SECTION III
DESCRIPTION OF THE FOSSIL PLANTS

A. GENERAL

1. Naming of the fossils

Because of the poverty of preservation in most instances and also the small number of representatives of any particular plant, the nominating of new genera and species has been avoided as far as possible and, wherever a reasonable similarity was evident, the South African plants have been incorporated in established taxa. This placing of most of the plant fossils in the group which they most nearly resemble may not always be regarded as botanically justifiable but in practice is of greater value to the field geologist than the adoption of some non-committal term such as 'indeterminable lycopod' for the former method may have local stratigraphical significance.

2. Order of description

The vascular plants will be described first, according to their complexity. This follows the classification adopted in most modern Palaeobotanical text-books, e.g. Andrews (1961) "Studies in Palaeobotany". It is not necessarily in their chronological nor in stratigraphical order although a general evolutionary advancement can be discerned in fossils from the older to the younger of the rocks of the Cape System. The Algae are described last, because both genera described are somewhat problematical.

3. Growth-Environment of the plants

Many of the plants described were obviously drifted to the position where they were found and little can be determined about the nature of their growth environment. A few are found in certain areas in a dense mass of stems of one species which suggests preservation where they grew.

The general climatic conditions indicated by the proximity of glacial sediments and by the pale colouration suggest a cold and wet land environment but many may have been semi-aquatic in habitat.

4. Classified list of plants fossils described (See Table 2)

B. SUB-DIVISION PSILOPSIDA

1. General

This group of very simple land vascular plants characteristic of the late Silurian and Lower to Middle Devonian plant life was at one time believed to represent the earliest form of land plants from which all other divisions arose. Increasing knowledge of areas in which the plants occur and more detailed studies of these plants, as better specimens become available, have shown that, in almost every case, among the earliest known land plants in any area there are some which can no longer be classified with psilophytes and must be regarded rather as the progenitors of other sub-divisions, and grouped as proto-lycopods, proto-articulates, proto-ferns, etc. The number of true psilophytes has thus been reduced and the plant assemblages in which they occur are considered to belong to the Psilophyte Stage of plant development which is sometimes called a "Psilophyte Complex".

Because no record of these plants has been published previously in South Africa the main features of the sub-division are described very briefly below. *Psilophyton* was first described by Sir William Dawson (1859) from Gaspe Peninsula, New Brunswick, Canada, but it was not recognised as the type of a new sub-division of the Plant Kingdom until 1917 when beautifully preserved specimens were found silicified in a band of chert of Middle Devonian Age near the small town of Rhynie in Scotland and described by Kidston and Lang (1917). Sections could be cut and every detail of the plants could be studied and they were then universally accepted as representing a vital and important stage in the history of plant life.

In all these extremely primitive plants there is an undergound stem or rhizome from which a small erect stem arises and branches several times. The stems are usually naked but may have a number of tiny hairs or spines in lieu of leaves, but no true leaves occur. The tips of several branches are enlarged and modified to form sporangia. The plants exhibit therefore the first essentials of land plants for they were anchored in the ground to obtain mineral salts and water and have a simple vascular strand to transmit this nutriment to the tips of the branches. The stems and spores have a waxy cuticular covering to protect them from the variations in humidity and temperature of an aerial, as opposed to an aquatic, environment and finally the shoots have stomata, or breathing pores which are clearly indicative of terrestrial life.

(Specimens of the Rhynie plants collected in 1964 can be seen in the Palaeobotanical Collection of the University of the Witwatersrand).

2. The Genus *DUTOITIA* Hoeg

SUB-DIVISION: Psilopsida Order: Psilophytales

Dutoitia pulchra Hoeg
Locality: Near Knysna

Horizon: Upper Bokkeveld Series
At Present: Pal. Museum, Oslo, Norway

In 1930 Hoeg described the first psilopsida known from South Africa. He found the plants in a blue clayish shale exposed on the western side of the valley of the Blaauwkrantz River on the Knysna—Port Elizabeth road. The occurrence was in Bokkeveld Beds and the affinities of the plants suggested a lower or Middle Devonian age. Hoeg named the plant *Dutoitia pulchra* (Hoeg 1930, p. 93, Fig. 1). He had been directed to this area by the specimens 2969 and 4553 in the South African museum on which some of the plants were preserved but had not been described.

In this occurrence the stems were abundant and often crowded in a small layer of shale about 1 foot thick. Only one species was preserved in the form of white impressions. The small straight stems, measuring 1-4 mm. in width, did not taper at all but often bifurcated so that one branch was longer than the other and a "kind of sympodium" was formed. Some of the stems had small spinose or hemispherical protuberances. The lower part of the plant was unknown but a most characteristic feature was the presence of large sporangia terminating many of the stems. These were described as being "bladder-like" organs, obconical in shape with a flat top and 2.5-5.5 mm in diameter. All the specimens collected by Hoeg are now in the Pal, Mus., Oslo. I have been unable to locate the two specimens in the South African Museum mentioned by Hoeg. There are several specimens in the Albany Museum which appear to be of the same genus and which I had believed to be of the same species but I was able to submit photographs of these specimens to Professor Hoeg at the Xth International Botanical Congress in Edinburgh, 1964. He agreed that they could be included in the genus *Dutoitia* but stated that they were probably of a different species. Since the specimens all came from Port Alfred I propose to name the species *Dutoitia alfreda*.

Dutoitia alfreda sp. nov.

Plate I, Figs. 1-3

Locality: Port Alfred (Kowie)
Horizon: Upper Bokkeveld Series
At Present: Albany Museum, Grahamstown.

In the Albany Museum there are several groups of specimens of black carbonaceous shale labelled 4418, 4173 or 4165, which were collected from the Station Quarry at Port Alfred.

It is possible that the Port Alfred beds represent the same horizon as the Knysna shales, but their exact position in the Bokkeveld Series is unknown. Rennie and Mountain (1942) pointed out that although the outcrop of overlying Main Witteberg Sandstone is half a mile distant from the Port Alfred Quarry,

the intervening area is covered by alluvium and the Cape Beds are highly folded so that the true depth below the Witteberg cannot be assessed.

On the best of the specimens, number 4418a which is figured on Pl. I, Fig. 1 and nominated as the type, a bedding surface is covered with stems of *Dutoitia* preserved as light-coloured markings on the dark background. The preservation is apparently not as good as that of the Knysna specimens but there is no doubt, I think, of their generic identity.

The thickest stem is only 2.5 mm in width and no spines or protuberances can be seen but this could be due to the coarser matrix. The characteristic branching is, however, clearly evident and a number of large terminal sporangia are preserved. They are club-shaped with a flat top and measure 7 × 4 mm Several can be seen in section as small circles of 4 mm diameter. Pl. I, Fig. 2 is an enlargement of the right hand top corner of Pl. I, Fig. 1 showing a club-shaped sporangium 'a' and one in cross-section marked 'b' in which there is a suggestion of small spherical objects, which must be spores but of this there is no proof.

In addition to the specimens marked 4418 in the Albany Museum there are several slabs and flakes of graphitic phyllite numbered 4173 and 4165. All are from Port Alfred (The Kowie). On these a number of specimens of *Dutoitia* are preserved but they are difficult to photograph because they are graphitic and are only visible on the dark matrix by reflected light. A branched stem on a 4173 flake is shown in Pl. I fig. 3. It resembles the type of sympodial branching described by Hoeg (1930) whose paper included only one illustration which was of a branched axis on which the shapes of the sporangia do not appear to be identical with those from Port Alfred. The consistently naked axes of the latter are a further justification for the separation of the two species.

Dutoitia maraisia sp. nov.

Plate II

Locality: Howisons Poort near Grahamstown
Horizon: Near the base of the Witteberg Series
At present: Palaeobotanical Collection, University of Witwatersrand, Johannesburg

What is possibly a third species of *Dutoitia* was sent to me during 1964 by J. Marais of the Geological Survey office in Grahamstown. I had heard of the presence of psilophyte impressions in the rocks of Howisons Poort near Grahamstown, on the Port Elizabeth road. I am grateful to Mr. Marais for locating them, and have named them in his honour.

The horizon is the so-called "Shale Band" and lies near the base of the Witteberg Series. It is one which has yielded several other plant genera described later in this monograph, for the originally argillaceous sediments allowed a better preservation than that in the quartzites above and below. It is a higher

horizon than the Knysna shales studied by Hoeg or the graphitic shales of the Kowie, both of which are included in the Upper part of the Bokkeveld Series. The length of the time interval between them cannot, however, be calculated accurately in the Grahamstown area because the transition from Bokkeveld to Witteberg is buried beneath a cover of much younger sediments beneath which the Cape rocks are highly folded.

The rock is a carbonaceous micaceous shale on which some of the bedding planes are covered with fragments of a small psilophyte. The shales show poor fissility and bedding planes are only well defined where a layer of plant fragments, now altered to graphite, provides an easy parting plane.

The numerous small fragments indicate that the plants were torn from their position of growth and transported although their number suggests that they could not have been carried any great distance. Their fragile nature prevented the preservation of any whole plants.

The small branching stems normally range in width from 1-0.5 mm and less, but a few fragments with a width of 3 mm and a clearly marked central vascular strand can be seen. It is not possible to determine whether the broad and narrow stems are parts of the same plant, but it is probable. Two surfaces are shown on Plate II, Figs. 1 and 3 on each of which a few broad axes and a number of smaller branched axes can be seen.

The stems are thinner and therefore more fragile than those of *Dutoitia* from the Kowie. The sporangia, where preserved, are likewise smaller but, what is more important, they appear to be of a different shape. A flat top is not visible in any instance and instead of standing erect at the end of an axis, they tend to droop and hang in a pendulous fashion (see Plate II, Figs. 2 and 3). In addition several stems, e.g. at the tops of figures 2 and 3, show projections. For these reasons the Howison's Poort plants are not included with the Kowie species and despite their poor preservation have been placed in a new species. The resemblances to *Dutoitia* are sufficient to place them provisionally in the same genus.

Comparison of *Dutoitia*

The size and shape of the sporangia of the three species of *Dutoitia* appear to be unique but the rest of the plant suggests comparison with a number of small psilophytes from other parts of the world. Hoeg compared his specimens of *Dutoitia pulchra* from Knysna with *Psilophyton*, *Rhynia* and *Hicklingia*. For the naked axes of *Dutoitia alfreda* from Port Alfred the most obvious resemblance is with *Cooksonia* from the uppermost Silurian or lowermost Devonian of Victoria, Australia (Lang and Cookson, 1935). They may be compared also with *Cooksonia* cf. *hemisphaerica* from the Upper Silurian of Pridoli (Obrhel, 1962a, Plate I, Figs. 1-3).

3. ? Psilophytalean Axes

Plate III, Figs. 1-10

Locality: De Doorns
Horizon: 3rd Bokkeveld Sandstone
At Present: Palaeobotanical Collection, University of the Witwatersrand, Johannesburg, and Geological Survey Museum, Pretoria.

Occurrence

In 1962 in the course of re-mapping the area Mr. J. N. Theron of the Geological Survey collected specimens T.D. 77-83 from the third Bokkeveld Sandstone in the De Doorns District. This horizon is marginal between the lower marine and upper fresh water phases of the Bokkeveld Series and is therefore lower than any of those in which *Dutoitia* was found.

The rock is from an outcrop and is weathered to a deep red. A great many small organic fragments are included. There is usually no colour contrast between them and the rock matrix but, when split, the fresh rock is more yellow in colour and the fossils of a dark maroon colour and therefore far more conspicuous.

The nature of these fragments is open to doubt and the possibility that some, at least, are of animal origin cannot yet be excluded. They are treated here as plants because some of them are closely comparable with primitive plant fossils (Cookson, 1935) from Victoria, Australia, whose vegetable origin was proved by organic residue.

Some of them resemble also a new group of Thallophyta described by Kräusel (1960) from the upper part of the Lower Devonian beds at Ponta Grossa in the state of Parana. Their preservation permitted chemical treatment and microscopical examination through which an algal rather than an animal origin could be implied. Since the Cape specimens are too poorly preserved to allow this type of study, only the outward form can be compared and subdivision would be unreliable. They are therefore grouped provisionally and in a very general sense under the term Psilophytalean axes but it is probable that several different genera are present and that some may be thallophytes.

The rock breaks unevenly and the stems can be seen lying in all directions and at different angles. They were probably of drift origin and deposited in water where no marked current directions existed. The stem fragments are rarely more than 2 cm in length and are often only 3 to 4 mm wide. On one surface of specimen T.D. 77B which is approximately 70 sq. cm in area, about fifty portions of different stems were counted but many other surfaces exhibited only a few. Their undulating character suggests soft herbaceous plants. Most of the stems are covered with very small round or oval "lumps", or alternatively hollow scars on negative surfaces—any elongation is longitudinal

and never transverse with reference to the stem. In a few cases the scars are circular and they may therefore have formed the bases of small round spines but no projections of this type are visible on either margins or surfaces. In all cases the distribution of scars appears to be most irregular. Some of the surfaces like those in Plate III, Fig. 1 have uneven longitudinal ridges or corrugations due probably to shrinkage. It is not known whether the marked relief on these small stems represents outer or inner surfaces of the plant, but in addition to the punctate stems and interspersed with them there are a few which are of the same size but have fine longitudinal striae with only a faint suggestion of round scars (see Plate III, Fig. 4). Only one of the stems, of a much smaller size, exhibits any type of branching but the rough transportation implied by the short fragments would probably have destroyed any such evidence. No reproductive organs of any kind have been seen and no other fossils appear in the rock although the horizon is within or on the boundary of the marine invertebrate zone of the Lower Bokkeveld.

Description of Specimens

Specimen T.D. 77B

A few of the stems have been selected to illustrate different types of surfaces and of relief. Plate III, Fig. 1 is of several corrugated or crumpled stems with small round or oval and raised or ring-shaped scars. The stem on the upper left hand side is broader than most. Fig. 2 has on the left a stem, 'a', with very marked relief in which the raised scars are irregularly arranged and are ovate with the sharp end pointing downwards. On the right hand side there are several fragments of corrugated stems, 'b', without round scars and above them, at the point marked 'c', a small but distinct bifurcated stem. This is the only example of branching in this collection. It is slightly out of focus in the photograph, being on a different level, and unfortunately the tips of both branches are missing so that their possibly reproductive nature cannot be confirmed. It is not improbable that all three stem types in this figure may belong to one species of plants.

Specimen T.D. 80—Plate III, Fig. 3 illustrates the very small size and irregular distribution of the outgrowths and their longitudinal elongation. In addition there is a distinct groove which may indicate the presence of a vascular strand (cf. Cookson, 1935, Plate II, Fig. 45) and at 'b' a possible bifurcation.

