THE FORMATION OF PLANT COMPRESSION FOSSILS:
EXPERIMENTAL AND SEDIMENTOLOGICAL INVESTIGATIONS

by

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To Bob
"The simple, qualitative experiments described below are only justifiable in so far as they give good ideas and they can discredit bad ones. For me they did both".

Professor Tom M. Harris (1974)
A B S T R A C T

The mechanisms and processes that lead to the formation of a plant compression fossil have been experimentally reproduced and studied in the present investigation. This research has used two main lines of investigation: firstly, experimental modelling of the fossilisation process; and secondly, a detailed examination of plant compression fossils. Early experimental modelling was based on the simplest system possible. A dry compression apparatus was used in which artificial materials, representing plant and matrix, were subjected to vertical deformation. Forms were produced which closely resembled vertical sections of Sawdonia, Stigmaria, Calamites and Lepidodendron.

Further apparatus was subsequently constructed, in which wet sediment and actual plant material were compressed, thus more closely reproducing the natural system of compacting sediment. Using this apparatus, factors, such as the role of grain size, change in dimensions of the plant organ, and rigidity of plant tissues were investigated. A recirculating laboratory flume tank was used to examine the flow conditions, and other parameters that were required to produce burial of plant material and infill of hollow stems. The results obtained formed a basis for interpreting the conditions of formation of observed fossil stem infills. Experimental compression of the stems buried in the flume indicated the effect of an infill on the eventual form of the fossil.

Examination of plant compression fossils in the present investigation has been mainly based on a study of vertical sections through the matrix. These reveal the overall structure of the compression, and the processes leading to its formation. The Carboniferous plants, Cyperites, Alethopteris, Lepidostrobus and Trigonocarpus, have been investigated in this way.

An understanding of the factors that dictate the final form of the fossil, using the techniques described above, gives new insight into the fossilisation process. This is of potential value in reconstructing plants from fossils only known in the compression state of preservation. This is illustrated with reference to Permian ovulate glossopterid fructifications from Gondwanaland.

Computer modelling provides an alternative method for studying the compression process, and an account is given of a computer-based investigation of the degradation process.
ACKNOWLEDGEMENTS

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I appreciate the support and encouragement given by my parents, especially during the last months of writing. Last, but not least, I thank my husband, Bob, whose patience, encouragement and understanding enabled me to complete this thesis.
This thesis consists of two published papers and a submitted paper, and also the main part of the thesis. The order in which it should be read is: the Introduction to the thesis, the paper in Appendix A, Chapter 3 of the thesis, the paper in Appendix B, Chapter 5 of the thesis, the paper in Appendix C, and then the remainder of the thesis.

Unfortunately, there is some unavoidable repetition. This is mainly in the introduction of the thesis and in the introductions to the papers. This is because of the necessity to introduce the field of study to the reader in the publications.

The references at the back of the thesis are a comprehensive list of all the references quoted in the published papers and those in the main part of the text.
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C. REX, G.M. A laboratory flume investigation of the processes involved in the formation of fossil stem infills. (submitted to 'Sedimentology')
CHAPTER ONE: Introduction
1.1 General

Plant remains may be preserved in a number of different states in the fossil record. These preservation states reflect different aspects of the original plant. The most common preservation of plant organs is as compressions. These are formed when plant organs are buried in sediment and suffer vertical flattening as the sediment compacts. The residual plant tissues are commonly diagenetically altered to coaly matter, giving a coaly compression fossil in typical Carboniferous fossils, but in younger fossils the plant tissues may not have reached that stage of coalification and may be in the form of brown coal or lignite. Other modes of preservation of fossil plants are less common. They include permineralisations, where the cellular detail of the plant has been preserved in silica or calcite, and authigenic preservation, where the plant was buried in sediment that underwent early cementation before compaction occurred, resulting in the original configuration of the plant being preserved.

In the research described here, only the compression form of fossil plant preservation has been investigated. The prime interest in this study has been the mechanisms and processes that are involved in the formation of plant compression fossils. This has involved, to a large extent, experimental modelling of the compression process, accompanied by a close examination of plant compression fossils. Schopf (1975), in his discussion of the modes of preservation of fossils, stated that "of the various modes of preservation it seems that coalified compression is least understood, although it represents one of the most common forms of fossil plant preservation". The general view of plant compression fossils is that they are simply flattened versions of the original plant. This is exemplified in a statement by Marie Stopes (1910), who placed compressions and impressions in the same category and called them all impressions. She stated: "Impressions in thin sheets of fine rock may be compared to dried specimens pressed between sheets of blotting paper; they are flattened, preserved from decay, and their detailed outline is preserved". This may be true, to a certain extent, of plant organs, such as fronds and leaves which originally had little vertical dimension but structures, such as stems and fructifications with considerable original vertical dimension, evidently underwent distortions during the compression. It is the nature of these distortions, and the factors that dictated the form of a plant compression fossil, that have been studied during the
course of this work.

Three types of fossil have been examined in this research, all of which belong to the general category of "plant compression fossils". These are:

(a) Plant compression fossils sensu stricto: in which no infilling of the plant structure has occurred and the plant organ deforms as the sediment compacts. These fossils form layers of coal (not necessarily in a single plane) which are exposed on bedding planes and fracture surfaces.

(b) Pith casts (and other casts): these fossils are in the form of sedimentary infills of parts of the plant structure and from which the organic matter has been lost as a result of weathering, e.g. Calamites, an infill of a pith cavity.

