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The sphenopsida of the south african upper permian

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Eggert and Gaunt (1973, p.757) say that present evidence indicates that Sphenophyllum had a horizontal rhizome from which abundantly branched aerial stem systems arose, which bore the whorls of leaves. The branching may be in the form of several laterals or a single lateral per node or even equal dichotomies in the distal orders. The aerial stem systems had limited growth potential and were probably determinate, with associated anatomical changes and progressively fewer and simpler leaves per node.

The anatomy of the Sphenophyllum group has been extensively studied from well preserved coal ball remains mainly from North America. Good and Taylor (1972, p.619) report on the anatomy of Sphenophyllum apices. "The apical region consists of whorls of leaves which surround a conical apex bearing leaf primordia beneath the apical cap." They also mention that in all sphenopsid genera examined, the branch buds appear to be identical miniatures of the main axis apex. There is a single tetrahedral apical cell with a triangular upper surface and three triangular internal cutting faces. It would appear that the production of apical cell derivatives is species specific and occurs in either a dextrorse or sinistrorse direction around the apical cell (Good and Taylor l.c. p.623). Derivatives of the apical cell form procambium to the inside and leaf primordia and intercalary meristems to the outside of the apical cap. An intercalary meristem can be seen beneath the youngest leaf primordium, which appears to have a delayed activity as internodal growth begins at about the eighth node, mainly through cell elongation of cells already present, the meristem at this level serves to increase the diameter of the node. Only between the twelfth and fifteenth nodes does the intercalary meristem add to the tissue of the internode above it. The intercalary meristem is composed of one to two rows of small cells at the base of each internode.

Good and Taylor (l.c. p.624) say that once the leaf primordia form in most Sphenophyllum species, the leaves do not lengthen enough to overtop the apex until usually about the eighth node; but in one species already at the fourth node. Equisetum arvense leaves overtop the apex at the third node and Calamites sp. leaves at the second node.

Schabilion (1975, p.104) notes that the Sphenophyllum stems in which intercalary meristematic development has been observed have all been small (nodal diameters about two millimetre, internode length four millimetre) and that decay and breakage commonly occured in these areas before and during the process of fossilization, resulting in the frequent occurence of disarticulated stem fragments.

There appears to be a cessation of intercalary growth as in studied basal portions of small stems the cells of the intercalary meristem attain a thick walled appearance, as if fully differentiated; this may be ascribed to the determinate growth pattern of Sphenophyllum. Apparently intercalary meristems have not been observed in larger Sphenophyllum stems.

Sphenophyllum stems have a characteristic triarch configuration of the primary vascular bundle. Good (1973, p.931) states that three protoxylem groups mature a few nodes below the apex and continue as separate strands until the level of metaxylem differentiation, which is usually somewhat delayed, this delay being characteristic of all Sphenophyllum species. Large stems show abundant secondary xylem and secondary cortex or periderm.

The primary phloem occurs in three groups, alternating with the arms of the primary xylem. Eggert and Gaunt (1973, p.762) state that the secondary phloem varies in structure depending on whether it occurs opposite the arms of the primary xylem, or opposite the concave area between the arms of primary xylem. An actively meristematic vascular cambium has not been observed, as this layer changes histologically after the cessation of growth in determinate aerial stems. Sphenophyllum represents the only well-documented example of a fossil pteridophyte that had secondary xylem and phloem produced by a bifacial vascular cambium.

Small branches may occasionally show some signs of secondary xylem at the nodes. Eggert and Gaunt (1973, p.760) thus suggest that the potential for some secondary thickening was present in these branches but that the rarity of such branches indicates that in most cases the plants did not live long enough for secondary thickening to have extended upwards to these branches.

Wilson and Eggert (1974, p.327) mention that the roots they investigated of tree-sized Sphenopsids (Calamitales) were typical roots, clearly distinguishable from stems in the arrangements of the primary vascular tissues and in the lack of evidence of nodal structure. The roots of Sphenopsids as a whole appear to be more like those of typical seed plants rather than other pteridophytic plants such as lycopods.

Good (1973, p.931) reported a specimen with a small lateral bud which shows that the bud originates from one protoxylem strand of the main axis. The bud occurs at the node above the leaf trace. The leaf and branch trace are contiguous for a short distance. Baxter (1948) showed whorled branches alternating with whorled leaves. Phillips (1959) suggested that the branches are axillary to corner leaves, while

Baxter (1972, p.45) states there is no evidence for Phillips' suggestion, as in a true nodal section (see Baxter 1972, pl.3, fig.1) the traces to the branches and leaves all arise at the same level, and no evidence of leaf traces subtending branch traces was seen. Zeiller (1879, p.29) already noticed this arrangement of branches arising in isolation at the nodes between the insertion of two contiguous leaflets.

Schabilion and Baxter (1971) put forward the interesting concept that some anatomical forms of Sphenophyllum are due to damage to the meristematic areas during development. The "trauma" may be caused by mechanical wounding, or such unfavourable factors as frost.

Schabilion (1975, p.108) proposed that the similarity shown between Calamites, Sphenophyllum and Equisetum in the presence of a single apical cell, intercalary meristems and determinate growth patterns suggests that these features were present early in the evolutionary history of the Sphenopsids, before divergence of the Sphenophyllales, Calamitales and Equisetales.

The epidermal cells of Sphenophyllum have typically sinuous walls as shown by Surange (1966 a, p.27, fig.12), Maheshwari (1968 b, p.284), Pant and Mehra (1963, text fig.2) and many North American and European authors, such as Good (1973, p.934) who published a beautifully clear figure (fig.31, p.937) showing these sinuous outlines. The stomata of sphenophyllalean leaves consist of two bean-shaped sunken guard cells surrounded by two to four unequally sized subsidiary cells. Stomata appear to occur on the abaxial leaf surface, randomly placed in some species.

Storch (1966, p.200-241) presents a chronological sequence of the historically more important contributions to the genus Sphenophyllum using as his source mainly Northern Hemisphere literature. He suggests (p.267) that although one could divide the Sphenophyllum group into several sections, none of them would be natural divisions as separation on grounds of leaf morphology are not supported by the fertile structures falling within the same delimitations. There is thus no point in merely creating more form-genera until all the fructifications are known and a more natural division using leaf morphology and fertile structures together can be used.

Asama (1966 b, p.577) suggests that for Cathaysia there are two evolutionary series of Sphenophyllum. In the one, including S.speciosum, the leaves become larger with geological time, in the other, including S.thonii the leaves become smaller. For the first series, the enlargement

of leaf size may be ascribed to a worsening of environmental conditions which causes a reduction in branching and fusion of segments resulting in the enlargement of the segment (Asama l.c.p.573).

Asama later (1970, p.292) proposes a classification of the Cathaysian Sphenophyllum on the degree of anisophylly and the venation. There are thus four groups, the trizygoid and non-trizygoid groups each with the veins from the base following either a straight course to the distal leaflet margin or the side veins curving outwards ending on the lateral margin. The groups with the curving type of vein are designated with the prefix "Para-", thus the four groups are: non-trizygoid, straight veins, Sphenophyllum; non-trizygoid, curving veins, Parasphenophyllum; trizygoid, straight vein Trizygia; trizygoid, curving vein type, Paratrizygia.

Kawasaki (1934, p.79), however, defines the lateral margins of the leaf as being restricted to the part parallel to the veins, thus veins do not end on lateral margins. This classification is not supported by fertile structures and is thus a grouping of convenience rather than a taxonomic reality.

Halle (1928, p.230) mentions, that although in fossil plants it is difficult to ascertain whether anisophylly is the result of heredity or modifications produced during the ontogenesis as a response to various stimuli, whatever the cause, anisophylly has a strong ecological significance. Many Sphenophyllum species show some degree of anisophylly resulting in definite leaf mosaic, S.speciosum showing constant anisophylly with probably almost perfect leaf mosaic, while S.oblongifolium has transitions of isophyllous to anisophyllous leaflets (Zeiller 1900, p.138).

Although Sphenophyllum generally is possibly one of the best documented Sphenopsid genera its anatomical details being very well known for a fossil genus, its taxonomic position is still rather vague. It has been included within the Sphenopsids under its own order, Sphenophyllales (Boureau 1964, p.47), although its stem anatomy is completely vascularised while the stems of other Sphenopsid genera such as Phyllotheca and Schizoneura have a hollow pith.

In the present collection only specimens attributable to Sphenophyllum speciosum have been found.