Plate III, Fig. 4 is from the same slab and is of two stems with striated surfaces which possibly represent a different aspect of the same plant. A fragment of a punctate stem can be seen overlapping one of them.

Specimen T.D. 79—Plate III, Fig. 5 is of two punctate stems, presenting negative and positive surfaces, on the left and right hand side respectively. On the same surface Fig. 6 shows the variation in size and shape of the lumps and their extremely irregular distribution.

Specimen T.D. 83—Plate III, Figs. 7 and 8 show a more pronounced elongation of scars but in addition a surface indicative of cell structure. The latter is only visible in Fig. 8 where it is magnified six times. Fig. 7 must be viewed from the left to show the correct relief.

Specimen 57f and counterpart S.A.M.—Plate III, Figs. 9 and 10. The only other specimen of this type known to me is one in the South African Museum which was collected by Schwarz in 1905 from the farm Uitkomst in the district known as the Warm Bokkeveld which lies on the northern limb of the folded Hex River Mountains. Theron's specimens from De Doorns were collected from the southern limb of the same range and possibly from the same or a close horizon. Schwarz (1905, p. 276) described the area as one from which a great many well-preserved marine invertebrate fossils had been collected. This specimen appears to be the only one placed in the plant collection but its vegetable origin might have been regarded as doubtful but for the occurrence of so many fragments of comparable stems from De Doorns. Two surfaces are displayed, a convex one magnified three times in Plate III, Fig. 9 and a concave counterpart shown natural size on Plate III, Fig. 10. A probable outer surface can be seen on the top right hand side of Fig. 9. The stem is 7 mm in width and a little larger than any from De Doorns but the scars are comparable in size and shape and in irregularity of distribution cf. the left hand stem in Fig. 1.

Discussion and Comparison of the De Doorns specimens

These very poorly preserved and incomplete fossil plant fragments from the lower part of the Bokkeveld Series can be compared with primitive plants from several areas. As an assemblage they have most in common with fossil plants from Victoria; Australia, described by Cookson and Lang (1931) and especially Cookson (1935) and regarded as of Upper Silurian age. For many years these were the oldest known land plants and famous on that account. Several fossil plant sites in Victoria, Australia, have yielded primitive vascular plants. The age was fixed by finding *Monograptus* associated with some of the plants and this Graptolite is known to be "not younger than Lower Ludlow". The interrelationships between the plants of all four sites is such that their contemporaneity is assured. Recently the Silurian age was questioned but it has now been re-established.

The plants themselves were comparable with Lower Devonian types of Europe and it is possible that in Australia they may have ranged through Upper Silurian into Lower Devonian periods.

From the site near Alexandria, Victoria known as Mount Pleasant (Cookson, 1935) several stems have been described which appear to be very similar to those collected by Theron from the Third Bokkeveld Sandstone in the de Doorns district. Cookson described the plant remains as being small and fragmentary and normally preserved as encrustations of brown mineral matter on which a few

carbonaceous particles may remain. In a very few cases organic material was sufficient to allow chemical treatment and thus to ascertain that the fragments were those of vascular land plants. She was able to isolate a fragment in which a few tracheids were preserved (Cookson, 1935, Plate 10, Fig. 23) which showed remains of thickening on their walls and regarded this type of structure, which had been found also in other areas, as probably characteristic of most of the plant assemblage. It is unfortunate that no such evidence is available from the highly weathered Cape specimens but every one of the specimens on Plate III can be compared to a certain extent at least with those from Australia.

Cookson (1935, Plate II, Fig. 38) can be compared with Plate III, Fig. 1 from De Doorns. The Australian stem was labelled cf. *Baragwanathia longifolia* for it resembled leafless stems of this plant preserved under better conditions in the other sites. The stems classified by Cookson (1935, p. 142 and Plate 11 Figs. 43-45) as "stems with small spirally arranged elevations" are, in size and relief, comparable with most of the De Doorns stems. The elevations were round or oval with the long axes parallel to the length of the stem (cf. Cookson, Plate 11, Fig. 43 with Cape Plate III, Figs. 7 and 8). Scars were sometimes ovate with point downwards (cf. Australian Plate II, Fig. 44 with Cape Fig. 2, Plate III). Scars were sometimes well-spaced and sometimes crowded (cf. Australian Plate 11, Fig. 45 with Cape Plate III, Fig. 3). One of the specimens showed a small central vascular strand from which the tracheids were isolated. There were, in addition, some striated stems (cf. Australian Plate 11, Fig. 37 with Cape Plate III, Fig. 4).

Although a considerable number of examples was available for investigation, Cookson regarded the nature of the elevations on the stems as obscure. As in South Africa, she found no evidence of small leaves on either margins or surface but considered that in all probability the raised scars were either small leaf bases or emergences serving a similar function.

The small branched stem on Plate III, Fig. 2 can be compared with the Australian *Hostimella* (Cookson, 1935, Plate 10, Figs. 16-18) or *Hostimella* sp. (Lang and Cookson, 1931 Plate 11, Figs. 3-9). Cookson stated that the small spiral Australian axes might be related to *Psilophyton* and with this I agree.

Fine surface markings which may represent cell structure can be seen on Plate III, Fig. 8. This can be compared with Cookson, 1935, Plate 11, Fig. 40 with similar markings which she regarded as epidermal structure. It was visible only by reflected light on a surface encrustation.

Other psilophytes have been recorded from Spiti in the N.W. Himalayas by Sahni (1953, Plate 1). They were small axes which divided into two short branches of equal length. Sahni was not completely convinced of their vegetable origin and believed them to have been of Silurian or possibly of Ordovician age.

The plants described by Kräusel and Dolianiti (1957) from the lower Devonian Beds of Picos in Brazil are the only others known and may even be specifically identical with these Cape axes.

Dawson (1862, Plate XII, Fig. 6b) illustrated as small stem with tiny scars, which he called the punctuated variety of *Acanthophyton spinosum*. The size and markings were rather similar to the specimen shown on Plate III, Fig. 3, but no enlargement was given. The stem was of Middle Devonian age. Some of the lumpy stems could be compared with *Lepidodendron gaspianum* Dawson 1862, Plate XIV, Figs. 26-28. But their arrangement is more regular.

Palaeostigma sewardi Krausel and Dolianiti

Plates IV, V, VI and VII

Localities: 1. Steytlerville
2. Near Bathurst
Horizon: 1. Upper Bokkeveld
2. Upper Bokkeveld
At Present: 1. S.A. Museum, Cape Town
2. Albany Museum, Grahamstown and No. 1806 South African Museum, Cape Town.

History of the genus

One specimen of this plant from the Steytlerville District of the Cape was originally described by Seward (1932, Plate XXIII, Figs. 1, 3 and 4 only and Plate XXIV, Fig. 8, Text Fig. 1, p. 360) who regarded it as being specifically identical with other Cape stems and included it in the species *Haplostigma irregulare* (Schwarz) Seward.

In 1954 Kräusel drew attention to the probability that at least two different plants had been united by Seward but they were only separated taxonomically by Kräusel and Dolianiti (1957, Plate I, Figs. 1 and 2) when additional specimens of the present plant were found in the Lower Devonian of Brazil. As a result these authors separated the smaller-scarred stems described by Seward from the larger-scarred ones which remained in the genus *Haplostigma*. The former were placed with the new Brazilian specimens in a new genus and species as *Palaeostigma sewardi* but they nominated the South African specimen 10744 S.A.M. (No. 836 Haughton) as the holotype of the new genus. They believed it to be a much simpler plant than *Haplostigma irregulare*, describing it as a stem probably without real leaves and with various spiny appendages which were rounded or conical and were arranged irregularly.

The type specimen and a number of new specimens are described and discussed below but the nature of the plant is still problematical and even its systematic position is somewhat uncertain. As it is closest to certain *Psilophytes* the plant has been included in this section.

Description of Specimens

Holotype 10744 S.A.M. and its counterpart 10741 S.A.M. (No. 832 of Haughton).
Plate IV, Figs. 1 and 2.

This specimen was collected by Haughton (1935) from the upper part, i.e. the fresh water facies, of the Bokkeveld Series on the farm Schietkraal in the Steytlerville district of the 'Cape Fold Belt', about 80 miles northwest of Port Elizabeth. It was described and illustrated by Seward (1932, text Fig. 1, p. 360, Plate XXIII, Figs. 1, 3 and 4 and Plate XXIV, Fig. 8). In the present publication Plate IV, Fig. 2 is an enlargement of Sp. 10741, S.A.M., the counterpart of the holotypes. It illustrates clearly a comparatively smooth stem on which a number of very small, transversely elongated scars appear. Some of these are hollow and others raised and they are apparently arranged irregularly. Seward's interpretation was that the surface represented the resistant cylindrical cuticle of a stem of which all other tissue had decayed, so that the raised lumps were on the upper surface and seen from the outside, while the hollow scars belonged to the lower surface and were being viewed from the inside.

In support of this he illustrated two enlargements of better preserved cuticular surfaces from a South African specimen No. V. 240 in the British Natural History Museum (Seward, 1932, Plate XXIV, Figs. 9 and 12) which show the details of a few raised scars.

Kräusel and Dolianiti (1957) illustrated an enlargement of the epidermis of a Brazilian specimen (K. & D. 1957, Plate 1, Fig. 2) and this is strikingly similar to Seward's enlargement of the British Museum specimen from South Africa but their impression of a stem (K. and D., Plate 1, Fig. 1) is less like those of the South African type specimen.

Specimens 4344 *Albany Museum and* 1806 *South African Museum.*
Plate IV, Fig. 3, and Plates V, VI and VII.

A number of additional specimens of *Palaeostigma* are preserved in the Albany Museum, Grahamstown, on slabs of carbonaceous shale metamorphosed almost to a graphite schist so that the surfaces are highly reflective.

The specimens which are numbered 4344 and a few 4173 were collected from Sweet Fountain (formerly Estments Farm) in the Bokkeveld Beds, 3 miles east of Bathurst Station. There is also a specimen from this area preserved in the South African Museum, Cape Town, and numbered 1806. The largest of the Albany Museum specimens is illustrated on Plate IV, Fig. 3. Unlike the type specimen the whole surface, and indeed every layer in the rock, is covered with the plants lying in all directions so that it is extremely difficult to measure individual stems but those clearly defined appear to be between 1 and 2 cm in width (see Plate V, Fig. 1).

The occurrence indicates that the plants grew in a tangled mass possibly in an aquatic environment but, if so, the thick cuticles suggest at least periodical exposure to the air.

All the stems are covered with the characteristic small, raised and hollow scars which are irregularly arranged. As in the Schietkraal specimens they may be round, but are usually oval, being elongated transversely and never vertically.

Some of the stem surfaces are wrinkled but there is neither vertical nor horizontal corrugation of the stems such as commonly develops in *Haplostigma* stems.

No appendages were seen on any of the stems and no indication of the presence of vascular tissue. In at least two small areas brownish patches of original cuticle have been preserved and a wrinkled skin-like appearance is apparent, showing that mineralisation of the plant matter had not been completed (see the area at the top of Plate VII, Fig. 2). This would provide an answer to the doubt expressed by Kräusel and Dolianiti (1957) that the fossils might conceivably have been of animal origin. An attempt to scrape and macerate material from one such surface was made but no significant residue remained.

In some areas epidermal cell structure is visible (Plate V, Fig. 2). These features appear to be identical with those illustrated by Seward (1932) of a South African specimen number V. 240, which possibly came from the same site, and also those by Kräusel and Dolianiti (1957) of a Brazilian specimen and I believe that this is an important factor in establishing their specific identity.

Specimen 1809 *Albany Museum*

On specimen 1809, Albany Museum, which was collected also from Sweet Fountain, a few fragments of *Palaeostigma* are preserved with *Calamophyton* (see left hand side of Plate XVII, Fig. 1). It is the only instance in which any other plant has been found associated with *Palaeostigma*.

Details of the scars and discussion on their origin

In view of the contradictory explanations of the projections and hollow scars, they have been rather profusely illustrated in this monograph in order to show as many aspects of the stems as possible. Seward's interpretation of the stems as overlapping surfaces of cuticle is justifiable in some of these specimens, e.g. Plate VI, Fig. 1 in which the hollows are clearly defined but the projections are either immature or masked. In places also the distance between concave and convex pairs of scars can be seen to increase with the relative position of the two surfaces but in most stems there are certain features which seem to demand another explanation.

A careful analysis of enlarged surfaces of the stems suggests that in some areas, at least, the detail is far too clear on both sunken and raised scars for them to represent upper and lower cuticular surfaces. An alternative suggestion is therefore preferred, but cannot be fully substantiated at present. It is thought that the raised scars are equivalent to small vegetative buds or bulbils which when ripe separated from the stem to form a new generation, leaving behind a saucer-like depression. (Since the term bulbil is used for similar detachable

vegetative buds on some flowering plants and also on certain fungi, I consider it to be applicable in this instance.)

The development of a central scar on the raised projections may be indicative of the stage of development. It is not always present—cf. Plate V, Fig. 2 and Plate VI, Fig. 1—in which some of the 'lumps' are smooth and others display a small central dimple, the size of which apparently increased until a crater-like opening can be seen on many of them. See Plate VI, Figs. 2, 3 and 4 and VII, Fig. 4. Occasionally the opening is in the form of an elongated slit, see Plate VI, Fig. 5.

Plate VII, Fig. 1 may represent a stem on which bulbils were just beginning to form.

An examination of the surfaces on Plate V, Figs. 2 and 3 shows a certain cyclic arrangement of hollow scars but a haphazard arrangement of raised ones. Possibly such surfaces represent stems on which the bulbils were nearly ready to be detached but had not separated at the time of burial until the sliding action of the overlying stems loosened them. The pressure could have damaged some of the bulbils because in several instances, e.g. left hand side of Plate VI, Fig. 1 and the top of Plate VII, Fig. 4, remains of tissue appear to have been left in the smooth saucer-like depressions.

On Plate V, Fig. 3, which is an enlargement of Plate V, Fig. 1, I suggest that some bulbils still lie in their hollow cups; some are partly removed; others still lie near the cups; a few are missing. Many examples can be seen on the other illustrations. The isolated but well-developed bulbil on the right hand side of Plate VII, Fig. 3 may represent one which has been detached. Radiating structure is visible in many well developed bulbils and is sometimes apparent in the cups also (see Plate VII, Fig. 4 and Plate V, Fig. 3).

Fractured sections of the bulbils likewise sometimes exhibit strong radiating structure and the suggestion of a central core or column. One of these is particularly clear on Plate VI, Fig. 2.