(c) Combination of (a) and (b): composed of an infill containing or surrounded by a "compression fossil", e.g. the endocortical infill of Stigmaria which may contain a compression of the stele.

1.2 Previous research

The first palaeobotanist to consider the processes involved in the formation of a plant compression fossil was Walton (1923). He developed the transfer technique, where the lower surface of the fossil in contact with the matrix, was revealed by removal of the matrix by maceration in hydrofluoric acid. Walton (1936) wrote a hypothetical account of the compression of stems and leaves in fine-grained sediment. He postulated the change in dimensions a plant organ underwent during compression, based on his observations of actual fossils. The main theory of Walton's, that has prevailed in the literature since the 1930s, was that the horizontal dimensions of the plant organ do not change during compression, but are the same in the fossil as in the uncompressed plant. It is believed that Walton conducted experiments on the compression process, but the results of this work were never published (Harris 1974).

The first experimental work on the compression process, of which details were published, was that of Harris (1974). He was interested in modelling the compression of pollen grains using artificial materials, to see
If the same features could be produced as were observed in *Williamsoniella* pollen grains. He used hollow balls composed of various materials, and compressed them between flat surfaces. His results showed that distortions of the models produced similar features to those seen in pollen grains and miospores. He conducted a further sequence of experiments which involved compressing the models in matrix. This did not produce any change in the horizontal dimensions of the models of the pollen grains. He concluded that Walton's (1936) hypothesis, as it applied to spores, was probably correct. But the behaviour of a rigid spore wall is mechanically very different from the compression of the much more compressible plant tissues in a stem.

Niklas (1978) experimented on the compression of plant stems using artificial and actual plant material in a compression apparatus. The apparatus used is not described in detail nor is the experimental procedure. The only illustration of the work shows folding in the bedding after compression (Fig.3.1). Folding is usually produced by stress acting parallel to bedding, and not in a compressive stress system where the maximum stress is perpendicular to bedding. The brief results of the work state that the horizontal dimensions of the plant stem only alter by up to 10% after fossilisation. The experimental conditions that produced this change are not described, so that his results and conclusions remain enigmatic.

Recently, there has been some experimental work conducted on the preservation of invertebrates (Briggs & Williams 1981; Williams et al 1982). These invertebrates, Middle Cambrian arthropods and Upper Ordovician graptolites, have a similar preservation state to plant compression fossils, i.e. they have suffered flattening and some distortion as the sediment, in which they were buried, became compacted. Briggs & Williams (1981) proposed that soft-bodied organisms did not undergo any lateral expansion during collapse, as a result of decay, or compaction. Assuming this absence of lateral change, they consider that these fossils are analogous to two-dimensional views of three-dimensional objects. They developed a technique of photographing simple models of an arthropod (*Odaria*), and a graptolite (*Dicellograptus*), to show that the structures shown by the fossils are related to the orientation of the organism to the bedding plane. Different original orientations of the animal resulted in certain structures being distorted or hidden from view during the compression process.
Williams et al (1982) took the work a stage further by making models of graptolite rhabdosomes and compressing them in a wooden box filled with loosely compacted dental plaster. After the box had been loaded, it was immersed in water and the dental plaster hardened. The solid plaster block was then split open to reveal the compressed models of the graptolites. The results of the modelling were compared to fossil graptolites, but no lateral expansion of the graptolite models had occurred. However, examination of fossil graptolites indicated that these had undergone lateral expansion during compression. The modelling produced the same pattern of thecal flattening as seen in the fossil rhabdosomes. Williams et al (1982) concluded that their models were too rigid, and so prevented lateral expansion occurring to the extent that had occurred in the fossil graptolites.

Seilâcher (1976) considered the criteria that dictated the form of compressed ammonite shells. He demonstrated how different genera of ammonites collapsed and compressed in different ways, depending on the nature and degree of infilling of the shell that had occurred during burial. For example, Amaltheus, from the Jurassic of Southern Germany, had only a sedimentary infill of the body chamber. The remainder of the whorls were occupied by phosphatic concretions. The presence of the phosphatic concretions prevented deformation of the shell during compaction. In contrast, Leioceras fractured as it collapsed, as the body chamber and the phragmacone were devoid of any infill. In another genus, Oppelia, depressions termed "caldera collapse" were seen in the bedding plane above the specimen. These depressions resulted from the collapse downwards of the phragmacone due to the overlying sediment burden. This behaviour of the degree of infilling dictating the form of the compressed ammonite shell also occurs in plant fossils where the form and nature of the infill of, for example, a stem cavity, is directly responsible for the final form of the fossil.

1.3 Brief outline of the research

This research has concentrated on experimental modelling of the compression process to determine the factors that dictate the form of a plant compression fossil. In the first instance, the simplest system possible was used. This involved a dry compression apparatus, in which artificial materials representing plant and matrix were compressed. The results of this work indicated that models of the original plant structure
could be constructed and, on deformation, produced the same structure, in vertical section, as that seen in compression fossils. A second apparatus was subsequently designed and built in which wet sediment and actual plant material could be compressed. This apparatus enabled much closer modelling of the natural system of compacting sediment and plant tissue. Using this wet compression apparatus, several more lines of investigation could be pursued that were not possible in the dry apparatus; for example, the effect of grain size on the form of the fossil, and the change in dimensions of a plant organ as it undergoes collapse and compression in wet sediment. The results of this work have shown that plant stems embedded in different compressibilities of sediment produce very different forms of "fossil" on compression, and that the plant organ suffers substantial changes, not only in the vertical dimension, but also in the horizontal dimension.