3.1.1 Sphenophyllum speciosum (Royle) McClelland

Holotype No. V4190 British Museum Natural History, London

Isotypes Nos. 850-950 Pant Collection, Botany Department, Allahabad University India

Pant and Mehra (1963, p.54) gave an emended diagnosis for Sphenophyllum speciosum based mainly on their epidermal work.

Emended Diagnosis Macroscopic features only.

"Foliage shoots having slender articulated stems, nodes slightly swollen, stem surface longitudinally ribbed, ribs continuous in successive internodes....

Leaves inserted in whorls, superposed, each whorl consisting of six leaves, arranged in three pairs of unequal size, each leaf free at the point of attachment, cuneiform, ovate to ovate linear, ... spreading, lamina usually entire and simple but occasionally somewhat lobed on distal edge of leaves in smallest pair. Veins usually forked thrice or four times, forks free, usually a single vein entering the base of the lamina, but leaf base also often showing two or three veins ... substance of lamina thin. ...".

Morphologically S.speciosum is typical of the Sphenophyllum group, having slender, articulated stems that have three ridges and two grooves continuous at the nodes which are slightly swollen, bearing whorls of superimposed leaves at the nodes. The species is typified by the anisophyllous arrangement of the leaves, with a wide leaf gap separating the two largest leaves, the leaves are in three pairs, the lowest pair being the smallest. The venation is typically dichotomous, with usually two veins apparent at the base of the leaf. These veins dichotomize from three to five times reaching the apex in relatively straight lines. The margin is entire, although Pant and Mehra (1963, fig.1) show slightly lobed smaller leaves in some whorls. The leaflets are elongate ovate. Surange (1966 a, p.25) mentions that the shoots are dorsiventral, and according to Halle (1928, p.239) the smaller leaves would be placed on the upper side of the shoot and thus pointing to its base and the leaf gap would be pointing towards the apex of the shoot, with the leaves placed below the stem. This arrangement is verified by the fossils found. Hirmer (1927, p.369) already drew attention to the leaf mosaic of the species. Pant and Mehra (1963, p.54) and Maheshwari (1963, unpublished, in Surange 1966 a, p.25) both record sinuous walled epidermal cells (typical of the genus) and haplocheilic stomata, probably only on one surface.

Pant and Mehra (1963, p.55) say that S.speciosum is distinct from the Northern species of the genus, but that its epidermis "strongly suggests that it belongs, in all likelihood, to the same natural alliance".

In 1839 Royle instituted the genus Trizygia to accommodate the trizygoid specimens from India, which he designated Trizygia speciosa. McClelland (1850) and Unger (1850) both included the genus with Sphenophyllum; McClelland as S.speciosum, Unger as S.trizygia. Feistmantel (1876 a + b) retained Unger's combination on the grounds of it recalling the original generic name which at the same time stressed the trizygoid nature of the specimens, always six leaves arranged in three pairs. By 1879(b) Feistmantel reverted to using Trizygia speciosa as the European carboniferous Sphenophyllum had been linked together with Asterophyllites as belonging to the Calamites by Stur (1879, p.256, 260), Feistmantel (l.c.) thus considered the trizygoid form as differing from the true Sphenophyllum and retaining its independent generic status. This view was upheld in Feistmantel's 1880-81 work where he again mentions (p.70) (as he did in 1879 b, p.166) that the form referable to Trizygia has the whorl incomplete and only on one side of the node. This was a misobservation.

In both 1880-81 (p.70) and 1886 (p.22) Feistmantel states that the original impression gained from specimens from the Raniganj and Barakar group as showing a difference in size, was not upheld by further collecting and these later discoveries showed there was no substantial distinction between the specimens from the two geological groups, only one species being represented.

Zeiller (1891, p.673) reinstituted Sphenophyllum for the Indian trizygoid form feeling that Trizygia merely represented a particular form of Sphenophyllum which could be observed next to normal Sphenophyllum, as shown for specimens from Europe, although the anisophylly for S.speciosum was constant (Zeiller 1900, p.138). This move was supported by Seward (1898, p.411) who commented that the question of locality should not unduly influence the choice of a separate generic name. Sphenophyllum speciosum was used until Maheshwari (1968 b, p.284) again advocated the use of the generic name Trizygia on the grounds of morphological and epidermal differences and palaeogeographical separation from the true Sphenophyllum group.

This suggestion does not appear to have met with general approval as further publications such as Plumstead (1969), Rigby (1969 b), Archangelsky (1970), Lacey and Huard-Moine (1966) and Lacey et al (1975)

all retain the name Sphenophyllum speciosum without comment. Asama (1970, p.293), however, indirectly supports the retention of Trizygia by placing his straight veined, trizygoid group under that name. Within that group fall Trizygia oblongfolia, T.speciosa, T.densinervia, T.sino-coreana and T.grandifolia.

Solms-Laubach (1891) hints that he does not consider S.speciosum as being a bona fide member of the Sphenophyllum group. He finds it difficult to decide where the group should be placed.

> It will be best therefore to renounce for the present all forced attempts at classification and to regard the group as sui generis, as standing by itself and independent.

The specimens that are included within Sphenophyllum speciosum are predominantly found in India (Jacob 1952, p.156) from the Barakar and Raniganj groups. (Feistmantel (1878, p.113, pl.18, fig.1), Feistmantel (1880-81, p.69, pl.11A, figs.1-9, pl.12A, figs.1-2), Arber (1905, p.35, pl.1, fig.1, 1a), Maheshwari and Prakash (1965, p.118, pl.1, fig.5, Text fig.2), Surange (1966a, p.23, figs.10-13), Surange (1966 b p.56, chart 1) and Pant and Mehra (1963, text fig.1)).

Walkom (1922, p.7, pl.1, fig.3,4) rerecords and refigures the only specimen from Queensland, Australia (found in 1912 by Ball, pl.4, fig.6). The specimen recorded and figured by Feistmantel (1878, p.33, pl.2, fig.1 and 1890, p.85, pl.2, fig.8) from New South Wales, does not appear to be very Sphenophyllum-like, and is perhaps more like a ?Psygmophyllum.

Archangelsky (1957, p.42; 1958, p.27, fig.3; 1960, p.30, pl.7, figs.2,3) reports S.speciosum from Argentina, Santa Cruz (Bajo de La Leona) where he had collected many specimens. Arrondo (1972, p.38, pl.1, fig.2, pl.2, fig.1, pl.5, fig.1) records the species from a second Argentinian locality also in Santa Cruz. Lundqvist (1919) does not list it for Brazil. Neither Plumstead (1962 b) nor Rigby (1969 a) record Sphenophyllum from Antarctica.

Walton (1929, p.64, pl.A, fig.2) reported the first S.speciosum from Wankie, Rhodesia, followed by Bond (1952, p.215), Huard-Moine (1965, p.68, pl.G, fig.1,2, Pl.H, fig.1) and Lacey and Huard-Moine (1966, pl.15, pl.1, fig.2), Plumstead (1969, p.48, pl.10, fig.8).

Teixeira (1947, p.26, pl.12, figs.1,2) reports some fragmentary whorls of S.speciosum from near Tete (Mocambique) and Lacey and Kulkarni (1969, p.263, fig.1 e) from Southern Malawi. These references together with the few mentioned below conclude the reported finds of Sphenophyllum speciosum from Africa. Arber (1905, p.37, fig.11) referred the first South African specimen (from Natal) of Sphenophyllum speciosum to S.sp. noting that the leaflets seem to be united into a short sheath.

Du Toit (1932, p.376, pl.40, figs.5,6) reported specimens from near Bergville, Natal, as S.speciosum. Lacey et al (1975, p.357-358) report and figure S.speciosum from near Mooi River, Natal. The many new records of S.speciosum from various sites recorded further on will thus greatly extend the knowledge of the geographic distribution of the species in South Africa.

Specimens attributed to S.speciosum have been reported from the Cathaysian floral province by Kawasaki (1927, p.24, pl.13, figs.68,69), Kim and Asama (1970, p.324, pl.1, fig.4), Kon'no (1968, p.170, pl.11, figs.6-10) and Kon'no et al (1970, p.505, pl.1, figs.7-8) amongst others.