I would therefore suggest that in the light of this new evidence a solution involving detachable vegetative reproductive buds provides a more realistic explanation of the irregularity of the observable depressions and elevations on the stems of these plants.

Comparison and Remarks

As far as I know, apart from the Brazilian specimens from a Lower Devonian horizon of Picos (Kräusel and Dolianiti, 1957) which are believed to be specifically identical, no other plants of this type have been described.

Several authors have drawn attention to projections or tubercles on certain early vascular plants and have suggested that they might have some reproductive significance, notably the hemispherical bulges on stems of *Rhynia gwynne vaughni*.

The feature is reminiscent of certain Red algae and it would seem to support the theory first advocated by Arber (1921) that Psilophytes and indeed

all lower vascular plants had an algal origin. Arber actually considered Psilophyton to be a Thallophyte which probably belonged to an "obsolete race of Thallophyta, higher in the scale of complexity than any living Algae".

Plants like *Palaeostigma* could almost be regarded as transitional between Thallophyta and vascular plants.

In this connection the radiating structure to be seen in some of the small round or oval bulbils of *Palaeostigma* is reminiscent of that in *Pachytheca* and, in fact, when separated from the parent plant might, save for the smaller size, be mistaken for these small, spherical, lower Devonian plants.

Up to now *Pachytheca* has not been recorded from South Africa, but occurs in Australia as well as in many norther hemisphere formations of this age.

Further references to an algal origin and relationship will be found in the final chapter.

There is, however, an important alternative suggestion. A very interesting paper has recently been published by Pant (1962) in which he presents a strong case for regarding the stems of *Rhynia gwynne vaughni* with its much discussed hemispherical projections as the gametophyte of the other psilophytes in the Rhynie chert beds. He finds support for his views in the closely comparable vascular gametophytes of the living *Psilotum.* He demonstrated that the tissue of the hemispherical bulges of *Rhynia gwynne vaughni* was clearly demarcated from that of the parent axis by an abscission layer at the base and believes that they became detached to form a young sporeling—a new sporophyte generation. In the light of this new evidence the theory of detachable vegetative bulbils is less revolutionary. It is possible that there may be a close parallel between the Scottish and Cape plants in the manner of their reproduction although in the absence of the marvellous preservation in colloidal silica, proof may not be possible. It would explain the apparent absence of vascular tissue in *Palaeostigma* which would probably have to be regarded as an aquatic generation of *Haplostigma* or *Dutoitia* or some other primitive psilophyte associated with it. *Spongiophyton* Kräusel (1960) from South America may fall into this category also and a new vista of dual relationships between primitive land plants and associated plants formerly regarded as thallophytes is open.

C. SUBDIVISION LYCOPSIDA

General

This is the most important subdivision of fossil plants found in the Cape System, both from the point of view of numbers of genera and also numbers of occurrences. All the specimens, without exception, can be placed in genera of proto-lycopods which is highly significant, for it is indicative of Devonian age.

Like the Psilopsida, all the plant fossils described in this section are fragmental and often very imperfect. No sporangia have been found and classification has had to be based on superficial resemblances only. Nevertheless a much

larger number of genera has been recognised than had been known previously from Southern Africa. Some of them provide interesting and significant comparisons with other areas.

Classification

The early lycopods have been the subject of a number of recent investigations and revisions in other countries. Unfortunately none of the reviews originated in a southern hemisphere country but once again it can be emphasized that comparisons at the level of Orders and Families are common between northern and southern hemisphere Devonian fossil plants. They are less common in Genera and only occasional in species. In later geological periods they become even more rare.

Genus *DREPANOPHYCU* Göppert

Order: Archaeolepidophytales Family: Drepanophycaceae

Plate VIII

Systematic position

The genus *Drepanophycus* Göppert now includes many specimens originally described as psilophytes. Hoeg (1942, p. 184) in discussing the origin and development of the spines and the evolutionary position of the genus emphasized the necessity of separating it from the Psilophytales. Kräusel and Weyland (1949) placed *Drepanophycus* together with *Baragwanathia*, the primitive Upper Silurian — Lower Devonian plant from Victoria, Australia, in the family Drepanophycaceae of the order Archaeolepidophytales. Pici-Sermolli (1958) included it in the class Protolepidodendridae, order Drepanophycales and family Drepanophycaceae. Banks (1960) and Grierson and Banks (1963) reviewed former classifications and, for this genus, accepted the terminology of Kräusel and Weyland (1949) which is used above.

General Distribution

Grierson and Banks (1963, p. 230) provided the following generic diagnosis —"Dichotomously branched robust axes with falcate leaves; leaf bases large. Central vascular strand with annular tracheids". The stems are among the best known of Devonian plant fossils and the genotype *D. spinaeformis* which now includes *Arthrostigma gracile* Dawson (Kräusel and Weyland 1935) is known in considerable detail. It had a creeping underground stem from which upright dichotomously forked spiny stems arose. A single sporangium was borne on the upper surface of some of the spines and it was this feature which caused the plant to be regarded as amongst the most primitive lycopods rather than as a psilophyte.

The genus is widely distributed in the Northern hemisphere but is little known from the Southern. It has been reported from Canada, U.S.A., Scotland, Wales, Norway, Germany, Bohemia, France and Portugal, and from Western Siberia and China. In the south the only reference known to me is of *Arthrostigma* from the lower Devonian of San Juan in Argentina by Frenguelli (1951) but unfortunately no figure was included in his paper.

In the vast majority of recorded occurrences, *Drepanophycus* has been found in Lower Devonian rocks but sometimes continues into the Middle Devonian. It is regarded as typical of these horizons.

Drepanophycus schwarzi sp. nov.

Plate VIII, Figs. 1-4.

Holotype Specimen 2903 S.A. Museum, Plate VIII, Figs. 1 and 2.

This specimen, on which several different stems are preserved, was collected by Schwarz from weathered pinkish grey Bokkeveld shales which outcrop in the grounds of the Mental Hospital at Port Alfred (the Kowie). All the stems were originally combined and described and figured by Seward (1909) as *Bothrodendron irregulare* Schwarz, but later (Seward, 1932) as *Haplostigma irregulare* (Schwarz) Seward. Although Seward recognised that there were "two fairly distinct forms" preserved on the surface he regarded them as specifically identical. Two stems can be seen on Plate VIII, Fig. 1 and it is evident that the nature of the projections, and the size, shape and distribution of the scars on the two forms differ radically. The larger stem has been retained in the genus *Haplostigma* (which was illustrated also by Seward (1909, Plate XXVIII, Fig. 3)) but the smaller is here transferred to the genus *Drepanophycus* Göppert. The specific name *schwarzi* has been selected in honour of Professor Schwarz who found the original specimen.

The stem is 10 cm long and 1.2 cm wide. It branches on the right hand side (see Plate VIII, Fig. 2) at an angle of 60 degrees and the curvature suggests an herbaceous but fairly rigid plant. On the surface of the stem there are closely spaced round scars arranged in definite longitudinal rows. These are controlled by the fact that although the growth of spiny projections was probably spiral, the vertical interval between them is much less than the horizontal, so that the scars which alternate in adjacent rows are almost touching in vertical alignment. The scars are round or oval in shape and are elongated vertically, being 1.5 to 2 mm in the longer diameter while the interval between them is less than 1 mm On Plate VIII, Fig. 1 an upper layer of the stem can be seen in two places and although the scars are flatter and more distinctly separate on the lower surface, the vertical arrangement remains conspicuous.

Along both margins but especially on the left hand side, a row of closely-spaced, stiff spines is preserved. They are 3 to 4 mm in length, broad at the base

but taper to a sharp point and are falcate or curved upward, so that they overlap. These features are clear in Plate VIII, Fig. 2 which was photographed with different lighting and shows the branching more clearly.

The type specimen is the only one on which the spines are preserved clearly but a few other stems with similar scars are known from the Albany Museum Collection. All are from the Bokkeveld Series in the Port Alfred area but occur in carbonaceous shale which is often altered to a graphitic phyllite on which organic impressions are clearest by reflected light but details are absent. Two of these are described below.

Specimen 4165A, Plate VIII, Fig. 3.

This stem is slightly broader than the type, being 15 mm wide and 6.5 cm in length. The longitudinal rows are clear and the vertical interval between scars is less than the horizontal. Remnants of poorly preserved spines occur on both margins. There is a short length of *Haplostigma* on the same surface.

Specimen 4165*A*, *Plate VIII*, *Fig.* 3.

This has stems only 6 mm wide branching at 60 degrees as on the type specimen. The plant matter has been altered to graphite and although the longitudinal rows and close spacing are apparent, all detail has been obscured.

Discussion and Comparison

Among the many small herbaceous Devonian plants with spiny leaves, the stems described above would seem to fit best into the genus *Drepanophycus* with which they agree in having simple falcate leaves arranged on an otherwise smooth surfaced stem. In the Cape specimens neither creeping stems nor sporangia have been seen, but the rocks in which they occur are highly altered by folding and the preservation is poor. Comparison must therefore be based on the outward form of upright vegetative shoots. Among published figures of *Drepanophycus* the closest resemblance is to one of *D.* cf. *spinosus* from the Lower Givetian of Central New York State, illustrated by Banks (1960, Plate I, Fig. 3). The scars are ring-shaped and there is evidence of vertical alignment but the spines are longer and less falcate and the vertical rows far less pronounced than in the Cape specimen. The species is best known and was first described from Central Bohemia by Krejci, and reviewed by Kräusel and Weyland (1933). Obrhel (1961) cast some doubt on the inclusion of the New York specimen in the species but Grierson and Banks (1963) reaffirmed it as *D. spinosus* var. *typica*.

There is a partial resemblance also to *Drepanophycus* sp. from Spitsbergen (Hoeg, 1942, Plate XIII, Fig. 9) and to a stem from Lower Middle Devonian of Portugal (Teixeira, 1951) while the size and vertical alignment of scars is comparable with *Archaeosigillaria vanuxemi* (cf. Grierson and Banks, 1963, Plate 35, Figs. 1 and 2). I know of no fossil plant from the southern hemisphere which is comparable with *D. schwarzi*.

Drepanophycus kowiense sp. nov.

Plate VIII, Fig. 5.

There are several fragments of stems in the Albany Museum collection which in size and general appearance are similar to those of *D. schwarzi* but both scars and spines are smaller and their arrangement is so different that it seems wiser at present to place them in seperate species. All known specimens of these stems are from the Bokkeveld Beds of the Kowie. The specific name *kowiense* is suggested and Specimen 4173c of the Albany Museum is nominated as the type.

Type specimen 4173*c*. Plate VIII, Fig. 5.

The stem fragment is 5.3 cm long and 9 mm in width with scars 1 mm or less in diameter. They are arranged spirally but the horizontal distance between adjacent scars, in alternate rows, is only 1 mm and is much less than the vertical interval between those immediately below, with the result that a pattern of horizontal rows resembling whorls 3 mm apart is the dominant feature. The spines on the margin are controlled by the vertical interval and are 6 mm apart, i.e. on every alternate horizontal row. They are far smaller at the base and shorter than those of *D. schwarzi*, averaging 1.5 mm in length, and are not normally falcate. Only one showed an upward curvature but they may have been truncated: The ring-shaped scars suggest that the spines were cylindrical at the base.

Specimen 4173*A*.

A 2.5 cm length of stem of *D. kowiense* is preserved on the back of this specimen (not figured).

Fragments of others are visible on some of the slabs of carbonaceous shale from this district.

Comparison

It is not unusual for Devonian stems of both hemispheres to exhibit a pseudo-whorled leaf scar arrangement due to a very tight spiral. *Colpodexylon deatsii* from North America (Banks 1944, Figs. 1 and 13) can be cited and several other Cape stems described in this publication exhibit portions in which a transverse line of scars simulates a whorl. The short-spined specimens described above are perhaps closest to *Drepanophycus gaspianus*, a species which includes the original *Lepidodendron gaspianum* Dawson from Gaspe Peninsula in Canada (Dawson, 1862, Plate XIV, Figs. 26-28). The species was renamed *Drepanophycus gaspianus* by Kräusel and Weyland (1948) who found it in the Lower Devonian beds of New York State. It has been refigured recently by Grierson and Banks (1963, Plate 33 of which Fig. 4 shows horizontal pseudo-whorls near the base). The leaves of *D. gaspianus* are dorsi-ventrally flattened beyond the

base which does not appear to be true of the Cape specimens in which the leaves are stiffer and rounder, while the leaf scars are ring-shaped.

Genus *PROTOLEPIDODENDRON* Krejci

Order: protolepidophytales Family: Protolepidodendraceae

The term *Protolepidondendron* has been used by different authors for various plants which were considered to be primitive lycopods. However, in 1932 Kräusel and Weyland redefined the genus to apply only to a group of herbaceous lycopods, characteristically of Lower and Middle Devonian age but which has occasionally been found also in Upper Devonian beds. They bore spirally arranged leaves which had enlarged bases and were bifurcated near the tip. The genis is of wide occurrence in the Northern Hemisphere in Bohemia, Germany, New York State, probably Quebec and China. The type species *P. scharianum* is particularly widespread and is known in great detail. See Kräusel and Weyland (1932c). The genus has been recorded from a few places in the Southern Hemisphere, viz. Brazil, Argentina, New South Wales and Queensland in beds ranging from Lower to Upper Devonian. It has not been recorded previously from Africa.

Protolepidodendron eximium Frenguelli

Plate IX, Figs. 1-4.

Specimens J.T. 3, Plate IX, Fig. 1 and J.T. 22, Plate IX, Fig. 2, were collected from the Upper Witteberg shales in the vicinity of Vondeling, approximately 360 feet below the tillite, by J. Theron and will be stored in the Geological Survey Museum in Pretoria.

In a matrix of black carbonaceous and ferruginous sandstone which exhibits no bedding planes, there are numerous small stems stained yellowish-brown by iron oxides. They ramify through the rock in all directions, even vertically, and were possibly buried in a position of growth.

The surfaces of the stems are extremely undulating and many are curved, suggesting a soft herbaceous plant (see the right hand stem on Plate IX, Fig. 1). The nature of the matrix is not conducive to perfect preservation. The stems are from 4-7 mm in width and the longest unbranched portion preserved is 6 cm One of the stems on each of the rock specimens bifurcates at angles of 25 to 35 degrees. They bore numerous spiny leaves of which the longest measured was 3.5 mm, and 1 mm broad at the base but tapered sharply to a point. Most of the spines curve outwards and upwards but some are perpendicular to the stem and quite straight while a few curve downwards. A careful search of the many spiny leaves revealed only three which appear to divide at a wide angle near the tip. One of these can be seen on the right hand side of Plate IX, Fig. 3. Spines are preserved only on the margins while the surfaces of the stem bear

the leaf cushions and scars which are sometimes most irregularly arranged but in other places exhibit a marked horizontal, or sometimes vertical alignment causing corrugation after shrinkage. The uneven surface can be emphasized by oblique lighting. Four or five rows of scars are usually visible on a stem. Some of the raised leaf cushions have a small hole which probably indicates the passage of a vascular bundle into the leafy spine, and, on a few of the stems, longitudinal central strands indicate vascular tissue.