One of the problems that became obvious during this wet compression work was that very little was known about the degree to which infilling of cavities in plant organs occurred during burial. Therefore, it was not known whether the models, that were being used in the wet compression work, were close to the structure of the infill that would have formed during the burial of a plant organ. In order to investigate the degree to which infilling of hollow stems occurred, and the conditions under which this would take place, a small laboratory flume tank was constructed and used. This allowed sedimentation along an alluvial channel to be modelled. Using this apparatus, the effect of diameter and length of a stem on the formation of an infill, and the type of flow conditions that produced infilling, was investigated. The buried and infilled stems formed in the flume were then placed in the wet compression apparatus. This then allowed the entire process of infilling, burial and subsequent compression of a plant organ to be replicated in a system which closely resembles the natural sedimentary environment. This technique enabled the effect of an infill on the form of the fossil to be ascertained.

Closely associated with the experimental work was the detailed examination of plant compression fossils. One of the most useful techniques, that was used in this part of the work, was to section the fossil, either while it was still intact in the matrix, and/or by reassembling the part and counterpart and then sectioning the fossil in the vertical plane. This sectioning revealed the entire structure of the compression fossil, especially the vertical dimension, and not just the surface that is exposed
by the fracture plane. By reassembling the part and counterpart, and then
vertically sectioning the fossil, the pathway the fracture plane took to
expose the compression can be determined. This also reveals how much of
the fossil is exposed by a fracture plane, and the extent to which parts
of the fossil remain hidden in the matrix. One of the fossil examined
during the course of this work that demonstrates this technique well is
Cyperites. This apparently flat lycopod leaf is shown to have a complex
three-dimensional structure which is not exposed by the fracture plane,
but only revealed when the leaves are sectioned intact in the matrix.
Experimental modelling was used to elucidate the structure of the uncom­
pressed leaf. Other genera of plant compression fossils have been ex­
amined using these techniques; for example, certain pteridosperm leaves
and the more complex fructifications of Lepidodendron, known as Lepido­
strobus.

By using these experimental modelling techniques to reproduce the infilling
and the compression of plant organs accompanied by a close examination of
plant compression fossils, has enabled the factors important in the fos­
silisation process to be elucidated. By understanding the extent to
which these factors, e.g. sediment grain size, degree of infilling, path­
way of the fracture plane, dictate the form of a plant compression fossil,
allows a much more accurate interpretation to be made of the fossil.
This is especially useful when plant fossils are only known in the com­
pression state of preservation. This is explored in the case of the
ovulate glossopterid fructifications.

1.4 Terminology

A terminology has been developed during the course of this work, which has
been used throughout this thesis. This is illustrated in Fig.1.1. In
the literature, the terms "part" and "counterpart" are often used in des­
briving plant compression fossils. Here, these terms are used only when
referring to the two halves of a compression fossil. It implies no
orientation of the fossil, nor does it imply that either term refers to
any particular half of the fossil (e.g. upper or lower). It is simply
a general term to indicate that the fossil fractured along the bedding to
yield two parts.

When fossils have been collected in situ in the field, or the "way-upness"
of the fossil has been determined by, for example, sedimentological evi­
dence, then the fossil has a known orientation. If the fracture plane
that exposed the fossil has run along the coal/matrix interface, this results in a compression (bearing the coaly matter) and an impression (devoid of coaly matter) being exposed. These are called the upper impression and the lower compression, or vice-versa, depending on the orientation of the fossil in the field (Fig.1.1a,b).

Fossils collected, that are not in situ, e.g. from tip heaps, have an unknown orientation. In this case, the impression fossil is called impression B and the compression, compression A. This indicates that the orientation is unknown (Fig.1.1c).

In some examples there may not be a distinct compression and impression. The coaly matter may be present on both the part and the counterpart. These fossils are termed "incomplete compression" and, if the orientation of the fossil is known, can be referred to as the 'upper incomplete compression' and the 'lower incomplete compression' (Fig.1.1d).

Where the part and counterpart are topographic opposites of each other, they are termed conformable. Therefore, for example, the fracture plane can expose a conformable compression A and a conformable impression B (Fig.1.1e,f), e.g. Alethopteris (Fig.7.1a). In some instances, possibly if the coaly matter has been lost from the fossil, the part and counterpart do not show the same structure, e.g. the ovulate glossopterid fructifications (Plate 16). In this case, there is a non-conformable impression A and a non-conformable impression B (Fig.1.1g,h). These could be further specified as upper and lower if an orientation of the fossil was known.
Description of Figure 1.1

a. & b. When the orientation of the fossil is known the compression is termed the upper or lower compression, depending on its orientation.

c. When the orientation of the fossil is unknown the part and counterpart are referred to as compression A and impression B.

d. Where the fracture plane exposes a fossil in which coaly matter is present on both part and counterpart, the parts are termed incomplete compressions. They may also be termed A and B or upper and lower, depending on the orientation of the fossil.

e. Compression fossil before it is exposed by a fracture plane.

f. The fracture plane exposes a conformable compression and a conformable impression, i.e. the two surfaces are topographically opposite.

g. Fossil where the coaly matter has been lost before it is exposed by a fracture plane.