There is great controversy about the retention of S.sino-coreanum Yabe as a separate species or whether it should be included with S.speciosum. Yabe (1922, p.4) mentions that S.sino-coreanum is geologically the youngest species (Lower Triassic) showing features of S.speciosum "and is distinguished from it only by having more crowded nerves.", and "provided with four or five, sometimes even more, nerves at the base." Halle (1927, p.47) mentioned that it was with "considerable hesitation" that he referred some new specimens to Yabe's species, and that it was extremely difficult to ascertain whether there were in fact two or more veins entering the base of the leaf. From well preserved specimens it appeared that there were sometimes two veins that entered the base of the leaf and dichotomized immediately to give the impression of four veins entering at the base. Halle (l.c.p.45) thus states that a character of this kind cannot be regarded as reliable as the manner of preservation and distortion at the leaf base often make it difficult to be sure whether the actual base is visible. Halle (l.c.) puts forward that S.sino-coreanum has a wider morphological range than the Indian S.speciosum, which shows very little variation in the size and shape of leaves. Halle (1927, pl.9, fig.18) figures a specimen whorl with large leaves that have a shallow asymmetrical incision at the apex and a slightly crenulated margin. In Halle's collection there are apparently specimens which show a transition from S.speciosum to specimens that should be considered as S.sino-coreanum. S.sino-coreanum is accepted by many authors as a valid species, notably those describing specimens from the Cathaysian floral province. Asama (1966 b and 1970), Kon'no et al (1970), Boureau (1964, p.82) and Storch (1966, p.245) also accept it in their compilations. Many authors on the other hand reject it as a valid species and include it with S.speciosum (Kawasaki (1927, p.24), Lacey and Huard-Moine (1966, p.15), Lacey et al (1975, p.357).

Huard-Moine (1965, p.69), however, mentions that of the two species the epidermis of S.speciosum only is known and thus it might be more satisfactory to wait till the cuticle of S.sino-coreanum is known to confirm or reject the synonymity of the two.

It is suggested here that a possible solution to the problem would be to regard all the Cathaysian specimens as S.sino-coreanum as Halle (l.c.) already stated that he had a range of specimens showing the intermediate forms between S.speciosum and S.sino-coreanum. Such characteristics as entire or notched/crenulate margins, vein-densities and leaflet size are thus poor criteria to use for the specimens from Cathaysia, while S.speciosum from Gonwanaland appears to be fairly uniform in all the provinces of the area. The fact that morphologically the one end of the species range of S.sino-coreanum should overlap with the accepted range of S.speciosum should not call for these specimens to be designated as S.speciosum if they occur in an entirely different floral province. Boureau (1964, p.82) gives the Lower Gondwana of India and Australia as well as China and Korea as the distribution of S.sino-coreanum without giving the references for India and Australia. Without seeing the specimens so classified, it is suggested that they have been misnamed, and should actually be included with S.speciosum if only for the reason that if the two species are so difficult to separate anyway, why mix them in two floristic provinces?

The whole question of taxonomy of these species is further complicated by the typical Gondwanaland absence of fertile structures, an area onto which the new collection unfortunately does not throw any light. The mere recording of these specimens, however, from so many new sites is in itself important, and some interesting morphological observations are made.

Summary

Although Sphenophyllum speciosum is challenged as belonging to the Sphenophyllum group, for the present this name is retained, disregarding the generic name Trizygia, which emphasises the trizygoid nature of the Gondwana species, but which is not a unique feature distinguishing it from the Northern members of the genus. The epidermal features tend to indicate one natural alliance according to Pant and Mehra (1963) although Maheswari (1968 b) separates the Northern and Southern forms on epidermal differences.

S.sino-coreanum is the only species that appears to be confused

with S.speciosum. The suggestion is made to retain S.sino-coreanum for all the Cathaysian specimens in question, while the Gondwana specimens are designated S.speciosum. The reports of the species occuring outside their respective floristic provinces are regarded as mis-identifications.

Therefore S.speciosum is accepted as the only member of the Sphenophyllales in the Upper Permian of Gondwanaland and as such has been found to occur in the Daptocephalus zone fossil plant assemblages in South Africa.

3.1.1.1 Description of New Material of Sphenophyllum speciosum. Fig. 3-42.

The majority of specimens are preserved as single whorls and whorl fragments, two or more successive whorls are preserved from Estcourt, Kiesbeen, Bulwer, Mooi River and Loskop. Measurements for all the new specimens follow the descriptive section in table 3. The largest preserved shoot (fig.3) has five successive nodes with whorls attached which diminish only slightly in size over that distance and is thus possibly a section in the central area of a shoot. The internodes similarly become successively shorter towards one end. The three pairs of leaflets are typically anisophyllous, the topmost and middle pair are slightly sub-equal, the lowest pair being appreciably smaller, the leaf gap is just over 90°. The leaflets of successive whorls are slightly overlapping, as are the leaflets within a whorl. The individual leaflets are wedge-shaped at the base, with the straight edges continuing for between half and two thirds the distance of the entire length of leaflet, at which point there is a slow curving in towards the rounded convex apex. The veins only reach the margin on the curved area, not along the sides. The definition of the veins at the base of a leaflet, although well preserved, is not always clear. In some instances there would appear to be two veins entering at the base, in others there is one very thick vein that dichotomizes almost immediately. There are three to four dichotomies per leaflet, the veins across the leaflet dichotomizing roughly in steps. The veins are a unit strand. The stem internodes are all straight, with the lowest node bent at an angle from the remainder of the stem, but probably still attached. The two lowest nodes are slightly swollen. The narrow stem typically has a central raised broad ridge with two narrow grooves, and two marginal areas that are not as highly in relief as the central ridge, this leads to a three-scalloped end at the base of the stem, which is attached below the lowest node. The whorls are orientated with the

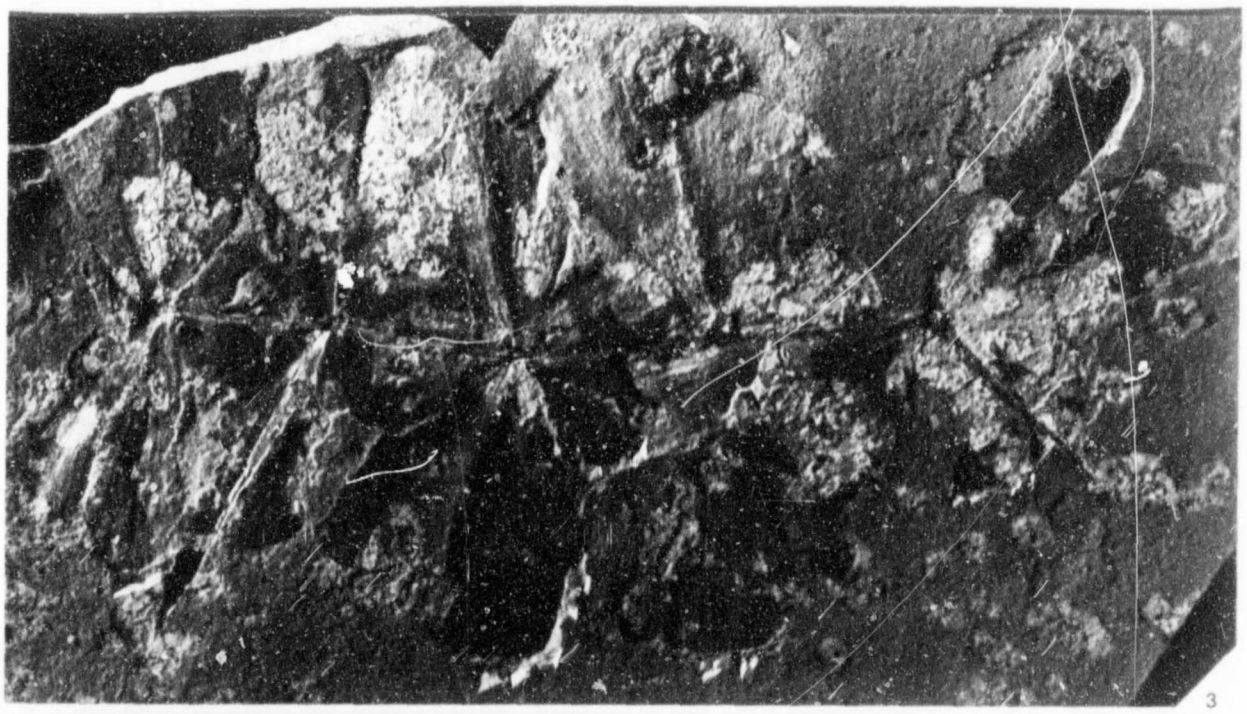
Figures 3 - 6 Sphenophyllum speciosum x 2

Figure 3 The longest intact section of a shoot, with large leaflets. There is only a slight decrease in whorl size and internode length from right to left in the figure, thus probably this fragment represents a mature, central section of a shoot. N-Blw 77a.

Figure 4 A typical section of a large whorled shoot, with the thin internodes visible. N-Lk 8a. (see also figure 7).

