the (k) measurement was preferably used as it represents the exact internode length, (m) gives the angle of the disc to stem.
In column one, marked "specimen No." 1),2),etc., represent isolated specimens on the same block surface. The number, followed by (a) (b) (c) etc. refer to successive nodes, the top most node representing (a). The number, followed by a + b merely denotes that the counterparts are preserved.
The measurements were taken under a binuocular microscope to reduce the percentage error as much as possible.

3.2.2 Phyllotheca australis (Brongniart 1828 b) Townrow 1955

Type specimen: No.3388 Muséum National, Paris

Synonymy list see Townrow, 1955, p.40

The specimens at Brongniart's disposal when he described the species in 1828 were not particularly well preserved, which as mentioned in the generic introduction, lead to a great deal of confusion in classifying new specimens of the genus. The emended diagnosis of Townrow (1955, p.42) describes the genus as a whole, and the species so succinctly that it is reproduced in full:

> " ..... Main stems, normally loosing leaves, 6-14 millimetres, usually 12 millimetres, wide at the node. Internode length 15-20 millimetres, usually about 20 millimetres, Width in the centre of the internode slightly (0,5 - 1,0 millimetre) less than the node. Node a transverse furrow, about 1,0 millimetre wide. Whole stem longitudinally ribbed, about twelve ribs on visible side of specimen. On internode ribs broad, slightly convex, separated by narrow furrows. At the node, and for 1,5 millimetre on each side, ribs higher, angular, furrows rounded, becoming indefinite. Ribs continuous over several internodes. Epidermal features as on leaf sheaths. Branches few.
>
> Leafy shoots small, borne on main stems, or on branches, internode length about 10 millimetre (3-12 millimetre) node about 3,0 millimetre wide (1,0 - 4,0). Exposed part of internode longitudinally ribbed, ribs small of semi-circular section, separated by wide, flat bottomed furrows. Ribs about one for every millimetre of width. Epidermal markings as on leaf sheath.
>
> Leaf sheaths about 3,0 millimetre long (2,0 - 4,0), covering from whole to just under half internode. Leaf-sheath showing ribs of same form as on internode and continuous with them, ribs also continued upwards as midribs of leaves. Furrows of same form as on internode. Epidermal markings, longitudinal cellular striae about 30 µm apart, with less distinct cross walls about 40 µm apart. Rows of pits running roughly longitudinally, about 16 µm in diameter. When detached, leaf sheaths cup shaped, ribs visible upon inner surface alternating with commisural furrows. Total leaves in a whorl 18 - 23 (usually 20).
>
> Roots arising in whorls from underground stem of same character and dimensions as main stem.
>
> Leaves flat, substance thin, margin entire. Width at base 0,5 - 0,75 millimetres, evenly tapering, around 10 millimetres long. (3 - 15 millimetres). Single fine midrib visible throughout whole length (except possibly apical 1,0 millimetre), traceable on to sheath. No transverse striae present. Cuticle exceedingly delicate (obtained only from main stem) showing longitudinally elongated cells 56 µm x 36 µm, and elongated pits 16 µm x 10 µm arranged in longitudinal rows.
>
> Cone borne on an axis of similar internodal form as main leafless stem. Dimensions: internode length, 7 - 10 millimetres; width, 5 - 7 millimetres; maintaining these dimensions to last (visible) node. Apex covered by at least two whorls of overlapping bracts, extending 11 millimetres, beyond last (visible) node. Node comprising

two lateral furrows, 4 - 7 millimetre apart, surface of stem between lateral furrows marked with longitudinal grooves or ribs, same in number as the sporangiophores and alternating with them. Bracts estimated at about thirty in a whorl, each bract about 10 millimetres long and 0,25 - 0,5 millimetres wide, arising from lower nodal furrow, and forming a sheath arching over the sporangiophores. Margins of bracts in lateral contact or possibly united, to the apex; apex truncated. Substance of bract delicate, midrib single.