h. The fracture plane exposes two unconformable impression fossils, i.e. the two surfaces of the fossils are not topographically opposite.
Fig. 1.1. The terminology of compression / impression fossils used in this thesis.
CHAPTER TWO: The experimental formation of plant compression fossils

(see appendix A)
CHAPTER THREE: An investigation of the compression process using a wet compression apparatus
3.1 Introduction

The work on the dry compression apparatus (Rex & Chaloner 1983) demonstrated that experimental modelling of the compression process enabled interpretations to be made concerning the structure of some plant compressions fossils. However, there were obvious limitations in a model so far removed from the wet-sediment environment of the natural fossilisation process. In order to get closer to the natural system of compacting sediment a second compression apparatus was designed and built. In this apparatus, wet sediment and actual plant material could be compressed in a system in which there was a strict control on the movement of water out of the compacting sediment. In this apparatus, some of the results from the dry compression system could be investigated further and other factors important in the preservation process determined. This had not been possible in a system based on artificial materials representing plant and matrix.

The lines of investigation which have been followed during the course of this experimental work are:

(a) The change in the horizontal dimensions of a plant organ during compression.

(b) The 'wayupness' of compression fossils.

(c) The formation of compression borders.

(d) The effect of sediment grain size on the form of the compression.

(e) The resistance of plant tissues to the compression process.

(f) The effect of a sediment infill on the form of the fossil.

It was demonstrated in the first compression apparatus that under these "dry" conditions the horizontal dimensions of the "plant" remained constant during compression. Walton (1936) had postulated that solid, woody cylinders and infilled, woody cylinders would not suffer any lateral displacements during the compression process. He considered that the tendency of a plant organ to bulge out, due to the pressure of the overlying matrix, would be prevented by the resistance of the matrix at the sides of the plant organ. Walton (1936) proposed two other important factors involved in the compression process. Firstly, that "the shape of the resulting fossil is principally based on the form of the lower surface of the original plant fragment". Secondly, that a hollow, woody cylinder infilled
Description of Figure 3.1 (from Niklas 1978)

Simulated compression failures in plant axes.

A-B The packing of a plant stem (seen in cross-section) and subsequent compression results in deformation of both sediment and the plant axis.

C-G The compression of a hollow plant axis results in the gradual collapse of the upper convex surface and the eventual flattening of the entire stem without observable horizontal deformation.

H-L The compression of a solid stem may result in the compression of the axis with minor horizontal deformation.

M-Q The compression of a solid stem that is allowed to undergo dehydration may result in a gradual decrease in its diameter, with major vertical deformation.
with an incompressible matrix would produce, on compression, an ellipsoid shaped infill bounded at the margins by compression borders formed from the compression of the woody cylinder. These theories on the formation of plant compression fossils, proposed by Walton, have not been challenged since the 1930s.

There have been two experimental investigations conducted to test Walton's theories: Harris (1974), modelling the compression of pollen grains; and Niklas (1978), who only gives a very brief report on his experiments. A small line drawing in the text of his account shows the apparatus used, which appears to consist of a box with a piston. There is no description of the apparatus. The piston apparently produced a buckling of the beds in the box (Fig. 3.1). How this effect is produced in a compressive stress system is not explained; buckling of layers is normally produced by stress parallel to the layers. A number of experiments were apparently conducted using artificial and natural materials. Four conclusions are offered:

(i) Horizontal deformation may occur during compression of a cylindrical body if the materials used are rigid and have elastic and plastic properties.

(ii) Upon lateral compression, hollow cylinders show a maximum diameter deformation of 3.5% (most buckling restricted to the upper arch of the circular cross-section).

(iii) Solid cylinders show a maximum 10% diameter increase.

(iv) Non-resilient materials follow in detail Walton's description of compression failure.

It is not clear how these result were arrived at, since no experiments are actually described.

3.2 The compression apparatus

The apparatus (Fig. 3.2a; Plate 1) used in this investigation consists of a hollow cylinder of perspex (44.0cms high) with a diameter of 14.0cms. The cylinder has a removable base which is sealed by 'O' rings when in position. The piston has a diameter of 14.0cms and consists of a solid disc of perspex (1.5cm thick), which has two rubber rings inset into the perspex to give a perfect seal at the margins of the cylinder. The disc
Description of Figure 3.2a

Diagram of the wet compression apparatus showing the dimensions and the components of the apparatus

(cb) cross bar; (gp) guide plate; (cnb) connection bar; (pr) piston rod; (sp) piston; (h) hole in piston; (r) rubber seal to piston; (p) perspex cylinder; (or) 'o' ring sealing base; (b) base plate; (wb) weight bar; (fb) filter papers underlying piston. (X 0.4).
Fig. 3.2a. The wet compression apparatus.
Description of Plate 1

The wet compression apparatus
is perforated by six large holes (3.5cms in diameter) near the outer edge of the piston, and six smaller holes (1.2cms in diameter) near the centre of the piston (Fig.3.2b). The surface of the piston, that is in contact with the sediment, has five layers of filter paper attached to it. This prevents the movement of sediment but allows water molecules to pass through as the sediment dewateres. The piston is attached to a rod which extends out of the cylinder, through a guide plate, and attaches to a horizontal bar above the cylinder. In turn, this is attached to a weight-bar underneath the apparatus from which a downwards vertical stress is exerted on the piston. Weights are added to the bar each day until the weight reaches about 54kgs. Four of these cylinders were built: two with a diameter of 14.0cms (in which a pressure of 0.3kg/cm\(^2\) could be exerted); and two with a diameter of 7.5cms (in which a pressure of 1.2kg/cm\(^2\) could be exerted).