On the right hand side of the branch on specimen J.T. 22 (Fig. 4) there is a small spherical object approximately 0.5 mm in diameter. It lies at the end of a leaf but not attached to it. This may be a detached sporangium but no other indication of fertile leaves was seen.

Comparison

Frenguelli (1954, Plates I-III) described and illustrated a number of stems, from the uppermost middle Devonian beds of Quebrada de la Charnela in the province of San Juan in Argentina, as *Protolepidodendron eximium*. They resemble the Cape stems so closely that there is little doubt of specific identity. Most of the Argentinian stems are a little narrower but some are of the same size. Frenguelli found a few bifurcating leaves but thought they were accidental.

In discussing this Argentinian plant Kräusel and Dolianiti (1957, p. 13) suggested that it should not be included in *Protolepidodendron* since the genus is founded on the bifid nature of its leaves. With this opinion Grierson and Banks (1963, p. 248) concur. I believe that since in both the Argentinian and the Cape plants a few bifid leaves have been found the retention of the classification proposed by Frenguelli is justified. It is possible that the paucity of evidence is due to the separate tips lying in different planes. This, however, raises the question of its possible inclusion in *P. scharyanum* Krejci, for Frenguelli considered that apart from bifid leaves the species were identical. With this opinion I cannot agree for the specimens of *P. eximium* from both Argentina and the Cape have leaves with very wide bases and borne at an acute angle. In this they differ considerably from the slender and pronouncedly bifid leaves of *P. scharyanum*.*

The closest Northern Hemisphere comparison known is with *Eleutherophyllum drepanophyciforme* Remy and Remy (1960, Plate I, especially Figs. 1 and 5) from the Namurian A horizon of Niederschlesien in which the general appearance of the stems is very similar, but the leaves of the Northern plant are longer and more delicate.

* Since this was written Menendez (1965b.) has reclassified Frenguelli's specimens as *Drepanophycus eximius* nov. comb. Since the S. American and S. African specimens are regarded as specifically identical, the South African specimen should also be renamed *D. eximius* (Frenguelli) Menendez, but in the light of the argument above this may not be wise until more specimens from each country are available and the argument of the existence or otherwise of bifurcating leaves can be settled.

Protolepidodendron theroni sp. nov.

Plate X, Figs. 1-5.

Two specimens, J.T. 31 and J.T. 24 which are from lower horizons than *P. eximium* differ sufficiently to be placed in a new species. They were collected by J. Theron, in whose honour the species is named, in the vicinity of the railway station of Vondeling between Prince Albert and Willowmore. J.T. 24 will be stored in the Geological Survey Museum, Pretoria but J.T. 31 has been donated to the Geological Museum of the University of Stellenbosch.

Specimen J.T. 31

The best preserved specimen is J.T. 31, Plate X, Figs. 1-4 and was recovered from the main Witteberg sandstone at approximately 1,900 feet below the tillite. It is a small stem preserved in weathered but still dense quartzite. At the base there is a bifurcating mould which branches at 40 degrees. An uncompressed limonite cast of the stem still occupies the right hand branch (Plate X, Figs. 1, 3 and 4). The stem is 1 cm wide above the point of bifurcation and bears spirally arranged, vertically elongated diamond-shaped leaf bases which measure 5 mm in length and 1 mm in breadth. The outlines of these can be seen only faintly on the top of the stem but they are clear on the left hand side where moulds of several leaves can be seen projecting into the quartzite. They were apparently 2-3 mm long and 1 mm wide. Most of them are truncated but the thick base tapers downwards into the stem at a steep angle. One of the leaves ends in a sharp point but the moulds of two others are preserved near the area where a quartz vein cuts the stem, and are clearly bifid in the last 1 mm (Plate X, Fig. 4). A transverse section of the stem shows the projecting leaf bases (Plate X, Fig. 3). Two slides numbered X4725 were cut and are in the palaeobotanical collection of the Witwatersrand University. It was hoped that even in this opaque medium it might be possible to determine the outline of the triangular xylem strand which is characteristic of the genus *Protolepidodendron* but unfortunately no structure was visible.

Specimen J.T. 24, Plate X, Fig. 5 is from the 2nd sandstone of the Bokkeveld Series in the Vondeling area. It is a negative impression in weathered quartzite of a bifurcating stem which is 2 cm wide just below the branching In certain areas the hollow moulds of diamond-shaped leaf cushions are clearly preserved, separated by a network of ridges. Near the base of the stem these are elongated to emphasise a vertical alignment. The size of stem and the size and shape of the leaf bases are comparable and the angle of bifurcation is the same as in J.T. 31, but no leaves are visible.

Discussion and Comparison

The specific differences between the specimens described above and *Protolepidodendron eximium* are obvious but it seems justifiable to place them provisionally in the same genus.

The size of the stems and angle of bifurcation as well as the size and diamond-shaped distribution of the leaf bases are similar but in particular the bifid nature of several spines of both species warrant this decision. Nevertheless, the slender nature of the evidence provided by only two specimens of *P. theroni* is

apparent and it is possible that more material and better preservation may disprove even the generic affinity suggested here.

Comparisons with other southern hemisphere species of *Protolepidodendron* and with some other genera are given below.

From Spitzbergen, Hoeg (1942) described *Protolepidodendron pulchra* of Upper Middle Devonian age. The specimens illustrated by him on Plate LIV, Figs. 1 and 2, and Plate LV, Fig. 2, are especially comparable in the size of the stems and in the size, shape and arrangement of the leaf bases with specimen *P. theroni* J.T. 24.

Walkom (1928, Plate XXIV, Figs. 1, 2 and 4) described two species of *Protolepidodendron* from Devonian rocks of Yalwal, New South Wales. The exact horizon was uncertain but was given as Upper Devonian. He named them *P. lineare*, in which the cushions are similar in size to the Cape specimens but the vertical arrangement is far more pronounced with a vertical groove separating adjacent columns, and *P. yalwalense*, in which the arrangement of cushions is comparable but they are larger and also less elongated. Well raised leaf scars were preserved which are not visible in the African stems. No projections were visible in the Australian specimens.

Kräusel and Weyland (1949) transferred these Yalwal specimens to the genus *Lepidodendropsis* but more recently Grierson and Banks (1963, p. 247) have supported Walkom's original comparison with the "Naples Tree" and regard them as possible *Lepidosigillaria whitei*. Only two other examples of southern hemisphere species of *Protolepidodendron* have been recorded. Kräusel and Dolianiti (1957) Plate 3, described *Protolepidodendron kegeli* from Lower Devonian beds of Picos, Piaui, Brazil, but this species differs from the Cape stems in having very long curved leaves.

Dawson (1881, p. 306 and Plate XIII, Figs. 15 and 16) described *Dicranophyllum australicum* from the Fanning River, Burdekin, Queensland. The rock was of Devonian age and occurred below the Star and Mount Wyatt beds. The plant has long and delicate bifurcating leaves and is therefore not comparable with the Cape specimen and Kräusel and Weyland (1933) combined it with the northern hemisphere *Protolepidodendron scharyanum* Krejci.

Genus *ARCHAEOSIGILLARIA* Kidston

Order: Protolepidophytales Family: Archaeosigillariaceae

Plate XI, Figs. 1-8.

The type species of this genus *Archaeosigillaria vanuxemi* was first described by Vanuxem in 1842 as a species of *Lepidodendron* and only received the present designation from Kidston in 1901. Recently Grierson and Banks (1963) have redescribed the Type specimen and provided a detailed history of the genus which need not therefore be repeated here.

It is a genus of mainly Middle Devonian protolepidophytes in which there is a general resemblance to the longitudinal arrangement of scars on Carbon-

iferous *Sigillaria* trunks. The scars may look round, rhombic or hexagonal according to the preservation but are always prominent and are closely packed. Their shape is due, according to Grierson and Banks (1963), to a "subepidermal net-like layer of resistant cells through which passed the leaf trace surrounded by parenchymatous cells like those of the cortex". Consequently the degree of decortication of the stem determines the shape of the scars.

In 1937 Arnold described stems from the type area under the name of *Gilboaphyton goldringiae*. They bore sharply pointed tapering thornlike leaves. The stem surface, where leaves were absent, was smooth between fairly well-spaced separate and almost round scars. In 1949 Kräusel and Weyland after examining the original specimens and related ones from the Devonian type area of New York State came to the conclusion that *Archaeosigillaria* and *Gilboaphyton* represented two aspects of the same plant and united them under the former name. They provided a number of illustrations of transitional stages between decorticated and outer surfaces. Grierson and Banks (1963, Plates 34-37) have given further proof of the relationship.

Leafless decorticated stems with small hexagonal or rhombic scars occur in South Africa and resemble some of the illustrations of *A. vanuxemi* fairly closely. They are described below. Because of minor differences and the fact that no leaves of any kind are preserved and having regard to the great distances from the type area, the specimens have been placed in a separate species for which the name given to the original South African specimen has been retained.

Archaeosigillaria caespitosa (Schwarz) nov. comb.

Plate XI, Figs. 1-8.

The only previous record of a stem of this type from South Africa was one described by Schwarz (1906, p. 357, Plate VI, Figs. 5 and 5a) as *Bothrodendron caespitosum*. I do not know whether Schwarz originally intended to call it *Bothrodendron* or *Cyclostigma*. He used the former term as a heading but on p. 358 referred to the specimen as *C. caespitosum* and all his comparisons were with specimens of *Cyclostigma*. In the text he nominated Specimen 142, Albany Museum, as the type of his species but in the description of the plates, specimen 145 is quoted. The drawings although not very clear are definitely of Specimen 142 which is therefore accepted as the type. A re-examination of this specimen suggests that it is far closer to the genus *Archaeosigillaria* than to either of the genera mentioned by Schwarz. It is redescribed and refigured below.

Holotype Specimen 142 A.M. Plate XI, Figs. 1 and 2.

This specimen was collected by Bain and is stated to have come from the Witteberg Beds of the so-called cold Bokkeveld area of the Ceres District, Western Cape. The exact horizon, however, is unknown.

It is an almost cylindrical cast of a stem 5 cm long and 1.5 cm in diameter, the centre of which is now filled with sediment. The scars are round or oval and about 1 mm in diameter or elongated longitudinally to 1.5 mm and are arranged in vertical rows in which the scars alternate in adjacent rows. They take the form of small raised areas or bosses which in a few cases are truncated and appear ring-shaped. There is no distinctive marking on any of them. On the right hand side of the stem in Plate XI, Fig. 2 an area can be seen where the projecting bosses have been flattened, leaving hexagonal scars crowded together. On Plate XI, Fig. 1 scars can be seen on the inside of the upper part of the cast showing that the stem had apparently branched at a very steep angle but the left hand branch is now missing.

Specimen J.T. 30, Plate XI, Figs. 3-4 will be kept in the museum of the Geology Department of Stellenbosch University.

This well-preserved small stem was collected by J. N. Theron (1962) of the Geological Survey from the main Witteberg Sandstone approximately 2,000 feet below the top of the Cape System in the vicinity of Vondeling in the district of Willowmore and was sent to me for determination. It is a limonite cast of a stem which bifurcates at a very acute angle like that of the type specimen. At the base only the mould is preserved. The matrix is of deeply weathered ferruginous sandstone. The left hand branch of the stem, after dividing, is 8 mm wide and exhibits 8 closely spaced rows of leaf bases which alternate in adjacent longitudinal rows. They form a closely interlocked rhombic and sometimes hexagonal pattern suggesting spiral growth. Some of the projections have a small hole and others a longitudinal slit on the top. The marks are not consistent but since similar marking can be seen on some of the American specimens (Kräusel and Weyland 1949, Fig. 6) it is possible that both are related to the emergence of a vascular bundle.

On the mould at the base of the stem the hollow scars are more hexagonal in shape and some still contain a round, ferruginous remnant of a leaf trace. No leaf or spine-like outgrowths now remain even along the margins and the specimen is almost certainly a decorticated one.

A slide, No. X4726, was cut to determine whether any broad pattern might have been preserved although there was no possibility of detailed structure in the opaque mineral replacement. None could be seen.

This specimen is regarded as being specifically identical with the Schwarz Specimen 142 A.M. from Ceres.

A few other stems from the Albany Collection have been included provisionally in the genus. They exhibit rhombic scars and far less relief but may represent other surfaces on the same plant.

Specimen 10739 S.A.M. (824 Haughton) Plate XI, Fig. 8 is a fragment of a similar stem. It was figured by Seward (1932, Plate XXIII, Fig. 5) as *Planta*

incertae sedis but he compared it with *Archaeosigillaria vanuxemi*. The specimen came from the Witteberg shales of Nourse Poort near Steytlerville.

Specimens 4172*b and* 4172*c*, A.M. Plate XI, Figs. 5 and 6.

Figs. 5 and 6 are counterparts on each of which two surfaces of a small stem are preserved, viz. a convex and possibly decorticated surface of the cast and a concave inner surface. I do not think that the latter represents the mould of an outer surface.

The matrix is of dark carbonaceous micaceous sandstone and the cast is a lighter coloured, bleached clay. The size of stem and of the rhombic leaf bases are similar to J.T. 31 but the latter do not project to the same extent.

The locality of the specimens is unknown.

Specimen 4140 *A.M.*, Plate XI, Fig. 7

In micaceous sandstone there is a 9 cm long and 9 mm wide hollow mould of a stem which is possibly of the same species. The small rhombic leaf bases are clear but no further detail is apparent.

All the specimens described above are of the decorticated *Archaeosigillaria* type. Stems with more openly spaced small protruberances or with thorny leaves which might be compared with the outer surface of the *Gilboaphyton* type are fairly common but since no transitional forms have been found they have not been included here but are described under headings of *Drepanophycus* and *Haplostigma*.