Figure 5 The orientation of the whorls is the reverse of normal, as the smallest pair of leaflets point in the direction of smaller whorls. The stem is particularly robust, clearly showing the broad central ridge flanked by two narrower grooves. N.-Blw 71a (see also figure 36).

Figure 6 The smallest whorls belonging to the species from the present collection. The leaflets are more tear-drop-shaped than wedge-shaped, but typically trizygoid. The venation is hardly visible. N-Kb 9a (see also figure 40).



3



4



5



6

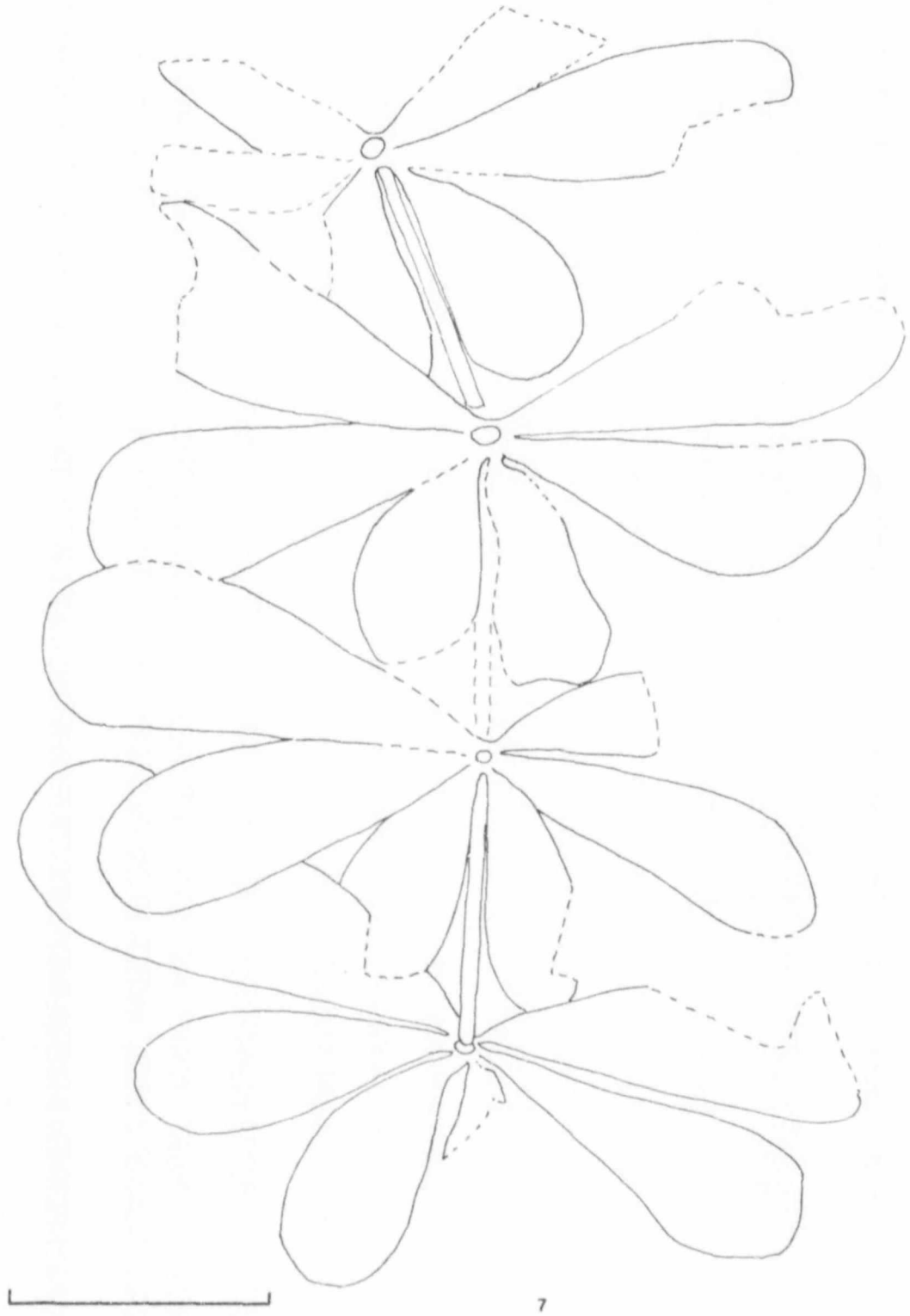


Figure 7 Sphenophyllum speciosum

The camera lucida drawing shows more clearly than the photographed specimen (fig.4) the degree of overlapping between individual leaflets and adjacent whorls. Scale is 1 cm. N-Kb 8a (see also figure 4).

smallest leaflets pointing downwards, lying over the stem, and the stem then emerging through the whorl to continue above the base of the largest leaflets. The detail on the surface of the specimen is interrupted by mottled concretions, spoiling the overall clarity of the fossil.

The specimen in figure 4 with four successive whorls, and that in figure 5 with three successive whorls are both typical examples of the species, except that in the latter the orientation of the lowest leaflets in relation to decreasing whorl sizes is the reverse direction of normal, that is, the smallest leaflets are pointing upwards, towards the smaller whorls. Whether this different position was present during life, or whether the shift was caused by the fossilization process is not known. The stem in figure 4 is thin, as is usual in the species; that of figure 5 is much thicker in relation to the whorl size than normal. Figure 6 has five continuous nodes with leaf whorls, all exceptionally small. The six leaflets are characteristically divided into three pairs, with the topmost pair the largest, showing the wide angled leaf gap. The individual leaflets are possibly slightly more tear-drop-shaped than wedge-shaped, but this may be caused more by the size of the leaflets than any real change of shape. The venation is hardly discernible, certainly the detail of dichotomy and number of veins entering at the base are not visible. Apart from one isolated whorl of leaflets some two centimetres away, these are by far the smallest chain of whorls from the present collection. The stem detail, and orientation of the whorl on the stem is quite normal. There is no indication apart from size that would justify the removal of this specimen from the species.

Figure 8 has two parallel shoots of three successive nodes each preserved. The whorls are of medium size. There is no indication of there having been a connecting branch subtending the two shoots. One set of whorls is preserved face up, while the other is preserved face down, making such a connection more unlikely. The parallel preservation is regarded as chance.

Figures 11 and 12 have three successive large whorls with a wide stem, while figure 9 has three successive large whorls on a thin stem; this specimen is interesting as a fragment of Raniganjia (not shown) lies next to it. Figure 10 is likewise next to two fragments of Phyllotheca. Usually the various groups of Sphenopsids are not closely associated in fossil positions.

Figures 13 to 15 each have two adjoining whorls, with the

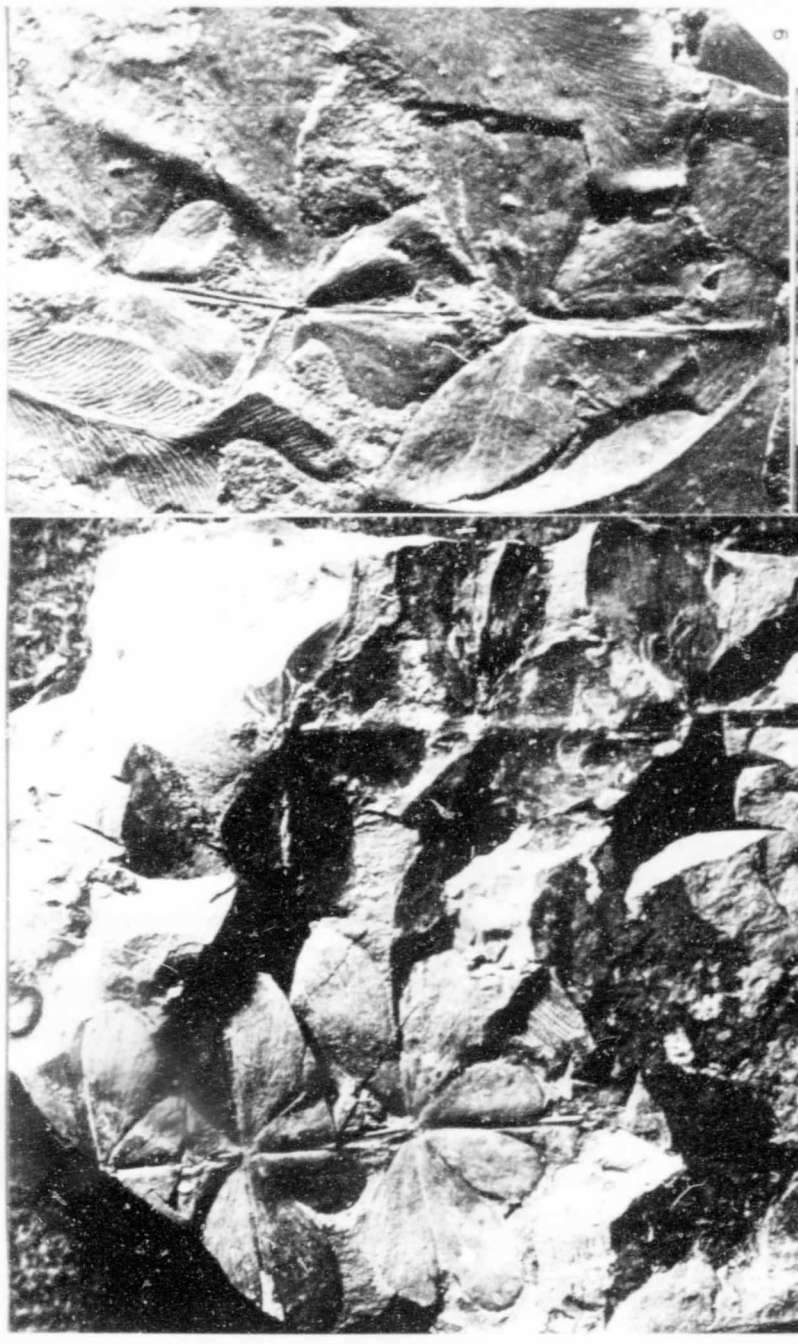
Figures 8 - 12 Sphenophyllum speciosum x 2