Scars of sporangiophores round, 1,5 millimetres in diameter, with one vascular trace. Sporangiophores about six in a whorl, twice branched, branching equal, basal portion of stalk 2 - 2,5 millimetre long, 1,5 millimetre in diameter, tapering, strongly wrinkled longitudinally: primary branches 2 - 3 millimetres long, 0,5 - 0,75 millimetres in diameter, not tapering, slightly wrinkled longitudinally; secondary branches 1 - 2 millimetres long, 0,2 millimetres in diameter, not tapering or wrinkled, bearing a few reflexed sporangia at their ends. Sporangia oval, 0,75 x 0,75 metre (millimetres ?) produced into a slight point, attached to sporangiophore by their upper and outer margins; bearing faint marks of elongated cells. Spores unknown."

The plants envisaged by Townrow (l.c.) as belonging to P.australis are thus fairly small, with a maximum diameter of 14 millimetres for a main stem, and thus, unlike other species of the genus they had very little, if any, secondary thickening. The forms of the leaf sheaths appears to vary with size and possibly age of the shoot (Townrow l.c., p.45). The young sheath is closely adpressed and covers almost the whole internode, the free leaflets departing at an angle of about 45° to the stem. As the whorl ages, the leaflets gradually become reflexed, the sheath bells out from the stem covering less of the internode.

Although many authors in the past have tended to synonymize P.australis with P.indica, Townrow (1955, p.50) suggests that two species should be maintained, as P.australis has leaves 10 millimetres long (3 - 15 millimetres) that taper evenly to a pointed apex, while P.indica has leaves 25 millimetres long (6 - 30 millimetres) not tapering till near the tip. Pant and Kidwai (1968) similarly regard the two species as distinct. Townrow (l.c., p.47) regards P.australis as a Permian species. In the sense of P.australis having leaves of about 10 millimetres length tapering evenly to a pointed tip, the species is represented in the present collection.

3.2.2.1 Description of New Material of Phyllotheca cf.australis. figs 45-61.

From Estcourt, Wagondrift dam comes a series of stellar shaped whorls, all preserved dorsi-ventrally on bedding planes. The leaflets taper markedly particularly in the smaller whorls (figs. 45 - 47). Figure 48 shows the specimen with the longest leaflets, which due to their length

Figures 45 - 61

Figures 45 - 49 *Phyllotheca cf. australis* x 2

Figures 45 - 47 Small whorls clearly showing the strongly tapering leaflets characteristic of the species.
45 - N-Ew 10b 46 - N-Ew 1 47 - N-Ew 6

Figure 48 The longer leaflets appear less tapering than the shorter leaflets such as those figured above. N-Ew 2.

Figure 49 A whorl with a well developed disc area and incomplete leaflets. N-Ew 9.

Figures 50 - 61 *Phyllotheca cf. indica* x 2

Figures 50 - 56 Small whorls with typically strap-shaped leaves.
50 - N-Bgv 114 51 - N-Bgv 70 52 - N-Bgv 524
53 - N-Bgv 74 54 - N-Bgv 211 55 - N-Bgv 539
56 - N-Bgv 107.

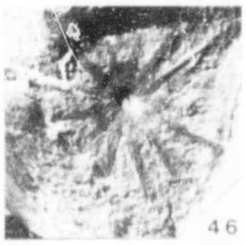
Figure 57 The strap-like leaves taper only towa the tip, in the leaflets that are almost complete. N-Bgv 544.

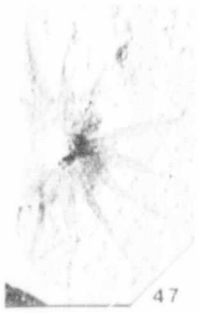
Figures 58 and 60 These specimens show the leaflets merging towards the united disc, having a sharp V-notch at the point of contact. 58 - N-Bgv 529 pto. 60 - N-Bgv 519 (see also figure 62A).

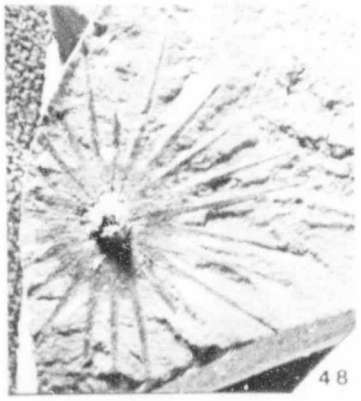
Figure 59 The gap between more widely spaced leaflets is filled by "webbing", forming a blunt U-shaped notch. N-Bgv 521 (see also figure 62B).