3.3 Materials and method

Each experiment was begun by loading the cylinders. This had to be done artificially, i.e. by hand. A layer of sediment was added to the cylinder and allowed to settle. The plant material was then added and buried by the addition of a further layer of sediment. The piston was then inserted and the weight-bar attached. Each day weights were added to the weight-bar, usually 5.4-6.3kgs, and the compression continued for 14 to 17 days. After this period the water that had collected above the piston was drained off by siphoning. The base plate of the compression cylinder was removed by unscrewing the four screws that kept the 'O' ring in position (Fig.3.2a). The compressed core of sediment and plant material was then pushed out of the perspex cylinder and into a "core-catcher". This was a plastic, hollow cylinder the same diameter as the compression cylinder, and fitted over the end of the cylinder via a collar (Fig.3.3). The core was then frozen in a deep-freeze at -10\(^\circ\)C and then sectioned in the vertical plane, while still frozen, using a hack saw.

The plant material used in the investigation was Hogweed (Heracleum sphondylium) to represent a stem with a degree of rigidity, and cucumbers and courgettes (fruits of Cucumis sativus) to represent stems which are considerably more compressible. The sediments used were clay, in a colloidal solution, to represent a very compressible matrix, and sands (approximately 1.0mm grain diameter) to represent a relatively incompressible matrix.
Fig. 3.2b. Plan drawing of the surface of the piston; (ps) small holes in piston; (pl) large holes in piston; (s) screws; (c) hole through which piston rod is attached.
Fig. 3.3. The wet compression apparatus with core-catcher attached.
In a further set of experiments, a laboratory flume was used to determine the formation of infills within hollow stems of varying length and diameter at different current velocities (this work is described in detail in Chapter 4). After the stems (Heracleum sphondylium and species of Sonchus) had been infilled and buried in the flume tank, they were compressed in the compression apparatus described above. The size and length of the stems that could be compressed were dependent on the diameter of the perspex cylinders in the compression apparatus. Coring cylinders were made (out of metal), which had exactly the same diameter (14.0cms and 7.5cms) as the compression cylinders. The buried plant material was removed by a metal plate being slid along the floor of the flume underneath the buried plant material. The corer was then pushed down into the sediment until it contacted with the base plate. The entire structure was then lifted out of the flume tank. The core could not be placed straight into the compression apparatus, since the sand was too wet and the core would collapse if removed from the coring cylinder. The core was accordingly placed in a deep-freeze (-10°C). frozen and then removed from the cylinder and placed in the compression apparatus. A small amount of water was expelled from the sand during the freezing process. The core of sediment and buried plant material fitted exactly into the compression apparatus. This was necessary, so that there was no room for lateral expansion of the sediment during the compression. The core was compressed in the same manner as described earlier. When the experiment was terminated, the core was removed, refrozen and then sectioned.

The stems were waterlogged before being introduced into the flume tank. This involved placing the stems in constantly running water for 2-3 weeks. The sediment used in the experiments was a fine sand (0.1mm grain size). Clay size sediment could not be used in the flume tank as it remains in suspension for very long periods of time.

Using this apparatus the natural system could be closely modelled. The stems were infilled and buried by sediment deposited from current activity and then subjected to compression.

3.4 Results

(a) Change in horizontal dimensions

Results from this experimental investigation have shown that the horizontal dimensions of the plant stems do change during the compression. The
Fig. 3.4. The terminology of the uncompressed (a) and compressed (b) stems used in this discussion.

OVD : overall vertical dimension
IVD : internal vertical dimension
OHD : overall horizontal "
IHD : internal horizontal "
T : thickness of original plant cylinder

MT : width of compressed plant at margins of infill
T' : thickness of compressed plant cylinder bounding upper and lower surfaces of the infill.
degree to which this occurs is dependent on the nature of the matrix that the plant stems are buried in, and the structure of the stem, i.e., whether it has rigid properties or is very compressible. The result of these experiments are given in Tables 1-4. The terminology used is shown in Fig. 3.4.

In the solid, non-rigid stems (Table 1), compressed in a clay matrix the overall horizontal dimensions (OHD) remained constant, except in 604 where it was reduced by 15% (Fig. 3.5a,b; Plate 2; E,F). The overall, vertical dimension is usually considerably reduced up to a maximum of 97.5%. The results were significantly different when the stems were compressed in a sand matrix. The overall horizontal dimensions were drastically reduced by 50-70% (Fig. 3.5c; Plate 2; A,B). This was accompanied by a reduction in the overall vertical dimension (OVD). It appeared that the sand and clay were behaving in a mechanically different manner during the compression and this affected the form of the "fossil". The clay matrix responded to the compressive stress by compacting in the vertical axis, and this resulted in a reduction in the vertical dimension of the plant stem. In contrast, the sand matrix appears to have responded to a hydrostatic stress system (3 principal stresses). This has resulted in a reduction in the horizontal and vertical dimensions of the plant stem and is not simply a compressive stress system. This is probably related to the incompressibility of the sand grains and the grains repacking and rearranging into a closer-fitting system as the sand begins to compact (Chilingarian & Wolf 1975). This process may result in the horizontal movement of the grains within the matrix.