Comparison and Age

In the Northern Hemisphere the likeness of these Cape stems to *Archaeosigillaria vanuxemi* has been mentioned already. The hexagonal and rounded scars of specimens 142 and J.T. 31 can be compared with the type specimen as illustrated by Dawson (1862, Plante XII, Fig. 7) and by Grierson and Banks (1963, Plate 34, Figs. 1 and 3 and Plate 36, Figs. 3 and 5). The rhombic scars of Specimens 4140 and 4172 are more like those shown by Banks 1960, Plate I, Fig. 2) and by Grierson and Banks (1963, Plate 35, Fig. 37) but they may also be compared in size and shape with a small specimen illustrated by Dawson as *Lepidodendron gaspianum* (1862, Plate XVII, Fig. 58) and others from Bear Island illustrated by Heer (1872, Plate LIV, Figs. 1 and 1b) as *Lepidodendron veltheimianum*.

Southern Hemisphere records of the genus are very limited but offer interesting comparisons. There is a very close resemblance which may amount to specific identity between type specimen 142 and J.T. 30 and *Cyclostigma con-*

fertum (Frenguelli 1954, Plate 4, Figs. 1 and 2) from the Middle Devonian beds of San Juan, Argentina, Both Kräusel and Dolianiti (1957, p. 14) and Banks (1960, p. 68 and 72) have expressed the belief that the San Juan plant is really *Archaeosigillaria* and that there is a strong resemblance to *A. vanuxemi* and Grierson and Banks (1963, p. 246) in a table of distribution doubtfully assigned the plant to this species.* In 1951 Frenguelli (Plate I, Fig. 11) illustrated a fragment of a stem with small rhombic markings. It was from the Middle Devonian beds of San Juan and he called it *Asteroxylon* sp. but it may well be *Archaeosigillaria*.

Specimens 4172 and 4140 can best be compared with *Archaeosigillaria picosensis* Kräusel and Dolianiti (1957, Plate IV, Figs. 1 and ?). This specimen was from the Lower Devonian of Picos in the State of Piaui, Bolivia. It is a small piece of stem broken at a point just below branching which is indicative of a steep angle. The scars in the upper half are almost oval but those in the lower half are distinctly rhombic and are elongated transversely.

Grierson and Banks (1963, p. 245-246) have expressed doubt about the inclusion of this species in the genus but there are some transitional features between *A. picosensis* and Frenguelli's specimen and those from the Cape. Kräusel and Dolianiti had suggested in 1957, the uniting of the two South American specimens but since the hollow mould of J.T. 30 also exhibits similar features, it is believed that all the specimens could be included in one species. If the San Juan and the South African plants should prove to be identical, and for this more specimens from each area are desirable, Schwarz' specific name would have priority.

A possible comparison may be made with an Australian specimen from Devonian rocks of Yalwal, New South Wales (exact horizon unknown) (Walkom, 1928, Plate XXIV, Fig. 3) which was described as ? *Lepidodendron clarkei*. Walkom compared his specimen with the rhombic scars of *L. australe*, but found that those of *L. clarkei* were considerably smaller. Most of them are more hexagonal than rhombic and although they are a little larger than those of the Cape specimens and the area of the stem illustrated is much larger than of any yet found in Africa, it agrees very well with the other southern hemisphere stems.

Corsin (1934) described *A. vanuxemi* of Dinantian Age from French African equatorial regions but I have not seen this paper.

According to Banks (1960) *Archaeosigillaria* is known to range from the Lower Devonian to the Upper Carboniferous. This is, however, misleading because the only Lower Devonian specimen is from Brazil (Kräusel and Dolianiti, 1957) and the only Upper Carboniferous one from Saxony, Germany. The vast majority of known specimens are from Middle Devonian while from the Upper Devonian the type specimen is the only one known. There are several occurrences in the Lower Carboniferous of Europe.

* Since this was written Menendez (1965a.) has re-described Frenguelli's species as *Archaeosigillaria conferta*. He was apparently unaware of Schwarz' type specimen described in 1906.

Genus *LEPTOPHLOEUM* Dawson

Order: Protolepidophytales Family: Leptophloeacea

N. Hemisphere: *Leptophloeum rhombicum* Dawson, 1862

S. Hemisphere:
- *Lepidodendron nothum* Carruthers 1872 (non Unger)
- *Lepidodendron australe* McCoy 1874
- *Lepidodendron nothum* | Feistmantel 1890
- *Lepidodendron australe* |
- *Lepidodendron albanense* Schwarz 1906
- *Leptophloeum australe* (McCoy) Walton 1926

General

The genus *Leptophloeum* is believed not to extend beyond the upper part of the Devonian and it is therefore of considerable value as a zone fossil. It is widely distributed in rocks of this age in both hemispheres and is essentially a type of lycopod stem in which a very pronounced pattern of regular rhombic and slightly convex or raised leaf cushions are separated from one another by comparatively wide margins. In many of the stems, but by no means in all, a small circular scar of the leaf trace occurs near the centre of the cushion or, more often, in the upper corner. In addition fertile specimens have a zone of closely spaced T-shaped sporophylls (see Walton, 1926) but these are seldom preserved.

Leptophloeum rhombicum Dawson

This name was applied first by Dawson to stems from the Upper Devonian of Perry, Maine, U.S.A. and his illustrations have often been reproduced (Dawson, 1862, Plate XII, Fig. 6 and Plate XVII, Fig. 52, also Dawson, 1863, Plate XVIII, Fig. 19). His reconstruction of the plant in 1863 which showed a terminal tuft of long, linear, single-veined leaves is no longer accepted but the nature of the stems is well supported.

Leptophloeum australe (McCoy) Walton, its history, occurrence and age in Australia

The naming of southern hemisphere representatives of the genus *Leptophloeum* has suffered considerable confusion. The first record was by Carruthers (1872) who described stems from Queensland, Australia, as *Lepidodendron nothum* Unger. He believed that these were specifically identical with Dawson's *Leptophloeum rhombicum* but also with Unger's specimens from Thuringia (1856) which had priority of naming. In this he was mistaken because the Thuringia specimens are now known to be unrelated, but the error was perpetuated for many years. Two years later McCoy (1874) described similar stems from Victoria, Australia, as *Lepidodendron australe*. Later Feistmantel reproduced McCoy's drawings of *L. australe* which were at that time believed to be of Lower

Carboniferous age, and illustrated also very similar specimens from New South Wales and from Queensland (Feistmantel, 1890, Plate I, Figs. 1-4, and Plate II, Figs. 1-6) for which he retained the name *L. nothum* because they were of Upper Devonian age. Modern stratigraphers have shown that the Australian plants from all these states are of Upper Devonian age so that separation on the basis of age is not valid. In addition, a number of authors in this century have agreed with Carruthers that the Australian plants were generically and possibly specifically identical with Dawson's *Leptophloeum rhombicum*. In particular, it was Walton (1926) who in redescribing the original Australian specimens advocated that all the Australian specimens in question should be combined with Dawson's *Leptophloeum* but that the small doubt of specific identification should be accepted because of the great distance which separated them. The Australian specimens should henceforth be known as *Leptophloeum australe*. Although a few other authors and notably Sze (1952) who found similar specimens in the Upper Devonian of China have concurred with Walton's views, the name *Lepidodendron australe* had become entrenched in Australian literature and is still used by a number of geologists but must be regarded as synonymous with *Leptophloeum australe*.

Through the courtesy of the Director of the Bureau of Mineral Resources, Canberra, I have received within the last few years a number of current but unpublished reports by Mrs. Mary White of plant fossils from many parts of Australia. These included photographs of *L. australe* in different stages of preservation which confirmed my belief that the Cape stems can be included in the same species.

In a recent composite description of the Devonian of Queensland, Bush et al (1960) described the thick sediments which accumulated in the Tasman geosyncline. They occur now in a number of basins in which the ages of plant horizons and of known marine invertebrate horizons can be compared. *L. australe* occurs in the Yarrol Basin, the Hodgkinson Beds, the Gilberton Formation and the Lower Burdekin Valley where it is found in both the Dotswood Beds and in the overlying Star Beds in association with *Cyclostigma* cf *kiltorkense*. It has been found also in the extreme north of the Drummond basin.

In New South Wales a recent revision of the Devonian sediments has been undertaken by Crook (1961). In the Parry Mudstone (formerly the Barraba Mudstone) Crook reported that *L. australe* is found throughout its thickness of 1150′ but especially at the base. Near the top, it is associated with an Upper Devonian plant known otherwise only from New York. In the overlying Kiah Limestone a very high Devonian goniatite is found. Crook places the Upper Devonian to Carboniferous, or Tournaisian to Visean boundary, in the Kiah Limestone and considers that *L. australe* is completely confined to Upper Devonian beds. He states that it has never been found associated with Carboniferous marine fossils in Australia. In addition, White (1957/53) has described the plant from Laurel Downs in Western Australia.

Leptophloeum australe in Africa

Plate XII, Figs. 1-6

General

In South Africa, apart from indecisive early records, such as Jones (1872) who mentioned that *Lepidodendron* had been found at Riversdale and also 50 miles to the south in the Swellendam district, by Dr. Atherstone, Thomas Bain and others, and Feistmantel (1889) who recorded a number of separate lycopods from Cape System rocks but did not describe them, the first description of the plant was by Schwarz (1906, Pl. VI, fig. 1). Under the name of *Lepidodendron albanense*, a specimen from the Witteberg Beds at Howisons Poort was described and figured. Schwarz compared this and other specimens with the Australian species and found a close likeness but was uncertain that they were identical since the Cape specimens usually lacked the characteristic vascular scar. Other authors e.g. Rogers, Seward (1907) have drawn attention also to the similarity. There are many references to such stems in the Witteberg Series implying that they are comparatively common but only a few specimens have been preserved in Museum collection. The best of these are described below. The lack of detail in most of them can be ascribed to the fact that all were preserved in coarse quartzites of the Witteberg Series so that they retain no organic residue and only broad features are evident, but one of the specimens, No. 4088 A.M., shows the small vascular scars quite clearly and I believe that there is no longer any justification for keeping them separate. The Cape specimens are therefore included as *Leptophloeum australe*.

Description of specimens

Specimen 150 *A.M.* (Schwarz 1906, Pl. VI. fig. 1) Pl. XII, fig. 1

This specimen from a quarry in Witteberg Series, south of Grahamstown, was formerly the type of *Lepidodendron albanense* (Schwarz 1906). It is the impression of a large stem on which the rhombic scars can be seen to decrease in transverse diameter from 15 mm to 8 mm within the preserved length of stem. No leaf trace scar is visible but Carruthers (1872) had pointed out that they were rarely preserved on large stems.

(*Specimen* 152 *A.M.* not figured here but quoted by Schwarz as a decorticated form of *L. albanense* does not appear to belong to the species.) Schwarz (1872) had mentioned other specimens in which there is "a slight protuberance near the upper corner of some of the leaf bases" and another with "larger rounded protuberances fixed centrally in the scar area".

Specimen 4088 *A.M.* Pl. XII, fig. 2

This hollow mould of a stem is also from the Witteberg Series and from Howison's Poort but is preserved in dense, recrystallised quartzite. On at least

six of the rhombic scars a small round protuberance is evident near the apex of the rhomb. It provides confirmation of the specific determination of *L. australe*.

In the Grahamstown Area Rennie and Mountain (1942) have stated that the rhombic scarred stems appear to be confined to the Witteberg quartzites.

Specimen 11403 *S.A.M.* Pl. XII figs. 3-6

This is the most interesting of the specimens and is from the Western Province. It is a cast of *L. australe* from Touws River 2 miles east of Nourse Poort, near the base of the Witteberg in which the external pattern of raised rhombic cushions is preserved in yellowish limonite. There are no signs of vascular scars on the outside but a number of thin limonite strands project into the sandstone filling of the cast. Each of these may be regarded as a vascular strand which terminated in a small hook. The longest of them is 2.5 cm, and since the radius of the stem is 2.7 cm, the pith must have been very small, as in most lycopods. Pl. XII, figs. 5 and 6 illustrate the two ends of the stem. Several of the strands can be traced to the upper corners of the rhombic scars but others have been misplaced for this resistant tissue obviously survived after the decay of the rest of the internal structure of the stem.

On Pl. XII, fig. 4, photographed perpendicular to the stem, the wide double-edged margins between the cushions can be seen clearly on the lower right hand side. These are common in a number of Australian specimens and provide further confirmation of identity.

Comparison with similar stems in other areas

In addition to the type area of Australia, *L. australe* has been recorded from several parts of S. America.

Frenguelli (1952) recorded a conformable succession of Lower Gondwana Beds on the eastern slopes of the Pre-Cordillera of San Juan, Argentina, in which *L. australe* has been found in the Cortadera Beds. These beds are overlain by the Tupe Beds in which abundant *Rhacopteris ovata* occurs. The latter fossil is essentially of Lower Carboniferous age and an Upper Devonian age can therefore be assigned to the Cortadera. No figure was included in this paper. The only illustration I have been able to find of a South American *Leptophloeum* was included in Frenguelli (1946) but was very poor and not altogether convincing.

From a Devonian horizon in Bolivia, I have been sent by Dr. Guy A. Chamot a number of small specimens which I believe to be *L. australe*. They occur in beds which lie conformably above a lower Devonian marine horizon with invertebrate fossils related to those of the Lower Bokkeveld.

From the northern hemisphere, apart from the specimens of *Leptophloeum* from New York State already discussed, a number of fossils with similar characteristics have been recorded from Devonian rocks of Europe and from China where Sze in a series of papers (1952-1956) on Devonian plant fossils in China has described *L. rhombicum*—from Upper Devonian beds in a number of provinces. Two groups of rhombic scarred Devonian stems, originally believed to be

Leptophloeum have now been separated into other genera and special mention must be made of them. The first group, from the Devonian of Spitzbergen was described by Nathorst (1894) and later by Hoeg (1942b, p. 128) who summed up the evidence and decided against including the Spitzbergen specimens in the genus *Leptophloeum* mainly on the grounds that the small fertile peltate leaves described by Dawson for *L. rhombicum* and by Carruthers and Walton for *L. australe* had not been found in Spitzbergen. He named them *Bergeria mimerensis*. His figures (Hoeg 1942, Pl. L figs. 1-3) can be compared in size with *Leptophloeum* but the strong vertical keel present on some of the rhombic scars has not been seen on any South African specimen. Recently Schweitzer (1965) has been able to confirm Hoeg's decision to keep *Bergeria* from Spitzbergen as a separate genus.

The second comparison is with Devonian stems from Russia which were originally described by Krystofovitch (1927) from the Middle Devonian of the Minusinsk Region of Central Siberia as *Leptophloeum sibiricum* but later transferred to the genus *Blaseria* by Zalessky (1934).

In almost every publication on Devonian floras from the earliest records, an association of rhombic scarred stems with round scarred stems has been reported. Some authors believed that they represented different aspects of the same plant. This will be discussed in more detail at the end of the next section in which the round scarred stems from the Cape System are described.