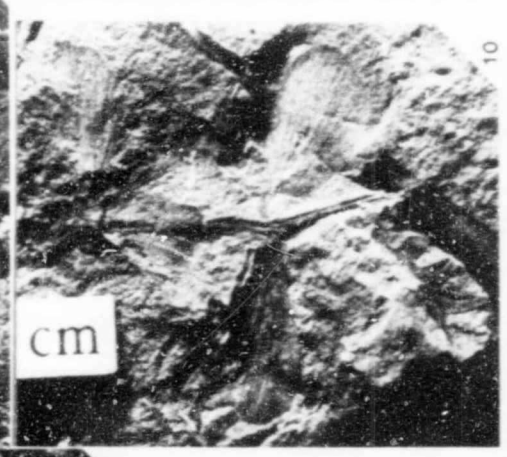
Figure 8 The specimen shows two parallel shoots of three whorls each. The left hand shoot is preserved adaxial side up while the right hand shoot is preserved adaxial side down. Both shoots typically have the internode below the lowest whorl preserved. The right hand shoot has a thick stem with clear ridges and grooves, the left hand stem is much thinner, but the central ridge is still clear. N-Lk 441a.

Figure 9 A large whorled specimen from Estcourt. N-Esb 257 (=cp of N-Esb 246) (see also figure 41).

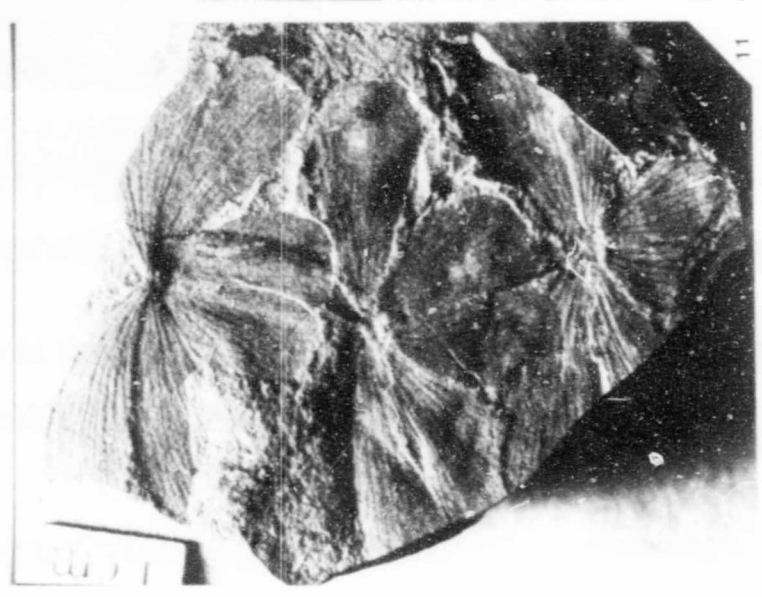
Figure 10 A poorly preserved specimen, which is unusually closely associated with two detached whorls of Phyllotheca (see left of figure). N-Lk 320.

Figures 11 and 12 Counterparts of a well preserved section, with a wide stem. Figure 12 shows the venation clearly. N-Lk 436a+b.


9
8
1 cm


10
cm


12



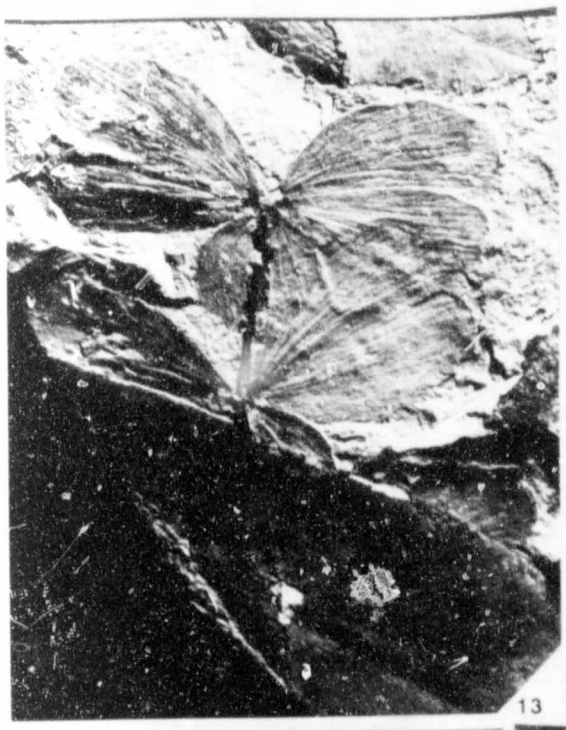
Figures 13 - 22 Sphenophyllum speciosum x 2

Figures 13 - 15 Successive whorls that have the basal internode attached. The specimen in figure 13 shows the delicate nature of the species.
13 - N-MN 1532 14 - N-Blw 70 15 - N-Lk 443
(figure 14 see also figure 38).

Figures 16 and 18 Two isolated whorls with clear venation. The connecting band is just visible around the stem attachment.
16 - N-Lk 102 18 - N-Lk 444
(figure 16 see also figure 39).

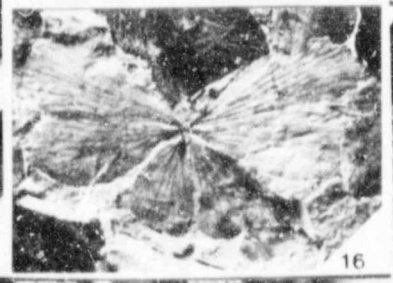
Figures 17 and 19 The leaflets are less anisophyllous than usual in both specimens. 17 - N-Lk 81 19 - N-Lk 442.

Figures 20 - 22 The basal internode is attached in all these specimens. Figures 21 and 22 have particularly long leaflets.
20 - N-Lk 445 21 - N-MN 979 22 - N-MN 1531.