In further experiments these non-rigid stems were hollowed out and infilled with the matrix the stem was buried in. Stems infilled and buried in a clay matrix showed a distinct increase in their internal horizontal diameter (IHD) after compression (see Table 2). The overall horizontal diameter (OHD) did not show the same increase, only increasing by 10% compared to the 30-40% increase in the IHD (Fig. 3.7b; Plate 3; D,F). Again, the results varied when these stems were infilled and buried in a sand matrix. In this case the OHD showed a reduction of 38%, whereas the IHD (the infill, basically) was virtually unaltered (Fig. 3.7c). The plant stem had been compressed to the same thickness around the sand infill, and again it appeared that the sand was compacting as a result of a hydrostatic stress system rather than a compressive stress system.

When more rigid stems, i.e., Heracleum, were compressed in the apparatus, there were also changes in the horizontal dimensions between the original
TABLE 1: Results of compression of solid, non-rigid stems

<table>
<thead>
<tr>
<th>Experiment No.</th>
<th>Plant material</th>
<th>Matrix</th>
<th>kg/cm²</th>
<th>MR</th>
<th>OHD</th>
<th>OVD</th>
</tr>
</thead>
<tbody>
<tr>
<td>604</td>
<td>Cucurbita pepo</td>
<td>clay</td>
<td>0.32</td>
<td>37%</td>
<td>R 15%</td>
<td>R 74%</td>
</tr>
<tr>
<td>608</td>
<td>Cucumis sativus var anglicus</td>
<td>clay</td>
<td>1.22</td>
<td>52%</td>
<td>constant</td>
<td>R 97.5%</td>
</tr>
<tr>
<td>610</td>
<td>&quot; &quot; &quot; &quot;</td>
<td>clay</td>
<td>1.14</td>
<td>41.9%</td>
<td>constant</td>
<td>R 84%</td>
</tr>
<tr>
<td>617</td>
<td>Rheum palmatum</td>
<td>clay</td>
<td>0.35</td>
<td>50%</td>
<td>constant</td>
<td>R 24%</td>
</tr>
<tr>
<td>618</td>
<td>&quot; &quot; &quot;</td>
<td>clay</td>
<td>0.35</td>
<td>50%</td>
<td>constant</td>
<td>R 26%</td>
</tr>
<tr>
<td>611</td>
<td>Cucumis sativus var anglicus</td>
<td>sand</td>
<td>1.14</td>
<td>7%</td>
<td>R 68.5%</td>
<td>R 54%</td>
</tr>
<tr>
<td>616</td>
<td>Rheum palmatum</td>
<td>sand</td>
<td>1.22</td>
<td>4%</td>
<td>R 52%</td>
<td>R 4%</td>
</tr>
</tbody>
</table>

MR : matrix reduction  
OHD : overall horizontal dimension  
OVD : overall vertical dimension  
R : reduction
Description of Figure 3.5
(all the diagrams show transverse-sections of plant stems)

a. Compression of a solid, non-rigid stem in a clay matrix (604). The resulting compression has a C-shaped structure. A slight reduction in the overall horizontal dimension of the stem has occurred during compression (X 2).

b. Compression of a solid, non-rigid stem in a clay matrix (608). The stem has been compressed to a fine line which has a slight upwards curvature. The horizontal dimension has been maintained from the stem to the "compression" (X 2).

c. Compression of a solid, non-rigid stem in a sand matrix (611). The resulting compression has a very distorted structure and has suffered considerable reduction in both horizontal and vertical dimensions. (X 2).
Fig. 3.5. Results of the experimental compression of solid stems in different grain-sizes of matrix.
Description of Plate 2

The results of the experimental compression of plant stems

A T.S of a compressed, solid, non-rigid plant stem (611) in a sand matrix. The "compression" has a very irregular distorted structure (X 1).

B T.S of a compressed, solid, non-rigid plant stem in a sand matrix (616). The "compression" has a distorted structure and has lost its original cylindrical shape. (X 1.5)

C T.S of a compressed, hollow, non-rigid plant stem in a clay matrix (601). The stem cavity has not been closed up during the compression but has been reduced. (X 1).

D L.S of C, showing the fractures produced in the plant stem during the compression. (X 1.5)

E T.S of a compressed, solid, non-rigid plant stem in a clay matrix (604). The "compression" has a C-shaped structure. (X 0.75).

F. T.S of a compressed, solid, non-rigid plant stem in a clay matrix (608). The stem (arrow) has been compressed to a fine line which has an upwards curvature. (X 1)

G. T.S of a compressed, hollow, rigid plant stem in a sand matrix (599). The stem cavity has almost closed up during the compression. (X 1)

H. L.S of an infilled plant stem that has been compressed. The stem was infilled (in sand) and buried in a laboratory flume tank and then compressed. The upper-stem surface has collapsed onto the infill. (X 0.75)
plant stem and the "fossil". In experiments where the stems were left empty (i.e. buried without sediment in the internal hollow) and compressed in a clay matrix, there was a substantial increase in the IHD of 20-30% (Fig.3.6a; Plate 2; C). This was accompanied by a less than 10% increase in the OHD (see Table 4). The experiments were repeated using a sand matrix, and on compression the stems were reduced in OHD and IHD as well as in the vertical dimensions. The hollow stems were almost completely closed after the compression (Fig.3.6b; Plate 2; G).

Heracleum stems, which were infilled and buried in a clay matrix, also showed a 20-30% increase in the IHD as the infilled non-rigid stems had shown (see Table 4). Again, very little increase in the OHD occurred, reaching a maximum of 15% (Fig.3.7a; Plate 3; A,C).