The controversial **Genus** *HAPLOSTIGMA* Seward

The confusion in early descriptions

Stems with spirally arranged round or oval scars are undoubtedly the most common Devonian plant fossils found in the Cape System. They occur in rocks of both Bokkeveld and Witteberg Series although the preservation differs in these respectively predominantly argillaceous and arenaceous formations. The history of their description has been one of considerable confusion and they have been regarded by various authors as decorticated or "knorria" forms of lycopod stems and alternatively as outer surfaces of psilophytes with round projections. Early authors compared them to both *Bothrodendron kiltorkense* Haughton and to *Cyclostigma australe* Feistmantel. The chief reason for confusion can be attributed to the fact that on three different occasions two separate genera were united under one name.

In South Africa, stems described here as *Palaeostigma* and *Drepanophycus* were formerly included in *Haplostigma* and in South America *Palaeostigma* and *Spongiophyton* have been separated from it by Kräusel. The pruning in both countries has left a plant which is constant in many features and probably a true genus but in the upper part of the Cape System some doubtful specimens preserved in quartzite are still included, and more collecting is necessary before the upper stratigraphical limits of the plant can be defined and the diagnosis emended to describe a single true genus.

In an attempt to produce some order out of the present chaos it has been necessary to photograph a number of early specimens, of which previously only drawings have been available, together with others discovered more recently and to undertake a general review of earlier literature on the South African examples in order to compare them with similar stems in other continents. The specimens named below represent the stages towards the creation of a separate genus by Seward. They will be described and discussed chronologically and summarised at the end of this section.

Haplostigma irregulare (Schwarz) Seward

Plates XIII-XVI

Bothrodendron leslii (Seward 1903 Pl. XI fig. 4)
Lepidodendroid stem (Seward 1903 Text fig. 8, p. 89)
Bothrodendron irregulare (Schwarz 1906, Pl. VI, fig. 4)
Bothrodendron irregulare (Seward 1909 Pl. XXVIII, figs. 1-4)
Haplostigma irregulare (Seward 1932 Pl. XXIII, figs. 2, 5, 6 and 7 —Pl. XXIV, figs. 11 and 13)

Description of Specimens—Old and New

Paratype of *Haplostigma irregulare*—Spec. B, S.A. Mus. Pl. XIII fig. 2
Bothrodendron leslii (Seward 1903, Pl. XI, fig. 4)
Paratype of *Bothrodendron irregulare* (Schwarz 1906, p. 356)

The earliest illustration of this type of stem from the Cape System was a drawing published by Seward (1903, Pl. XI, fig. 4) of a stem which he called *Bothrodendron leslii* under the mistaken impression that it was part of a collection of younger stems from Vereeniging to which it bore a superficial resemblance and which were described in the same paper. The latter are now known as *Cyclodendron leslii* (Seward) Kräusel and are unrelated but the scars of Spec. B. were smaller and it was the only bifurcating stem in the collection. Even at that time Seward drew attention to this feature and stated that Specimen B could be matched almost exactly with *Bothrodendron kiltorkense* from Bear Island (Nathorst 1902, Plate XI, figs. 1, 2, 5, 6, 10 and 11).

The mistaken identity was noted in a foreword to volume 4 of the Annals of the S.A. Museum (1903) and also by Schwarz (1906) who had collected the original specimen from Bokkeveld Shales near Triangle Station (now Matroosberg) in the Hex River Pass, Worcester Division, of the Western Cape. It can be seen in the S.A. Museum where I found a missing portion in the collection and have glued it into place. The present illustration Pl. XIII, fig. 2, is therefore larger on the left hand side than the drawing in Seward (1903). Signs of vascular strands are apparent in the left hand branch and a form of horizontal ribbing is developing at the top of the right hand branch.

This specimen was later nominated by Schwarz (1906) as a paratype of *Bothrodendron irregulare*.

Paratype of *H. irregulare* Spec. V. 236 Nat. Hist. Mus. Lond. Pl. XIII, fig. 4

This specimen came from the Atherstone quarry, Kowie (Port Alfred) from beds now regarded as Bokkeveld Series (Rennie and Mountain 1942). It was figured by Seward (1903, Text fig. 8, p. 89) as a "lepidodendroid stem". I am indebted to Dr. Chaloner of Imperial College for the photograph of this specimen reproduced on Pl. XIII, fig. 4, particularly since the stem is the best preserved of any yet found.

There are what Seward called "curved linear appendages, presumably leaves", attached along each margin almost at right angles to the stem. The preservation suggests that at the base they were inclined upwards and were thick, strong and rigid but tapered to a thin flexible apex. The stem, which is a flattened cast shows only a spiral arrangement of rounded scars and no suggestion of longitudinal or transverse ridges. Seward in a later publication (1909, p. 483) suggested that it might be regarded as specifically identical with the type specimen of *Bothrodendron irregulare* (Schwarz) which is described below. Although the stem is 2.5 cm wide and therefore considerably broader than the type, the spacing and arrangement of the scars is similar.

Type Specimen H. irregulare (Schwarz) Seward. Specimen 165 Albany Museum Pl. XIII, figs. 1 and 3. *Bothrodendron irregulare* Schwarz (1906, p. 3560357, Pl. VI, fig. 4)

Specimen 165 Albany Museum was nominated by Schwarz (1906) as the type of *Bothrodendron irregulare* and later (Seward 1932) became the type of *Haplostigma irregulare*. The illustrations on Pl. XIII figs. 1 and 3 are the first published photographs of the slab of graphitic phyllite from Bokkeveld beds on the farm Sweet Waters, near Bathurst. The specimen measures 18 cm x 10 cm and is covered with a mass of small stems, two of which must have been selected by Schwarz for his drawing which, however, did not express all the features adequately, and so may have been responsible for some of the later confusion. He stated that the species was common in the quartzites of the Witteberg Series at Port Alfred, i.e. in beds now accepted as Bokkeveld Series.

The stems are all approximately 1 cm in diameter and are covered with small spherical scars which are either convex or concave according to positive or negative preservation or to some degree of decortication. They are normally equidistant both transversely and longitudinally and exhibit a spiral arrangement but through later distortion or from drying of the stems, the scars may be arranged in either longitudinal or transverse rows and are sometimes contracted into ridges. The latter can be emphasized by the direction of the oblique lighting. The curvature of the stems shows that they were pliable and the wrinkling of some of the cuticular surfaces suggests that they were soft herbaceous plants.

No leaflike projections or spines are preserved on any of the stems but a circular hole on each raised scar suggests that a round spine has been truncated. Pl. XIII fig. 3 is an enlargement of the lower part of fig. 1 and shows a stem bifurcating at an acute angle.

Schwarz was so impressed with the similarity of these stems to *Cyclostigma australe* Feistmantel that he stated he would have included them in the Australian species had not Seward already placed Spec. B in the genus *Bothrodendron*. He thus perpetuated Seward's original error. His choice of *irregulare* as a specific name was scarcely suitable because a regular arrangement of scars is far more common.

It is a little difficult to understand why every stem on this type specimen No. 165 is so uniform in size. Can it be regarded as an entanglement of young plants all at the same stage of development or does it represent a smaller species of the same genus? At present not enough is known to justify the separation of the two forms.

Haplostigma irregulare from Port Alfred.

Spec. 2903-2905 S.A. Museum, Pl. XIV, figs. 1-5

Bothrodendron irregulare (Seward 1909 Pl. XXVIII figs. 184)

These specimens in pinkish grey talcose phyllite are from Bokkeveld Beds which outcrop in the grounds of the Mental Hospital at Port Alfred. Some of them were sent to Seward who described and figured a few (Seward 1909, Pl. XXVIII figs. 1, 2, 3 and 4) and considered that all could be included in *Bothrodendron irregulare* Schwarz (now *Haplostigma*). The stems present a number of different aspects of preservation and several show bifurcation but there is no doubt of their inclusion in Seward's later genus *Haplostigma* with the exception of the stem illustrated by Seward as fig. 3 which in the present paper is described as *Drepanophycus schwarzi*. The illustrations given here supplement those of Seward (1909) or emphasize some new aspect.

Specimen 2903 is illustrated on Pl. XIV fig. 1. Two of the stems have a flat surface with concave scars and represent negative impressions, but the central stem, the left-hand one in the figure, is part of a compressed cast and exhibits a columnar thickening which tapers downwards below each scar. This suggests the presence of strong fibrous, and probably vascular, tissue leading upwards into each projection.

The scars vary in form from prominent round swellings with a truncated top, giving the impression of two concentric circles, to circular depressions or crescent-shaped scars in which the deep groove marks the upper side of former projections.

Specimen 2909 *A*.1, Pl. XIV, fig. 2 includes a stem on which the marginal protuberances, which were so well shown on Spec. V236, Pl. XIII fig. 4, are

preserved. This specimen is of particular interest because it is partly decorticated and in the lower half of the stem a central vascular strand 2 mm wide, can be seen, while in the upper part similar strands of tissue curve upwards and outwards from the centre and run along the lower side of each projecting spine.

The lighting used for the photograph emphasizes the lateral fibres but unfortunately the median one at the base is scarcely visible. If, as seems probable, this is vascular tissue, and not merely strengthening fibre, the appendages can be regarded as primitive leaves and not mere outgrowths of surface tissue. It would mean that the plants were lycopods rather than psilophytes but without better preservation no confirmation is possible.

Specimen 2905, Pl. XIV fig. 3. The preservation of this stem is intermediate between that on Plate XIII fig. 4 and Pl. XIV fig. 2. No vascular strands are visible and the outgrowths, three of which can be seen clearly on the upper margin with a row of them faintly visible on the lower margin, are rather short and falcate, resembling spines rather than the long round outgrowths to be seen in other figures. They may have dried and the thin terminal portions withered. The outer surface of the stem, with raised scars, is preserved on the left and right-hand sides leaving a decorticated surface with sunken scars in the middle portion.

On *specimen* 2909 A_2 Pl. XIV fig. 4 there are portions of a large and a narrow stem. On both the scars are crescent-shaped, and I believe represent somewhat deeply decorticated surfaces. The smaller stem is 11 mm wide and the arrangement of scars is particularly regular giving rise to a rhombic pattern which can be emphasized by oblique lighting. A few of the scars at the top of the stem are round. Although this unusual aspect is the only one preserved, Seward believed it probable that the stem could be included in the same species but the small outgrowths on the left hand side make this somewhat doubtful.

Pl. XIV fig. 5 is another stem on Spec. 2905 showing an outer and inner surface and the development of ribbing.

Specimen 3750 *Albany Museum* Pl. XIV fig. 6

A completely different aspect of *Haplostigma* is illustrated on Spec. 3750, A.M., Pl. XIV, fig. 6. A piece of dark carbonised cuticle is preserved on micaceous sandstone. Faint cell structure is visible and the position of the leaf spines is indicated by round holes. The preservation implies a thick tough cuticle and indicates that most of the stems with projecting lumps represent outer surfaces with truncated spines and are not decorticated or "knorris" types of preservation as both Schwarz and Seward at various times suggested. Unfortunately the source locality of this specimen is uncertain.

Haplostigma irregulare from Schietkraal nr. Steytlerville

Specs. 10742-10746 S.A. Museum Pl. XIV, figs. 7 and 8

A group of specimens preserved in a hard fine-grained ferruginous quartzite was collected by Haughton in the course of mapping in the Steytlerville district (Haughton 1935) and sent to Seward who described them in 1932 (Pl. XXIII and XXIV).

Only two of the specimens are re-illustrated here in order to give a complete representation of S.A. specimens from different areas and preserved in different kinds of rock.

Most of the specimens were collected on the farm Schietkraal in the Steytlerville district about 80 miles northwest of Port Elizabeth and from the upper part of the Bokkeveld Series. The farm lies just off the west margin of Geol. Sheet 150 (Sundays River) and Haughton (1935) stated that the same plant fossils could be found also in the Witteberg Series in that area. One specimen (Seward 1932, Pl. XXIII, fig. 7) was from the Uitenhage district, east of Bezuidenhouts River and from the second Bokkeveld shales "well down in the marine beds". It has not been refigured here but represents the lowest horizon in which the plant has been found.

The Schietkraal specimens are preserved in a fine-grained, highly ferruginous bed which is dark grey when fresh but weathers to a hard yellowish brown surface on which the casts and moulds of stems stand out in marked relief. All the specimens are preserved in the South African Museum, Cape Town. For convenience both the present museum numbers and those of Haughton quoted by Seward have been given for the Schietkraal specimens described below.

Specimen 10742, *S.A. Museum* (Haughton 833). On Pl. XIV, fig. 7 there are two stems of different sizes and different degrees of decortication. A portion of this specimen was illustrated by Seward (1932, Pl. XXIII, fig. 6). The larger stem exhibits ribbing, truncated leaf spines and a surface texture which may well represent the outer cuticular surface. The smaller stem displays an inner surface, on the left hand side of which the scars are distinct and crescentic while on the right hand side a raised rhombic pattern can be seen separating the depressions. It may form a link with the smaller stem shown in fig. 4.

Specimen 10746 *S.A. Museum* (Haughton 838) Pl. XIV fig. 8, is another stem figured previously by Seward (1932 Pl. XXIV, fig. 11).

It is a stem with very small flat scars and a pronounced transverse ribbing. Seward considered that the scars were of the same size as those shown in the larger stem of the present Pl. XIV fig. 7 but he also compared the surface with that of the stem which is described here as *Palaeostigma sewardi* and illustrated on Pl. IV, fig. 1. I believe that the latter comparison is more reliable. Seward regarded all the specimens from Schietkraal, Steytlerville, including that of

Palaeostigma as specifically identical with those from Port Alfred which he had previously (1909) described as *Bothrodendron irregulare* Schwarz. He decided, however, to erect a new genus based on the combined specimens which he renamed *Haplostigma irregulare* retaining Schwarz' specimen 165 as the type. It is doubtful, however, whether Seward ever had access to this type specimen. His diagnosis was naturally influenced by the inclusion of the *Palaeostigma* (Seward 1932, Pl. XXIII, figs. 1, 3 and 4 and Pl. XXIV, figs. 8, 9 and 12) on which he had based his description of the cuticle and also probably his emphasis on the classification of *Haplostigma* which he regarded as intermediate between psilopsida and lycopsida. He described it as a simple stem in which the scars of the appendages showed no scars of leaf traces, parichnos strands or ligules. (At that time it was not recognised that southern hemisphere Palaeozoic lycopods lacked parichnos and ligular scars.) It thus served to separate the plants from *Cyclostigma* and *Bothrodendron*, the northern genera with which they had so often been compared. There were furthermore no long foliage leaves like those of *Cyclostigma*. The fructification of *Haplostigma* is still unknown.