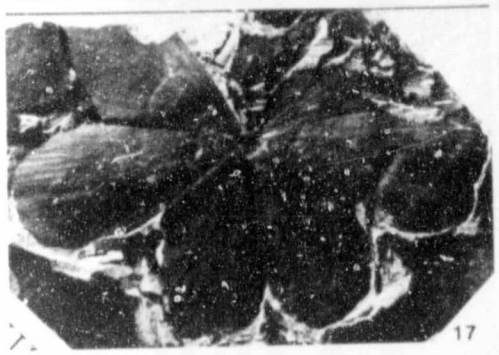

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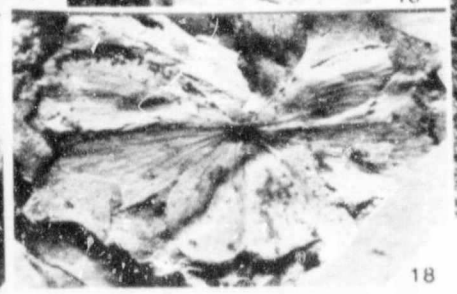

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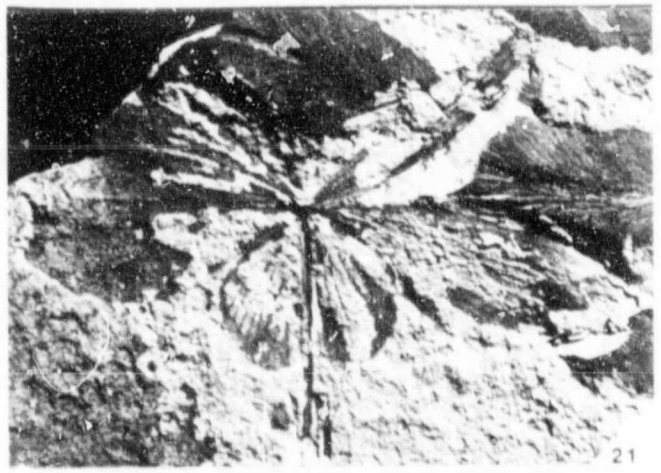

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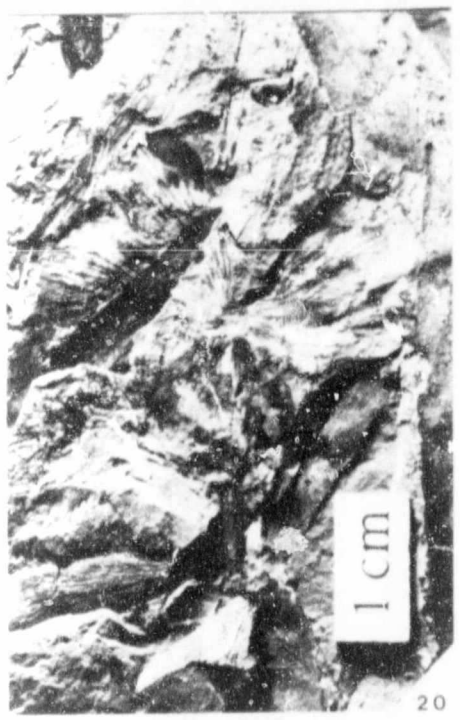

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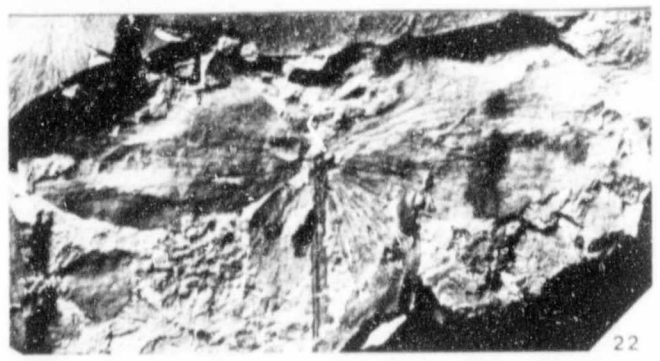

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basal internode attached. Usually if a portion of stem is preserved with a whorl of leaves it is the internode below the node that remains attached. Many whorls are intact, but not attached to a stem. Figures 16-26 all show single whorls, some with the basal internodes attached, the stalk ends in the three scalloped pattern (see fig.42), which is the result of the ridges and grooves of the stem. Several isolated whorls such as in figures 27 to 30 all show clear venation with the levels of dichotomy well marked.

Figure 27 shows the position of leaflet attachment at the node. The leaves are attached amplexicaully with the leaf gap between the two largest leaves arising just beyond the stem. The two largest leaflets are joined together by a small connecting band about 0,25 millimetre wide, figures 28 to 30 show this clearly too. Figure 28 shows the continuation of this band between the two lowest leaflets. The exact degree of cohesion between the middle pair of leaflets and the upper and lower ones is not quite clear, mainly due to the crowding of the leaf bases. The middle and lower leaflets appear to be attached opposite to a proturbance of the stem.

From the specimens that have a clearly preserved venation it becomes quite obvious that there is a variation in the number of veins at the base of the leaflet between one and two. In either case the first dichotomy occurs very soon after the entry of the vein into the leaflet. This variability in basal veins is thus not a reliable taxonomic characteristic. The margin of the leaflets is entire, any dentate appearance at the rounded apex is due to sediment infill between the veins at the margin of the leaflets that did not fall away during preparation.

Figure 33 has two lengths of stem that show the same tripartite arrangement of raised central ridge, narrow groove and flatter outer ridge on either side, as do the internodes as attached to the whorls of leaves belonging to Sphenophyllum. These fragments are 35,5 millimetres long, two millimetres wide, and 25 millimetres long and about two millimetres wide respectively, without showing any sign of node or leaflet in association. At this length they are longer than the internodes of large whorls. No specimens of Sphenophyllum have been recorded from Inhluzane, although these stem fragments might belong to the genus.

Figure 31 shows a similar ridge-and-groove effect as above, but the central ridge has a very slight spiralling ? effect, which is not usual. The specimen is 34 millimetres long and 2,3 millimetres wide, with the central ridge moving from one edge of the stem to the other.

Figures 23 - 33

Figures 23 - 30 Sphenophyllum speciosum x 2

Figures 23 - 30 Further examples of isolated whorls with the basal internode attached. Most of the specimens show clear venation with the levels of successive dichotomies well marked.
Figures 27 - 30 show the amplexicaul arrangement of the leaflets round the stem. The connecting band is most clearly visible in the leaf gap between the two largest leaflets.

23 - N-Lk 437 26 - N-Esb 337a 29 - N-Blw 75a
24 - N-Lk 439 27 - N-Blw 72a 30 - N-MN 977
25 - N-Blw 378 28 - N-Blw 73b
(figure 23 see also figure 42)
(figure 27 see also figure 35)
(figure 28 see also figure 34)
(figure 29 see also figure 37).

Figures 31 - 33 Possible sphenopsid stems x 2.

Figure 31 A stem that has a central ridge (strand?) with a slight spiral. The stem may belong to Sphenophyllum. N-In 366.

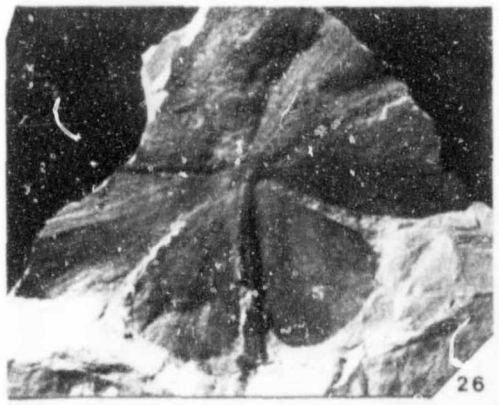
Figure 32 A stem fragment with regular ridges and grooves, possibly belonging to Raniganjia N-In 370.

Figure 33 Two stem sections with the typical Sphenophyllum speciosum tripartite arrangement of central ridge and two lateral depressed areas. No nodes are visible, thus the internodes are longer than any measured on foliar specimens. N-In 365.

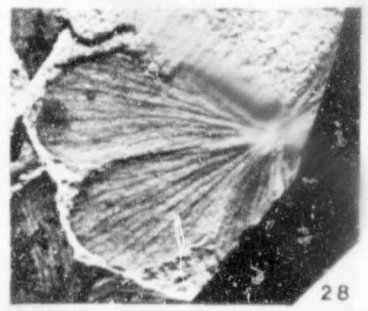

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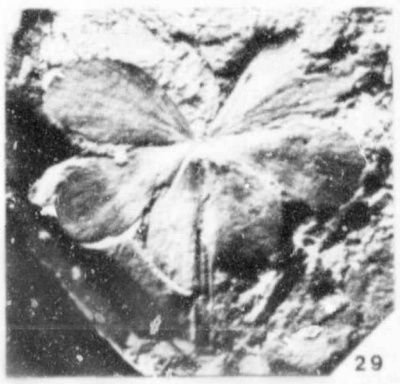

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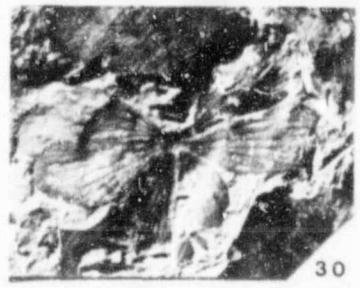