Figure 61 The leaflets show the typical heavy longitudinal strand with a small flange of tissue towards the margin. N-Bgv 543.


45

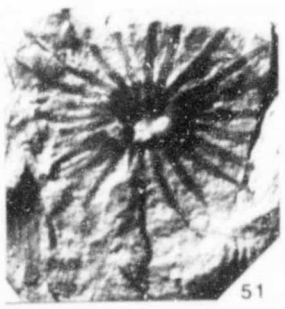

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51


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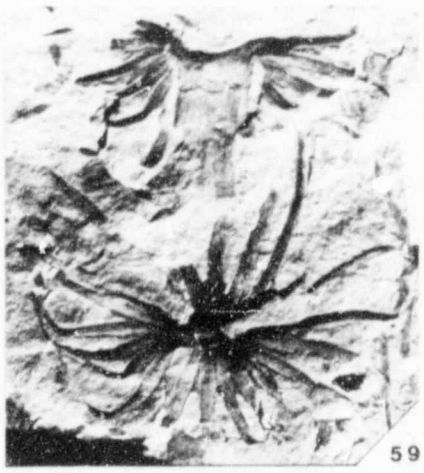

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58


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60


61

appear less tapering. The specimen in figure 49 is considered an intermediate between the figures 45 - 47 and 48 specimens, with incompletely preserved leaflets. The united disc area increases in width with an increase in the size of the whorl. The leaflets at their base widen out markedly to unite with the adjacent leaflet to form the disc. The commissural lines are very clear, while the mid-ribs are barely visible on some specimens. The free leaflet margins show the longitudinal strand clearly., but there does not appear to be a flange of tissue beyond the strand. Measurements for these new specimens are given in table 6.

3.2.2.2 Discussion and Conclusion of Phyllotheca cf.australis

The above whorls all (except fig.48) tend to have the free leaflets shorter than the average (10 millimetres) given for the species by Townrow (1955). Most of the specimens likewise have fewer leaflets per whorl (average 16 leaflets) as opposed to the 18 - 23 given as the normal range for P.australis. The generally small whorls with the strongly tapering leaflets would however appear to be representative of the species. The longitudinal strand (= ? inrolled margin) without an external flange of tissue further enhances the similarity. All the present specimens are preserved on flat planes, so that direct comparison with the sheath and angle of the disc are not possible, although the discs appear to be more flattend than cup-shaped, as diagnosed for detached whorls.

The similarity between the present specimens and the type material as described by Townrow (1955) is not as close as may be wished, but the short, tapering leaflets provisionally point to a classification as P.cf.australis. The definite [illegible]dering out" at the base of the leaflets removes them from the P.cf. indica group as described below, but would be acceptable for the P.[illegible]eridgei range. None of the leaflets, however, shows any sign of being recurved or reflexed as is considered typical of the latter species.

The systematic position of P.australis as figured by du Toit (1932, pl.40, figs. 3,4) is still unresolved. Townrow (1955) does not include it in the P.australis synonym list, and under P.indica he states "regarded as distinct" (p.47), but does not suggest an alternative classification. The du Toit (l.c.) specimens do not appear to resemble any of the new collection closely. An attempt will be made to relocate the collecting site and possibly resolve the problem at a later stage.

The few specimens here attributed to P.cf. australis do not greatly strengthen its cause for survival as an independent species, while at the same time the uncontrolled uniting of P.australis with P.indica seems undesirable. Without knowing what effects micro-climatic and edaphic factors can have on the morphology of the Phyllotheca group, and how prevalent heterophylly is in the group as a whole, the taxonomic resolving of the P.australis - versus - P.indica controversy appears to be unending.

3.2.3 Phyllotheca indica (Bunbury 1861) Townrow 1955
Type specimen V 19639 Hislop and Hunter collection, British Museum of Natural History

Emended Diagnosis (Townrow, 1955, p.47)

"Main stems without leaves, internodal length 12 - 25 millimetres, usually about 20 millimetres. Nodal width 5 - 15 millimetres, usually about 13 millimetres. Internode surface ribbed longitudinally, ribs convex somewhat flattened, furrows between narrow. Ribs becoming angular but lower at the node. Ribs cross node, are continuous over several nodes and internodes. Node a simple transverse furrow about 1,0 millimetre wide. Epidermal features as for leaves.