Round scarred stems preserved in sandstone Pl. XV

All the previous specimens were preserved in fine-grained sediments and all were from the Bokkeveld Series and therefore probably of Middle Devonian Age. There are, however, many stems preserved in sandstone and in some areas in dense quartzite, according to the degree of folding, in which only the main features survive. Many of these are comparable in size and arrangement with *Haplostigma* stems. Most of the quartzite and sandstone impressions are in rocks of the Witteberg Series and therefore a little younger but some are from Bokkeveld Sandstones. They are included here in the belief that some of them represent the same plant and because the absence of detail does not justify their separation. Others are included because this is the most convenient section for indeterminable lycopods. No organic matter survives in this matrix. The fossils are usually in the form of hollow moulds or sandstone casts and often not greatly compressed. The stems must therefore have been sufficiently rigid to withstand pressure until the rock had hardened around them. They include a few of the Albany Museum specimens to which Schwarz (1906) gave a number of different generic and specific names but which Seward (1909) on the evidence available considered should all be lumped together in *Bothrodendron*, and also a number of stems collected since 1932. They have been selected so as to represent as wide a range as possible.

*Specimen T.X.*18, Pl. XV fig. 1 was collected by J. N. Theron of the Geological Survey from Witteberg quartzite on the farm Elandsvlei in the De Doorns district. Two stems 1.4 cm in diameter are preserved as moulds in dense quartzite but only one has been figured. In this the original projecting spines have

left deep circular depressions while at the base of the stem mould a portion of a quartzite cast is preserved, which in turn has a cylindrical hollow centre 2-3 mm in diameter which probably represents the diameter of the more resistant vascular tissue. This is the commonest type of fossil and may well represent *Haplostigma irregulare*.

Specimen 161 *A. Museum*. Pl. XV fig. 2

This hollow mould from the quartzites of Grootriver Heights in the Steytlerville district was described by Schwarz (1906, pl. VI, fig. 2) as *Didymophyllum expansum* but is now included in *Haplostigma*. Some of the cavities contain casts of the spiny projections.

Specimen 143, *A. Mus*. Pl. XV fig. 3

This was described by Schwarz (1906, Pl. VI, fig. 2) as the holotype of *Lepidodendron kowiense*. It was collected in the "Cold Bokkeveld" of the Ceres District but the exact horizon, although probably Witteberg, is unknown. Schwarz believed it to be specifically identical with the British Museum stem spec. B 260, described earlier. The fossil is a sandstone cast with evenly distributed protuberances each of which is truncated to leave a circular hole. The arrangement of the scars shows both horizontal and vertical alignment giving a faint checker board effect which was not visible on any of the specimens described previously.

Schwarz thought that the regular arrangement justified separation from *Bothrodendron irregulare* but it has been pointed out that the regular arrangement in the latter is more common and would be more likely to survive on casts than on flattened cylinders of the outer tissue.

Both Seward (1932) and Rennie and Mountain (1942) considered that the *L. Kowiense* type of stem should probably be combined with *Haplostigma irregulare*.

Indeterminable Lycopods Pl. XVI

Large cast of Lycopod stem. Pl. XVI, fig. 1 (scale in inches)

This is the largest known lycopod stem to have been found in the Cape System. It was recovered by J. N. Theron from the main Witteberg quartzite and is now in the museum of the Geology Department of Stellenbosch University where I have examined it. The markings are regular but unfortunately too indecisive for even generic determination. I am indebted to Mr. Theron for the photograph produced here.

Specimen J.T. 26, Pl. XVI fig. 2 was collected in 1960 by J. N. Theron from the 2nd Bokkeveld sandstone ? near Vondeling. It shows the typical preservation of these stems in the form of a flattened sandstone cast and both sides of the mould.

Specimen J.T. 25 Pl, XVI fig. 1 is from the 2nd Bokkeveld Sandstone near Vondeling. The hollow mould of a narrow branched stem exhibits pits and faint ribbing but details are obscure.

Specimen Pl, XVI, figs 4 and 5

This specimen was collected by Dr. A. J. Bruwer from the highly folded Witteberg quartzite on his farm Mijmering in the Ladismith District of the Cape, and presented to the Witwatersrand University B.P.I. (Pal.) Collection.

The narrow tapering mould exhibits clean cut oval scars (the strong lighting makes some appear crescentic). These can be compared with Pl. XV fig. 5 and to a certain extent, with Pl. XIII fig. 1, but their size and relief differ from those of the Port Alfred and Steytlerville *Haplostigma*.

Comparison of *HAPLOSTIGMA* with fossil plants from other areas in the Southern Hemisphere

Throughout the Southern Hemisphere stems of *Haplostigma* type constitute, in a number of cases, the only or the most important Devonian records. Some of them are listed below.

From the Falkland Islands where the Upper Palaeozoic succession of the Lafonian System bears so close a relationship to the rocks of the Cape and Karroo Systems, a number of Devonian stems has been found. Halle (1912, Pl. 6 figs. 1-3) illustrated three, among which his figure 3, where both cast and mould are preserved, appear to be identical with those from the Cape. Halle called them "lepidendroid fragments" and was apparently unaware of similar stems in Africa.

Seward and Walton (1923, Pl. XIX, figs. 1 and 2) illustrated two more stems from the same area and in a lengthy discussion concluded that they were more closely related to *Bothrodendron irregulare* Schwarz from the Cape than to any other known plant.

From South America a few closely related, if not identical stems have been recorded. White (1908) figured a specimen from Brazil which Seward (1909 and 1932) considered to be identical with those from South Africa. Darrah (1941 Pl. I, fig. 3) illustrated a closely comparable specimen from Parana. I cannot understand why he separated the fossils specifically, for his illustrations closely resemble the Cape specimens in size, variation in size, ribbing and absence of ribbing and appear to be identical. They were of Lower Devonian age.

Barbosa (1949) described stems from the Lower Devonian beds at Ponta Grossa, Parana, which he named *Haplostigma lenticularis*. Kräusel (1960) after examining these from several localities concluded that most of them were unrelated and transferred them to a new genus *Spongiophyton* but he renamed two fragments *Haplostigma irregularis* (Kräusel 1960, Pl. XI figs. 87 and 88) which are closely comparable with those from the Cape.

Frenguelli (1952a) described *Haplostigma furquei* from the Pre-Cordillera of San Juan, Argentina. His illustrations appear to be specifically identical with the Bokkeveld stems from the Cape.

From Antarctica a hollow mould of a stem preserved in dense quartzite has been described as *Haplostigma irregulare* (Plumstead 1962, Pl. I, figs. 1 and 2). It is closely comparable, both as regards the preservation of the fossil plant and the rock matrix with Witteberg specimens like that illustrated on Pl. XVI, fig. 1. Subsequently a Lower-Middle Devonian age was confirmed by associated fish remains. The specimen came from rocks of the lower Beacon System on the Upper Taylor Glacier in the Ross Sea area.

Perhaps the most important southern comparison is with Australia from which the earliest records of similar stems in the Southern hemisphere were published. Both Seward and Schwarz drew attention to the close resemblance between *Haplostigma irregulare* and *Cyclostigma australe* as described by Feistmantel (1890 Pl. II, fig. 7 and Pl. XI figs. 2, 3 and 4). The stems which he called *Cyclostigma* sp. came from Devonian rocks (horizon unknown) at Goonoo Goonoo in New South Wales and were associated with *Leptophloeum australe*. Feistmantel compared them with *Cyclostigma kiltorkense* but said the scars were more closely set. The second group of stems *Cyclostigma australe* were found with *Rhacopteris* and certain species of Lepidodendron in Lower Carboniferous rocks at Smith's Creek, Stroud, New South Wales. From Feistmantel's published drawings (and, as far as I know, there are no published photographs of the Australian *Cyclostigma*) there appears to be no difference between fossil plants from the two occurrences and both so much resemble the Cape specimens that Schwarz (1906) was prepared to regard them as specifically identical.

The comparison of modern photographs with drawings like those of Feistmantel (1890) is never altogether satisfactory and despite the similarity, it is not known whether *Cyclostigma australe* and *Cyclostigma sp.* are specifically identical with *Haplostigma*. The objections raised by Seward to the use of the terms *Cyclostigma* or *Bothrodendron* in Africa would apply equally to the Australian specimens. The term *Haplostigma* has not, to my knowledge, been applied in Australia and there have been very few references to *Cyclostigma* since Feistmantel's time.

I have discussed this matter in correspondence with Mrs. Mary White who was describing fossil plants from all areas of Australia for the C.S.I.R.O. in Canberra. She stated that she had not found *Cyclostigma* among specimens from any of the recently investigated areas. It is possible, however, that certain stems of this kind in Australia have been described as *Stigmaria* to which they bear a superficial resemblance.

In 1964 I made a very brief examination of some of the Devonian stems in the Natural History Museum in London. The specimens labelled *Cyclostigma australe* v. 24410 did not appear to be identical with those from South Africa save in size and distribution of scars. Many of the latter had radiating grooves around them which are not apparent in any of the African stems I have seen.

Comparison with Northern Hemisphere Devonian Plants

The older literature abounded in comparisons of Cape and Australian fos-

sils with round scarred fossil stems from N. America, Ireland, Bear Island, etc. and many examples could be quoted of isolated stems illustrated by Dawson, Haughton, Nathorst (1902), Hoeg (1942), Zalessky, etc. which bear a close resemblance to some of the Cape Stems but Seward has shown that in certain features the genera to which these stems belong differ markedly. Further comparisons would be useless repetition.

Speculations on the common association of round and rhombic scarred stems in Devonian rocks

Reference must be made to this feature which recurs so frequently in Devonian literature. There would seem to be three possible causes. The first and most obvious is that the time range of these characteristic fossils overlaps, e.g. *Haplostigma* started earlier but existed with *Leptophloeum* in the Cape. In Australia also *Cyclostigma* and *Leptophloeum* have been recorded together and in Europe and China the same association is common.

Secondly, decorticated specimens of *Leptophloeum* as well as of the rather similar Devonian genera of *Bergeria* and *Blasaria* have a pattern of evenly spaced round scars thus justifying the frequent references in the past to a knorria form of stem.

This explanation cannot, however, be applied to the many southern hemisphere round scarred stems on which cuticle is still preserved, proving them to be outer surfaces.

A third possibility may not have been sufficiently explored and may still be kept in mind, namely that some, at least, of the round scarred stems represent the younger twigs of *Leptophloeum*. The suggestion is not new. It has been made in various forms by Feistmantel and others and it may be significant that it is very rare to find *Leptophloeum* stems narrower than 2.5 cm or Haplostigma wider. Recently Schweitzer (1965) has published a most interesting observation that *Bergeria mimerensis* and *Protolepidodendropsis* in West Spitzbergen are parts of the same plant.

Normally Devonian fossils are so fragmental that only isolated portions can be found and with time, other new relationships will undoubtedly be revealed. In South Africa the Bokkeveld *Haplostigma* occurs earlier than specimens of *Leptophloeum* and their relationship is therefore improbable.

Summary of *HAPLOSTIGMA* evidence and its systematic position

Knowledge of the genus *Haplostigma* has not increased very much since it was created in 1932 by Seward but it has been clarified by the removal of three other genera from it, and also by the evidence of possible vascular tissue in the spine-like leaves which would bring the genus nearer to the lycopods. It is obviously a primitive plant but in the absence of any known fructification further attempts at classification would be merely speculative.

Although only three stems have been illustrated on which the spiny projections are preserved, the quartzite moulds with deep hollows tapering upwards, indicate stems with persistent and strong spines which, like the stems, resisted decay until after the sediment had been cemented around them. This evidence is possibly not in agreement with the apparently soft and pliable smooth stems with smaller and closer scars, which occur on the type specimen on Plate XIII fig. 1. Both forms, however, occur at the same horizon and in the same area in Port Alfred and it would seem wiser to regard them at present as representing young and older aspects of the same plant than to separate them on comparatively slender evidence.

The fact that none of the recognised specimens of *Haplostigma* showed any but rounded scar patterns even when deeply decorticated suggest that specimens like the smaller stem on Pl. XIV, fig. 4 and the moulds on Pl. XV figs. 5 and 6, which up to now have been accepted as *Haplostigma* should be allocated to the long lists of indeterminable lycopods, at least pending further evidence, together with all those illustrated on Pl. XVI.

The geographical range of the genus, in all probability, includes South America, the Falkland Islands, East Antarctica and Australia and is thus confined to the Southern Hemisphere.

The stratigraphical range of the specimens described is from Lower Bokkeveld, which on marine invertebrate evidence is regarded as Lower Devonian in age to the Main Witteberg quartzite which is certainly not younger than Upper Devonian and much of it is probably of Middle Devonian Age.

SUB-DIVISION SPHENOPSIDA

Class Protoarticulatae

Genus *CALAMOPHYTON* Krausel and Weyland

1. General

In most Devonian plant assemblages there are a few plant fossils which may be regarded as forerunners of the articulates since they anticipate in various degrees the jointed stems and the whorls of branches and leaves which are so characteristic of this class of plants. None of the Devonian plants, however, exhibits the regularity in such features and habit of growth as are found in Carboniferous and later members of this plant division. Two genera are fairly well known: *Calamophyton* Kräusel and Weyland, and *Hyenia* Nathorst. In the northern hemisphere both are typically of Middle Devonian age. They have been described in numbers from Spitzbergen (Hoeg); Germany (Kräusel and Weyland); from Belgium (Leclercq and Andrews 1960) and the Greater Donetz Basin (Ischenko 1965) and recently from New York State, North America

(Bonamo and Banks 1965), but are little known from the southern hemisphere. Only Frenguelli (1954) has recorded *Hyenia argentina* from South America.

In discussing these genera Leclercq and Andrews (1960) have stated that the differences between *Calamophyton* and *Hyenia* are often difficult to determine for they are based on such features as the nature of the branching of the Sporangiophores of *Calamophyton* or the strong horizontal rhizome of *Hyenia* which gave rise to a number of upright shoots; but where neither of these features is preserved the differences may be negligible. Neither plant is known in its entirety and very little is known of their anatomy. They differ somewhat in their general habit of growth, *Calamophyton* normally being a stronger, larger plant with more conspicuous branching. Among the fossil plants from the Cape System there is only one which can, I believe, be included in this group and because of its size and branching it has been placed provisionally in the genus *Calamophyton*.

2. *Calamophyton capensis* sp. nov.