In summary, the horizontal dimensions of the plant stems do change during the experimental compression process. This change is mainly dependant on the nature of the sediment the plant stem is buried in. In clay matrices there is an increase in the horizontal dimensions of the stem. This is usually the internal dimension of hollow or infilled stems and is accompanied by a much smaller increase in the overall horizontal dimension. In contrast, stems buried in a sand matrix show a substantial reduction in the overall horizontal dimension, whereas the IHD shows virtually no change. It is concluded that the sand and clay matrices respond to the compressive stress exerted on the sediment in a different manner. This is related to the compressibility of the clay matrix as against the incompressibility of the sand grains. As the clay matrix compacts, there is some horizontal movement of the clay particles, as shown by the increase in the horizontal dimension of the infill. This expansion of the infill seems to be restricted by the surrounding plant stem, which shows little increase. This may be related to the fact that the plant stem has no, or few, plastic properties and cannot deform horizontally to the same extent as the clay. The sand matrix behaves quite differently. The vertical compressive stress exerted on the sand results in the repacking and rearranging of the grains into a tighter configuration by the grains sliding past one another (Chilingarian & Wolf 1975). This seems to occur in any direction, but since the plant stem represent a very compressible constituent with the matrix, the grains move inwards towards the stem from all directions. This results in a decrease in the horizontal and vertical dimensions of the plant stem (Fig.3.8a,b,c).
Description of Figure 3.6
(all the diagrams show transverse-sections of plant stems)

a. Compression of a hollow, rigid plant stem in a clay matrix (601). On compression the hollow stem begins to close, but the plant cylinder fractures along the upper and lower surface as a result of its non-plastic properties (X 2).

b. Compression of a hollow, rigid plant stem in a sand matrix (598). On compression the stem cavity is considerably reduced, and the stem has suffered reduction in both horizontal and vertical dimensions. (X 2).
Fig. 3.6. The results of experimental compression of hollow rigid plant stems.
# TABLE 2: Results of compression of infilled, non-rigid stems

<table>
<thead>
<tr>
<th>Experiment No.</th>
<th>Plant material</th>
<th>Matrix</th>
<th>kg/cm²</th>
<th>MR</th>
<th>OHD</th>
<th>IHD</th>
<th>OVD</th>
<th>IVD</th>
</tr>
</thead>
<tbody>
<tr>
<td>603</td>
<td><em>Cucurbita pepo</em></td>
<td>clay</td>
<td>0.94</td>
<td>40%</td>
<td>I 12%</td>
<td>I 47%</td>
<td>R 67%</td>
<td>R 58%</td>
</tr>
<tr>
<td>607</td>
<td><em>Cucumis sativus var anglicus.</em></td>
<td>clay</td>
<td>1.22</td>
<td>45%</td>
<td>R 5%</td>
<td>I 35%</td>
<td>R 71%</td>
<td>R 55%</td>
</tr>
<tr>
<td>614</td>
<td>&quot;</td>
<td>clay</td>
<td>1.20</td>
<td>45.5%</td>
<td>I 8.3%</td>
<td>I 33.3%</td>
<td>R 79%</td>
<td>R 66.6%</td>
</tr>
<tr>
<td>615</td>
<td>&quot;</td>
<td>sand</td>
<td>1.08</td>
<td>15.5%</td>
<td>R 37.5%</td>
<td>I 3.5%</td>
<td>R 41.6%</td>
<td>R 7.4%</td>
</tr>
</tbody>
</table>

**MR**: matrix reduction  
**OHD**: overall horizontal dimension  
**IHD**: internal "  
**OVD**: overall vertical dimension  
**IVD**: internal "  
**I**: increase  
**R**: reduction
TABLE 3: Results of compression of infilled, rigid stems:

<table>
<thead>
<tr>
<th>Experiment No.</th>
<th>Plant material</th>
<th>Matrix</th>
<th>kg/cm²</th>
<th>MR</th>
<th>OHD</th>
<th>IHD</th>
<th>OVD</th>
<th>IVD</th>
</tr>
</thead>
<tbody>
<tr>
<td>602</td>
<td>Heracleum</td>
<td>clay</td>
<td>1.08</td>
<td>40%</td>
<td>7%</td>
<td>I</td>
<td>26%</td>
<td>R</td>
</tr>
<tr>
<td>606</td>
<td>&quot;</td>
<td>clay</td>
<td>1.1</td>
<td>42%</td>
<td>15%</td>
<td>I</td>
<td>21%</td>
<td>R</td>
</tr>
<tr>
<td>612</td>
<td>&quot;</td>
<td>clay</td>
<td>1.32</td>
<td>39%</td>
<td>3.8%</td>
<td>I</td>
<td>33%</td>
<td>R</td>
</tr>
<tr>
<td>613</td>
<td>&quot;</td>
<td>clay</td>
<td>1.32</td>
<td>41%</td>
<td>4%</td>
<td>I</td>
<td>25%</td>
<td>R</td>
</tr>
</tbody>
</table>

MR: matrix reduction
OHD: overall horizontal dimension
IHD: internal " "
OVD: overall vertical dimension
IVD: internal " "