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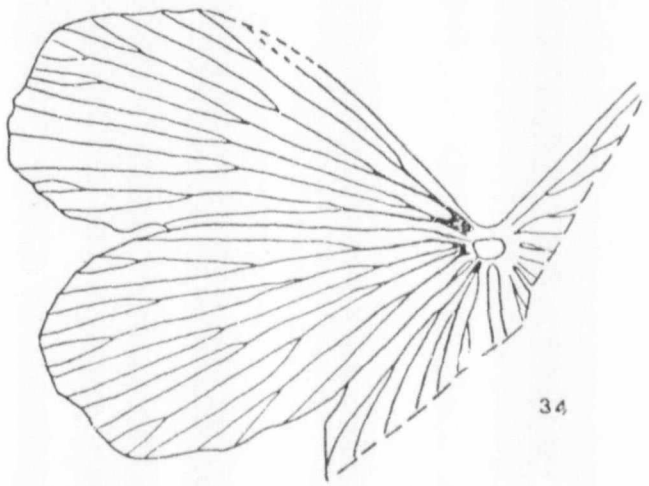

32

Figures 34 - 38 Sphenophyllum speciosum Scale is 1 cm

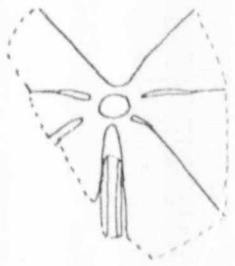
Figures 34, 34 A The specimen has very clear dichotomous venation and shows the connecting band clearly around the stem area, 34 A is shown without veins to accentuate this band. Although the veins are so clear, it is very difficult to distinguish their course at the base of the leaflets before union with the stem.
34 - N-Blw 73b 34 A - N-Blw 73a
(see also figure 28).

Figures 35 - 37 Specimens which further demonstrate the connecting band clearly.
35 - N-Blw 72a 36 - N-Blw 71b 37 - N-Blw 75b
(see also figures 27, 5 and 29 respectively).

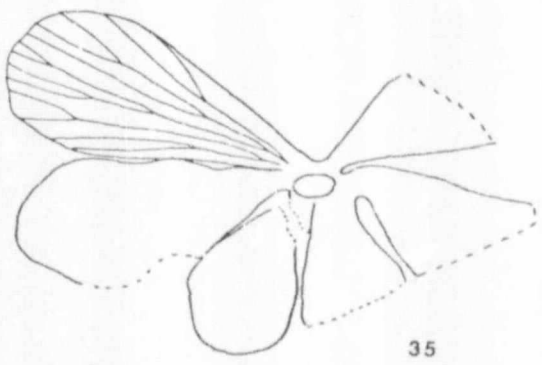
Figure 38 A typical two whorled specimen with the basal internode attached. N-Blw 70 (see also figure 14).



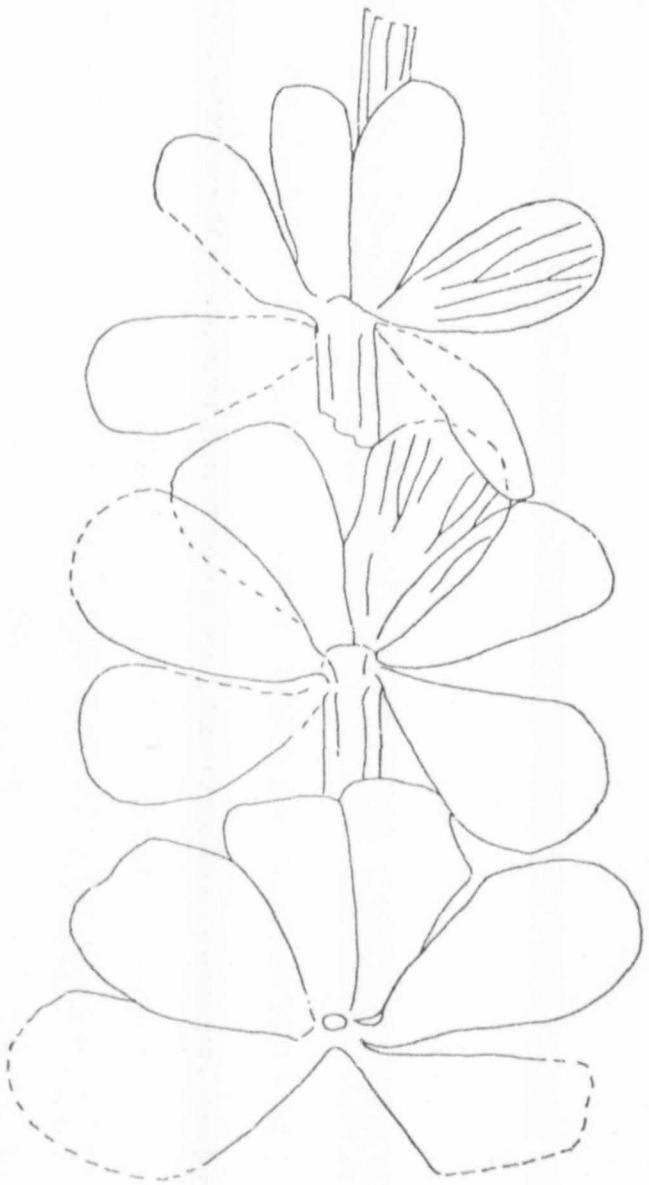
34



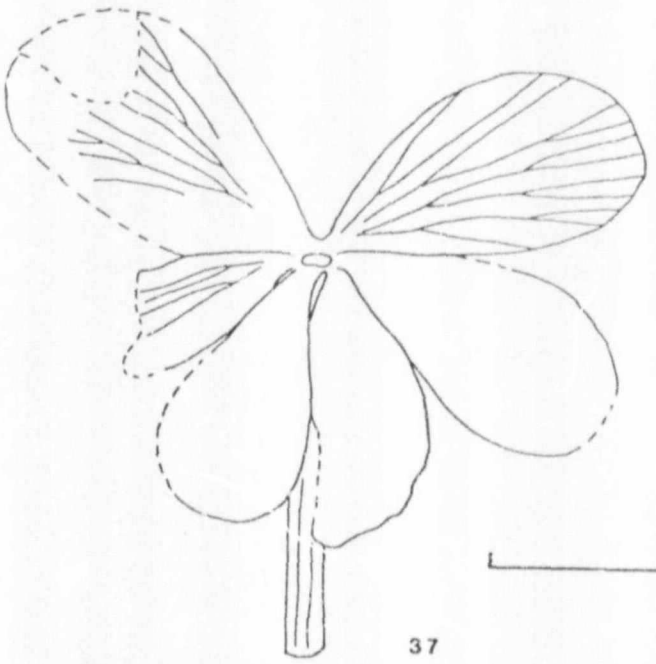
34 A



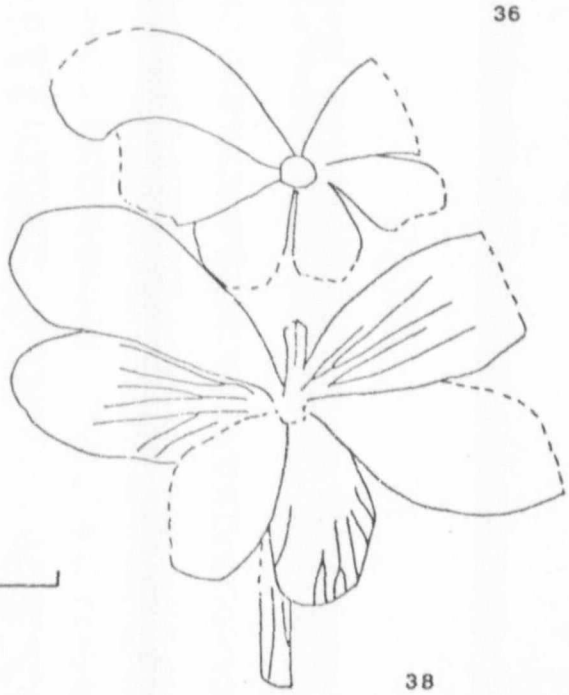
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Figures 39 - 42 Sphenophyllum speciosum

Figures 39 - 41 Scale is 1 cm

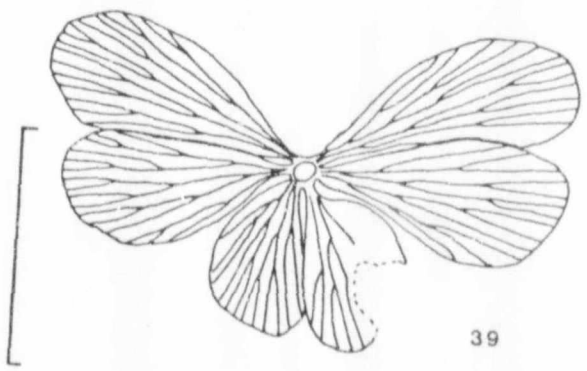
Figure 42 Scale is 5 mm

Figure 39 A small, almost perfect , isolated whorl showing the characteristic dichotomous venation, anisophyllous trizygoid arrangement of the leaves and the connecting band round the stem. N-Lk 102 (see also figure 16).