Pl. XVII figs. 1 and 2 and Pl. XVIII figs. 1-3

Locality:	Sweet Fountain (Estments farm) near Bathurst
Horizon:	Upper Bokkeveld
At Present:	Albany Museum, Grahamstown
Type Specimen:	No. 1809

The specimen, which has not been described previously, was collected many years ago from a quarry on the farm Sweet Fountain (formerly known as Estments Farm) which according to Rennie and Mountain (1942) lies three miles east of Bathurst railway station on the Kleinemond Road. The grey carbonaceous and highly micaceous shale is from the Bokkeveld Series and although the exact horizon is unknown, its age cannot be younger than Middle Devonian.

The specimen which is illustrated natural size on Pl. XVII fig. 1 consists of two main stems which are parallel and may have been parts of a single plant. Both are branched but that on the left is clearer. This stem is 19 cm long and approximately 1 cm wide at the base but tapers upwards. There are two apparent whorls of branches or digitate branching which simulates whorls—at the points marked a and b which are 4 and 14 cm respectively from the base. At both these points there are small transverse ridges which might be interpreted as nodes but which may be accidental. The outgrowths forming each "whorl" may be of branches, although no further branching is apparent on them, or they may be organs which functioned as leaves. The longest portion visible is 7 cm and they average 3-4 mm in width but do not appear to taper. They leave the main stem at an angle of approximately 30° and then curve outwards. Pl. XVIII fig. 1 is an enlargement of the lower "whorl" to show the branching and the apparent node.

The surfaces of all the wider stems have a film of light-greenish talc which contrasts clearly with the dark matrix of the rock. The mineral film often exhibits close transverse jointing but if it is removed the underlying stem is either smooth or finely striated longitudinally without any suggestion of joints. This can be seen on Pl. XVII fig. 2 which is a stem from which an oval cast, 15 mm wide, was separated. It is filled with sediment and compressed to a thickness of 1 mm The stem occurs on the lower part of the main surface of specimen 1809.

None of the branches of the type specimen can be seen to divide further but in the process of cleaving the stem shown in fig. 2, a small flake of rock was split off. On this surface there is a talc covered stem similar to the primary branches described above, 3-4 mm wide but with traces of several small branches on either side. See Pl. XVIII figs. 2 and 3. There is no marked transverse scar as in the larger specimen. The top branch on the right-hand side is the most complete. It curves outwards and upwards, dividing at one point into at least 4 branches each of which divides into two branches of unequal length and two of the longer sections can be seen to divide again. Some of the branch tips appear to be swollen and the whole system may well represent a fertile axis. The various portions lie at slightly different levels and are therefore difficult to photograph. Other fragments of small bifurcating stems occur on the same surface.

The whole rock specimen has a maximum thickness of 4 cm I was unwilling to risk damaging the main surface by further splitting of this type specimen but the abundance of plant material throughout its thickness suggests that further specimens of the plant might be found at the original site. On the same slab, small areas of *Haplostigma* occur and a few short lengths of *Palaeostigma* are preserved. The small oval scars on one of the latter stems are visible on the left hand side of Pl. XVII fig. 1 in the area marked c.

3. Discussion and Comparison

The preservation of this plant in the highly compressed Bokkeveld sediments is so poor that a reliable determination is impossible but its provisional inclusion in the genus *Calamophyton* appears to be justified. The best known specimens have been described by Leclercq and Andrews (1960) as *Calamophyton bicephalum* from the Middle Devonian of Belgium. Their material was excellent and plentiful but the painstaking separation of minute branches from the matrix by Professor Leclercq has probably never been surpassed by students of fossil plants and resulted in the most detailed reconstruction of the greater part of the plant. Both the main branching in pseudo-whorl-like manner and the monopodial and bifurcated branching of the small sterile and fertile axes can be matched to a certain extent at least in the imperfectly preserved Cape specimen.

Recently Schopf (1964) described *Calamophyton forbesii*, the first plant of this genus to be found in N. America. Although the species differs, his illustration on p. D.47 of a fertile shoot exhibits a type of monopodial branching very similar to that of the Cape branch, Pl. XVIII, figs. 2 and 3. Schopf suggested

that the apparent irregularity in his "ascending system of fertile branches" might be due to dichotomy in alternating planes and regarded the habit as of specific significance. Its appearance in Cape, Belgian and Argentinian species as well, suggests that this feature may well be of generic significance.

Schopf pointed out also that the limited range and well established age of *Calamophyton* could make it a very useful marker of the Middle Devonian (lower Givetian) of both continents. This is in keeping also with the Middle Devonian age estimated for the Sweet Fountain occurrence.

The two parallel axes seen on Pl. XVII fig. 1 could be due to growth from a common horizontal rhizome as in *Hyenia* but there is no indication of the fine leaves of *Hyenia elegans* for example (Kräusel and Weyland 1932). There is more likeness to *H. sphenophylloides* (see Hoeg 1935 Pl. III) in which the leaves are verticillate but the lower half of each is simple and looks like a stalk. Perhaps the closest resemblance is to the plant described by Frenguelli (1954 p. 366 Pl. IV fig. 3 and Pl. V figs. 1-4) as *Hyenia argentina* from the Devonian of San Juan. The size, striated stems, type of branching and above all the curvature of all the small branches in one direction are features common to both species. From the present limited knowledge of both the South American and Cape plants they could be specifically identical. Frenguelli compared his plant only with *Hyenia*, but it would seem to be more in keeping with the more recently described species of *Calamophyton*. Until more is known of both plants it is preferable to leave them in separate species.

E. PROBLEMATICAL MEGAPHYLLOUS DEVONIAN PLANTS

Genus *PLATYPHYLLUM* Dawson

1. General

A number of large leafed plants have been described at various times from the Devonian of the northern hemisphere but their affinities are doubtful since, in most cases, neither the plant as a whole nor the reproductive organs are known. A possible exception is *Enigmophyton superbum* from the Upper Middle Devonian of Spitzbergen of which a number of specimens were described by Hoeg (1942a pp. 88-115 and Plates XXXVI-XL). He added an interesting discussion on the origin, relationships and nomenclature of such plants. More recently Andrews (1961 p. 54) has compromised by grouping such leaves under the heading "Problematical Megaphyllous Devonian Plants" in which he included *Platyphyllum*, *Cyclopteris*, *Ginkgophyllum*, *Psygmophyllum*, *Germanophyton* and *Enigmophyton*. This seems to be the best solution pending further discoveries which may allow more accurate classification.

Among the plant fossils from the Cape a single specimen has been found which has been placed in the artificial form-genus *Platyphyllum* Dawson which

Hoeg (1942b p. 101) proposed as the most suitable for the inclusion of detached fan-shaped leaves with parallel bifurcating veins. The preservation of the South African leaf fragment scarcely merits a specific name but one has been given to facilitate reference since this is at present the only known southern hemisphere representative of the genus.

2. *Platyphyllum albanense* sp. nov.

Pl. XIX fig. 1

Locality: Howisons Poort near Grahamstown
Horizon: Near the base of Witteberg Series
At Present: Albany Museum, Grahamstown
Type Specimen: No. 4487

This specimen which has not been described previously, is a small slab of dark carbonaceous micaceous shale with the locality reference of Howison's Poort. The latter is a mountain pass, south of Grahamstown, which is cut through a syncline of Witteberg Quartzite flanked both to north and south by Bokkeveld Shales. Professor Mountain of Rhodes University, Grahamstown, has informed me that there is a narrow carbonaceous band near the base of the quartzite in this locality. Since the rock matrix is similar it is probable that the specimen was collected from this horizon which contains also a number of small psilophyte remains described as *Dutoitia maraisia* sp. nov. in this report. A middle Devonian age is suggested.

The specimen which is illustrated on Pl. XIX fig. 1 has the impressions of the venation of portions of two overlapping leaves on different levels. The total leaf area is 3.5 by 2 cm and unfortunately no organic substance remains and neither the base nor any part of the margin of either leaf is preserved. Nevertheless the light coloured impressions of veins are clear and leave no doubt of the megaphyllous nature of the plant and of the type of venation. Each vein bifurcates twice, within the area and one of them three times.

Significance

The specimen although so incomplete is of importance as the earliest indication of a broad leafed plant in South Africa. In view of the great influx of Glossopteridae at a later date, any such record is significant, especially since the Proto-Glossopteridae described recently (Plumstead 1966) exhibit a transition from a bifurcating ginkgoalean type of venation to a reticulate one.

Comparison

In size and spacing the venation is closely comparable with a leaf *Platyphyllum brownianum* from Perry in the State of Maine. It was described originally as *Cyclopteris browniana* by Dawson (1863 Pl. XVII fig. 6) who, even at that time,

questioned whether it was a fern or a ginkgoalean leaf. The plant was from Upper Devonian beds and was associated with *Leptophloeum* and *Psilophyton*. This type specimen of the genus was subsequently renamed *Rhacophyllum* by Lesquereux and *Psygmophyllum* by Arber, but was finally transferred by Hoeg (1942) to *Platyphyllum* (see photographs of the original specimen in Hoeg 1942b Pl. XLIII and also fig. 22, p. 100). The venation of the South African specimen also resembles that of *Enigmophyton* (cf. Hoeg 1942b, fig. 17 p. 90), but the latter is a true genus and is known in far greater detail.

? Archaeopteris— ? Psygmopyllum

Some poorly preserved plant remains were described by Schwarz (1906, p. 352) as *?Archaeopteris* and the single pinnules were stated to resemble those of *Archaeopteris obtusa* Lesquereux, a plant which was renamed *Psygmophyllum obtusa* by Arber (1912) and would therefore be included in this group. They were compared also with *Archaeopteris howitti* McCoy, which is found in Upper Devonian beds of Iguana Creek, Victoria, Australia. The leaves or pinnules were found by Schwarz in grey micaceous shales underlying Witteberg quartzites in Baviaans Hoek, Ceres. He stated that the borders were not much lacerated and that the preservation was too poor to show venation. Unfortunately the leaves were not figured, no museum numbers were quoted and the specimens cannot now be traced in the Albany Museum collection. They are mentioned here in the interests of completing the record and because it may be worthwhile to carry out a search in the original locality.

F. STEMS OF UNCERTAIN AFFINITIES

Pl. IV, figs. 1 and 2, and Pl. XIX, figs. 2-5

Among the plant fossils found in the Cape System are some stems of uncertain affinities. They are obviously of vascular plants and appear to be unrelated to any of the other plants described here, but their preservation is either too imperfect or fragmental to allow of more detailed classification.

A few of them, representative of different types, have been illustrated here with the object of indicating the existence in Africa of additional classes of plants during the Devonian and, by comparison, to demonstrate that similar stem types of the same age are known from other countries.

1. Stem Type A

Specimen 10741 S.A. Museum. Pl. IV, figs. 1 and 2

This stem has longitudinal grooves and short opposite branches. It occurs with *Palaeostigma sewardi* in the upper part of the Bokkeveld Series at Schietkraal

in the Steytlerville district. The counterpart of this specimen—No. 10742 S.A.M. on which far more of the stem is preserved, was illustrated by Seward (1932, Pl. XXIII, figs. 4 and 6 and Pl. XXIV figs. 8 and 10). He stated that the stem might represent the vascular strands of the stems from which the cuticular surfaces (of *Palaeostigma* and *Haplostigma*) had been separated but that it might be a different type of plant. In the light of modern knowledge the latter view is more probable. The branches have rather small paired projections at regular intervals on the stem and in the axils of some of them there are bud-like growths, possibly sporangia. There are several apparently identical stems in the S.A. Museum, all from the Bokkeveld but without accurate localities.

2. Stem Type B

Spec. 3708. Albany Museum Pl. XIX fig. 2

This stem is from the Lower Witteberg Series at Alicedale Poort.

It is a longitudinally grooved stem of dimensions similar to those of stem A, save that the branches are much longer and are alternate. There is a pronounced thickening or swelling in the axils of several of the branches, which may be indicative of the development of an axillary bud or of sporangia, but none is clear. Other fragments of these branched stems occur on the same slab.

Comparison

Similar stems occur in a number of places. One was described recently from East Antarctica (Plumstead 1962, Pl. XVIII, fig. 7, p. 69 footnote) from beds of Upper Middle Devonian age in the Lashley Mts., where the stem was associated with fossil fish remains which provided an accurate dating.

Hoeg (1942b fig. 14, p. 55 and Pl. XVIII) illustrated a stem which he named *Hostimella* with similar thickening and some axillary buds but the main stem of his specimen branched dichotomously, of which there is no evidence in the Cape System.

3. Stem Type C

Specimen J.T. 13, Pl. XIX, fig. 3

Short lengths of comparatively broad, 2.5 cm stems which appear to be woody, occur on this specimen collected by Theron from the Upper Witteberg shales on the farm Soetendal Vlei in the Willowmore district. The stems probably represent inner surfaces but no vascular or leaf trace-scars are apparent.

Comparison

A somewhat similar stem in size and striated surfaces was illustrated by Grierson and Banks (1963, Pl. 41). It was of Middle Devonian Age and was part of a large cast of a dichotomously branched arborescent plant and the surfaces, comparable with those of Spec. J.T. 13 proved to be subsurfaces, for

when the cast was removed a pattern of leaf scars was revealed in the hollow mould beneath. The Cape specimens may also be of subsurfaces but the fragments are too small for further speculation.

4. Stem Type D

Specimen 11551 S.A. Mus. Pl. XIX, fig. 4

This broad bifurcating stem with suggestions of longitudinal striae on what is possibly an inner surface presents no signs of leaf scars or leaf traces. The stem was collected by Du Toit from the base of the Upper Witteberg shales on the road from Laingsburg to Ladismith.

5. Stem Type E

Specimen J.T. 19 Pl. XIX fig. 5

This specimen was collected by Theron from the Upper Witteberg shales on the farm Soetendal Vlei, Willowmore District.

A number of different portions of stem occur on the specimen and may possibly be part of the same branched stem. All the stems are finely striated. A subsurface layer at the base of the central stem exhibits a distinct ribbed effect. There is a suggestion that several of the stems are hollow and in parts there is regular jointing. These combined characters suggest a plant allied to Arthrophyta and the closest comparisons are with such stems of which only two of many are quoted e.g. *Hyenia argentina* Frenguelli (1954, Pl. V) from the top of the Middle Devonian of the Precordillera of San Juan and *Calamophyton sp.* Schopf (1964, figs. i, h and j) from the Middle Devonian of Maine, U.S.A.

6. Discussion

From these poorly preserved stems few conclusions can be drawn. The branched stems may have psilophytalean or possibly pteridospermous affinities; the others which are all from the Upper Witteberg shales suggest the introduction at this stage of larger and more advanced plant life.