Leafy shoots; width at base of sheath about 30 millimetres. (2,2 - 4,0 millimetres), longitudinally ribbed, ribs fine, convex, not truly semi-circular, separated by wide flat-bottomed furrows. Epidermal features not seen.

Leaf sheath about 3,5 millimetres long (2,0 - 7,0 millimetre),width at top 2,75 to 5,0 millimetres. Ribbed at internode, ribs continuous with those of internode, and upwards into midrib. When preserved isolated showing commissural furrows upon inside. Leaves 18 - 22 in a whorl. Epidermal features as on leaves. Leaves 0,5 - 0,75 millimetres wide at bases, up to 30 millimetres long (apical region not known) not tapering in that length. Single midrib visible for whole known length of leaves. Epidermal features, longitudinal cellular striae about 65 µm apart, joined by indistinct cross walls."

The material Bunbury described was very fragmentary and as all the "australis group" (sensu Townrow 1955) of Phyllotheca are fairly similar, the species at its inception was already described as possibly identical with one or other (now all the same) of the Australian species, that is P.australis. Seward (1898, p.288) and du Toit (1932, p.375) consider them synonymous, the similarity in the sheaths being the deciding factor.

However, both species tend to have younger sheaths adpressed against the node, the sheaths becoming more lax with age. The character which separated the two species according to Townrow (1955, p.50) is the free leaflet shape. P.indica has long leaflets that do not taper till shortly before a pointed tip, while P.australis has short leaflets that taper the whole length to a pointed apex. This distinguishing feature is visible except on the most poorly preserved material, of which the specific designation should be left open.

Bunbury (1861, p.336)described the leaves as linear, very narrow and longer than the sheaths, with a distinct midrib. Feistmantel (1880-81, pl.12A, figs. 3-9) figured some new specimens attributable to P.indica. Townrow (1955, fig.2) redescribed and figured some of Bunbury's type material from the Hislop and Hunter collection. Maithy (1965), Surange (1966 a) and Pant and Kidwai (1968) all adding more specimens to the species, while Boureau (1964), Maheshwari (1968 a) and Rigby (1972) all synonymize P.indica with P.australis. From this it is clear that even now the taxonomy is not settled.

Townrow (1955, p.47) emended the diagnosis, and gives the main leafless stem maximum diameter as 15 millimetres. The width at the base of the sheath is given as 2,2 - 4,0 millimetres, with the sheath from 2,0 - 7,0 millimetres long and the width at the top of the leaf sheath 2,75 - 5 millimetres. The commissural furrows are visible on the inside, and there are from 18 - 22 leaves per whorl, which may be longer than 20 millimetres, and from 0,5 - 0,75 millimetres wide at the base, not tapering to an apex. The midrib is clear up to the apex. Pant and Kidwai (1968, p.111) further emended the diagnosis, giving the maximum width of leafless stems as 29 millimetres. The fused, spreading part of the leaf sheath is from 6 - 10 millimetres in diameter, with free leaflets up to 32 millimetres long and one millimetre wide with an acuminate tip and with 20 - 24 leaflets per whorl (on p.115 they say 18 - 22).

Over the free segments of the leaves the epidermal cells are "longitudinally elongated, slightly sinuous walled". (Pant and Kidwai l.c.), while over the leaf sheath the epidermal cells are straight or arch walled.

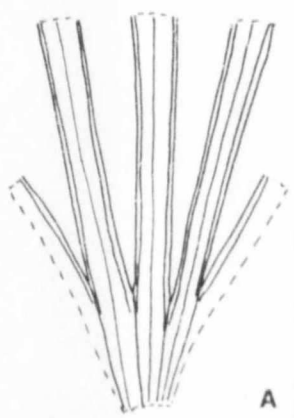
One or more branches may arise at a node at an angle of about 60^{o} to 70^{o}, then becoming deflexed to 90^{o} or more. Usually only one order of branching is postulated for the genus, but Maithy (1965, p.239, pl.1. fig.2 not clear) says "leafy shoots .... branched into two." (This is

Figure 62 Diagramatic sketch of the Phyllotheca whorl at the edge of the united disc area and the manner in which the leaflets approach one another, forming various types of notches.