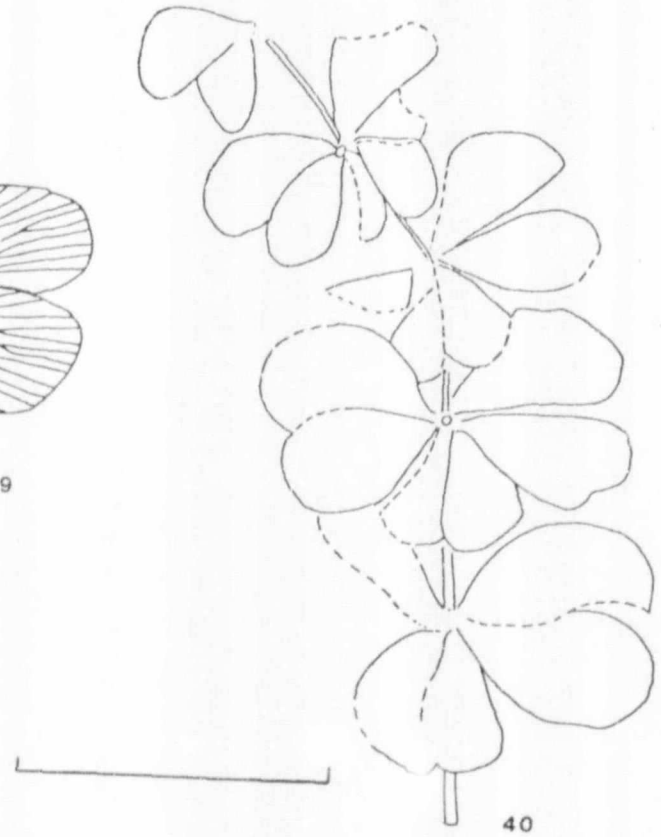
Figure 40 An outline of the shoot with the smallest whorls. No venation is clearly visible on the specimen. N-Kb 9a (see also figure 6).

Figure 41 As a contrast, a large whorled shoot at the same magnification. N-Esb 246 (see also figure 9).

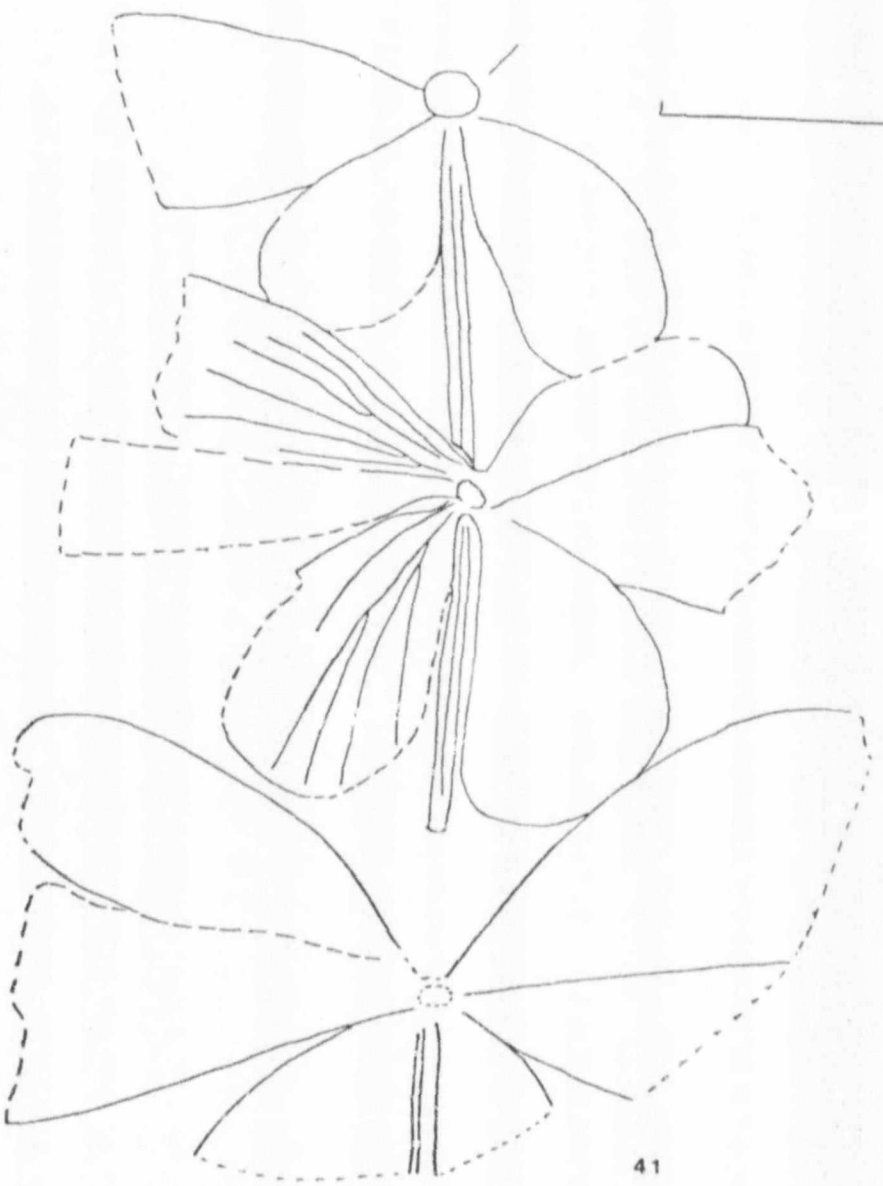
Figure 42 The basal terminal point of an internode to show the area of abscission, possibly in the region of the intercalary meristem. N-Lk 437 (see also figure 23).



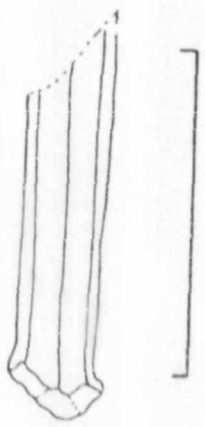
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TABLE 3 MEASUREMENTS OF SPHENOPHYLLUM SPECIOSUM SPECIMENS

Number	Length of Leaflets in mm.						Internode Length mm.	Stem Diam. mm.
	Leaflets Left			Leaflets Right				
	L	M	S	L	M	S		
N-Lk 6 b	11,3	11,3	-	-	-	-	-	0,7
N-LK 7 a	-	-	-	-	-	6,8	-	1,0
N-LK 81	16,0	16,0	14,0	-	15,9	13,4	21,0	-
N-LK 238	-	-	-	19,2	18,4	11,0	8,4	-
N-LK 436a	-	15,4	11,8	-	15,8	12,0		-
	-	-	12,7	-	15,0	12,7	14,3	1,9
	-	-	-	17,0	14,6	9,8	15,0	-
N-LK 437	-	-	12,0	-	-	11,7	18,8	1,2
N-LK 439	18,4	17,0	10,0	-	-	-	-	-
N-LK 441a left hand shoot	-	-	-	-	11,2	-	9,5	0,6
	-	12,6	7,7	-	11,6	8,0	10,8	0,8
	-	13,0	8,3	13,4	11,9	8,3	12,0	1,0
N-LK 441a Right hand shoot	-	-	-	-	-	-	11,9	1,3
	-	-	-	-	-	-	13,7	1,3
	-	-	-	-	-	-	15,3	1,3
N-LK 442	15,5	14,2	-	15,2	-	-	-	1,6
N-LK 443	? 7,8	8,4	7,1	-	-	7,1	9,8	-
	7,9	7,9	6,6	-	-	6,6	8,7	1,6
N-LK 444	-	-	8,6	-	-	8,4	-	-
N-LK 445	13,8	13,4	8,9	13,3	-	9,0	18,1	1,6
N-LK 102	11,8	10,0	6,9	12,0	11,4	7,6	-	-
N-LK 320	-	-	-	-	12,3	-	11,5	1,0
	-	12,9	-	-	12,9	-	12,2	-
N-LK 449a	-	-	8,4	11,2	10,6	9,0	-	-
N-MN 977	10,4	9,3	6,4	-	10,4	6,2	-	-
N-MN 979	-	-	11,1	-	20,0	11,0	15,9	1,0 (?)
N-MN1529a	20,7	-	-	-	-	11,0(?)	-	0,7

Author Benecke Anna Katherina
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