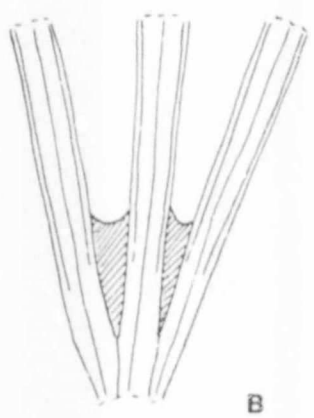
A Sharp V-shaped notch. The leaflets continue undistorted into the united disc. (see also figures 58 and 60).

B Blunt U-shaped notch, the strap-like leaflets being undistorted, but having webbing infill forming the edge of the disc. (see also figure 59).

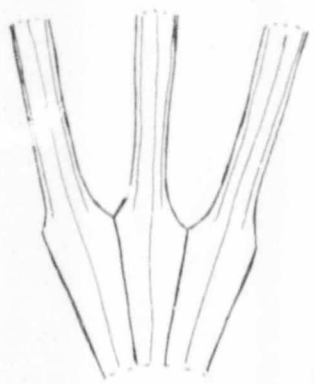
C The leaflets shoulder out as they form the united disc margin. (see also upper leaflets figure 78).



A



B



C

probably an abnormality and not a specific characteristic). Townrow (l.c.) considers P.indica a Permian species.

If P.indica is accepted in the sense of having long, non-tapering leaflets, the species is represented in the present collection.

3.2.3.1 Description of New Material of Phyllotheca cf.indica. Figs 63-96a, 104-105

The majority of the specimens from Bergville are attributable to this species. Typically the leaves are strap shaped, even in the smaller specimens (figs. 50 - 56), tapering markedly only for the second half to the tip (fig.57). The margin of the leaflet continues with very little, if any, distortion past the point at the margin of the disc, and narrows slightly only when it meets up with the neighbouring leaflets. This gives a very clear, sharp V-notch at the edge of the united disc (figs. 58 and 60 and 62A). If the leaflets are slightly more spread than usual one can still follow the line of the leaflet margin, even in the united disc area; the gap between the two leaflets till their margins meet is filled by thinner tissue forming a U-shaped notch at the edge of the disc (figs. 59 and 62B). In this case the commissural line on the disc is indistinct. In the former case, where the meeting of the leaflet margin forms the edge of the united disc area, there is a very distinct commissural line. In some instances there is a slight shouldering out of the leaflets (figs. 62C and 78). The margins of the free leaflets have a very heavy longitudinal strand with a small flange towards the outside (e.g. figs. 61,63), as do most of the other specimens of the species. This shows up particularly well in low incident light and gives the leaflets an accentuated margin. Most specimens show a midrib in the free leaflets, which tends to fade in the united disc area. Many laterally compressed specimens show the tight fitting sheath clearly, which expands rapidly into the disc area which in the preserved state may appear horizontal (e.g. figs. 64,65), slanting upwards (e.g. figs. 67,68) or recurved (e.g. figs. 66,69). Several specimens show consecutive whorls, from which it would appear that the sheath stretches almost the whole length of the internode and the average free leaflet is longer than the internode, but subtended at such an angle as to prevent direct overlapping (e.g. figs. 71 - 73). The commissural lines are a prominent narrow ridge on the sheath. Figure 74 shows a succession of nodes with short internodes, and figures 75 - 81 all show dorsiventrally flattened discs typical of the species.

Figures 63 - 71 *Phyllotheca cf. indica* x 2

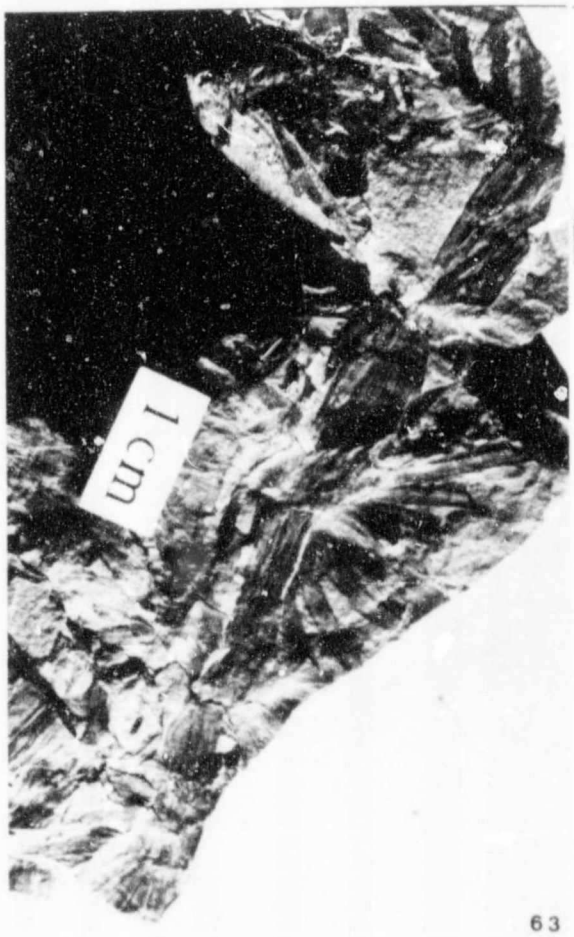
Figures 63 and 70 The flange of tissue between the longitudinal strand and the margin are clearly visible. 63 - N-Bgv 554. 70 - N-Bgv 529.

Figures 64 and 65 The united disc area in the preserved state appears to have been horizontal. 64 - N-Bgv 86 65 - N-Bgv 302b.

Figures 66 and 69 These specimens have recurved discs. 66 - N-Bgv 547 69 - N-Bgv 550.

Figures 67 and 68 The discs appear to slant upwards. 67 - N-Bgv 516 68 - N-Bgv 542.

Figure 71 A portion showing consecutive whorls. The tight fitting sheath stretches almost the whole length of the internode. N-Bgv 543.



63



64



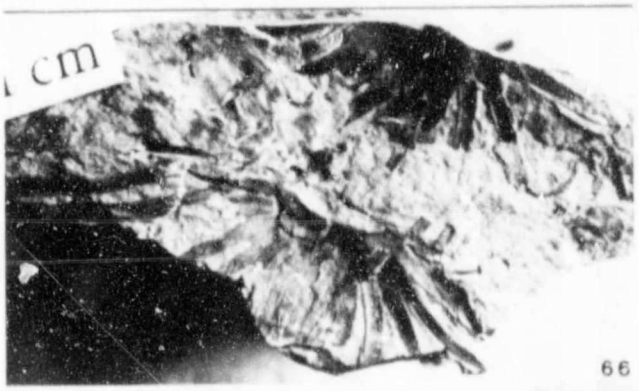
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67



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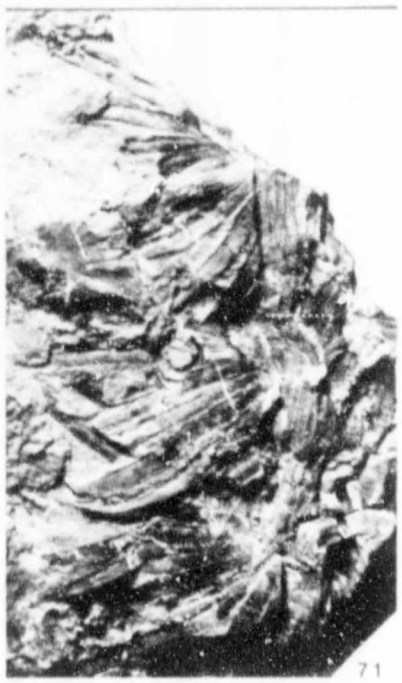
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69



70



71

Author Benecke Anna Katherina
Name of thesis The Sphenopsida of the South African Upper Permian. 1977

PUBLISHER:
University of the Witwatersrand, Johannesburg
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