I: increase
R: reduction
<table>
<thead>
<tr>
<th>Experiment No.</th>
<th>Plant material</th>
<th>Matrix</th>
<th>kg/cm²</th>
<th>MR</th>
<th>OHD</th>
<th>IHD</th>
<th>OVD</th>
<th>IVD</th>
</tr>
</thead>
<tbody>
<tr>
<td>601</td>
<td>Heracleum</td>
<td>clay</td>
<td>0.3</td>
<td>36%</td>
<td>I 7%</td>
<td>R 31%</td>
<td>R 33%</td>
<td>R 9%</td>
</tr>
<tr>
<td>605</td>
<td></td>
<td>clay</td>
<td>0.3</td>
<td>38%</td>
<td>I 9%</td>
<td>I 20%</td>
<td>R 52%</td>
<td>R 50%</td>
</tr>
<tr>
<td>599</td>
<td></td>
<td>sand</td>
<td>0.5</td>
<td>1.5</td>
<td>R 21.7%</td>
<td>R 58.8%</td>
<td>R 30.4%</td>
<td>R 58.5%</td>
</tr>
<tr>
<td>595</td>
<td></td>
<td>sand</td>
<td>0.5</td>
<td>1.5</td>
<td>R 46%</td>
<td>R 84%</td>
<td>R 42%</td>
<td>R 84%</td>
</tr>
</tbody>
</table>

MR : matrix reduction  
OVD : overall vertical dimension  
I : increase  
R : reduction  
OHĐ : overall horizontal dimension  
IHD : internal  
IVD : internal
(b) The "wayupness" of the "fossil"

Compression of solid, non-rigid plant stems in a clay matrix produced, in two experiments (604, 618), C-shaped structures (Fig. 3.5a; Plate 2; E). The upper surface of the plant stem had collapsed or been compressed into the lower. Which of these processes plays the most important role in the formation of the structure is difficult to assess. From the very compressed structure of the stem, it appears that the upper surface of the stem has been compressed into the lower rather than collapsed into it. Obviously, some collapse of the stem tissues has occurred, accompanying the compression of the stem.

In other experiments of this type (i.e. solid, non-rigid stems in a clay matrix), the stem was reduced to a very fine line not exceeding 1-2mms (Fig. 3.5b; Plate 2; F). The overall vertical dimension had been reduced by 84-98%. The "compression" has a slight upwards curvature, and the horizontal dimension has remained constant from the stem to the "fossil".

In further experiments these non-rigid stems were buried in a sand matrix and, on compression, were deformed into very irregular, distorted structures. These structures bore no relation (in shape) to the original stem (Fig. 3.5c; Plate 2; A, B).

When the rigid and non-rigid stems were infilled with a clay matrix and compressed, the infill was deformed from a cylindrical shape to an ellipsoid. Where these stems were infilled with a sand matrix, the infill maintained its cylindrical shape during the compression process. The shape of the infills, in both cases, did not produce any distinct "way-upness" character (i.e. the upper and lower surfaces of the infill showed the same curvature).

(c) The formation of compression borders

Walton (1936), as discussed earlier, postulated that a woody, hollow stem, when infilled with a less compressible matrix, would produce marginal compression borders on compression. A number of experiments were conducted to determine whether this would occur when using actual plant material and sediment. The experiments used rigid and non-rigid stems.

Compression borders were produced when the plant stems were infilled and buried in a clay matrix. The borders formed in both rigid and non-rigid
Description of Figure 3.7
(All the diagrams show transverse-sections of plant stems)

a. Compression of an infilled, rigid plant stem (606). The stem is infilled and buried in a clay matrix. On compression the infill becomes ellipsoidal in outline and there is an increase in the internal horizontal dimension of the stem. This is accompanied by an increase in the overall horizontal dimension of the stem. "Compression borders" (c) have formed at the margins of the infill as a result of the compression of the plant cylinder. (X 1).

b. Compression of an infilled, non-rigid plant stem (614). The stem is infilled and buried in a clay matrix. On compression the infill becomes ellipsoidal in outline and "compression borders" (c) form at the margins of the infill. There is an increase in both the horizontal dimensions of the stem, i.e. IHD and OHD. (X 1).

c. Compression of an infilled, non-rigid plant stem (615). The stem is infilled and buried in a sand matrix. On compression the infill maintains its circular outline and the plant cylinder suffers a reduction in both overall horizontal and vertical dimensions. No "compression borders" were formed. (X 1).
Fig. 3.7. The results of experimental compression of plant stems infilled and buried in the same sediment.
TABLE 5: Change in the thickness of the rigid plant cylinder during compression

<table>
<thead>
<tr>
<th>Experiment No.</th>
<th>Matrix</th>
<th>OHD (initial) (cms)</th>
<th>IHD (initial) (cms)</th>
<th>T (cms)</th>
<th>MT' (cms)</th>
<th>T' (cms)</th>
<th>Compression of T</th>
</tr>
</thead>
<tbody>
<tr>
<td>602</td>
<td>clay</td>
<td>3.4 (3.0)</td>
<td>2.4 (1.9)</td>
<td>0.55</td>
<td>0.55</td>
<td>0.55</td>
<td>0%</td>
</tr>
<tr>
<td>606</td>
<td>clay</td>
<td>2.3 (2.1)</td>
<td>1.5 (1.2)</td>
<td>0.4</td>
<td>0.4</td>
<td>0.01</td>
<td>97.5%</td>
</tr>
<tr>
<td>612</td>
<td>clay</td>
<td>2.7 (2.6)</td>
<td>2.0 (1.5)</td>
<td>0.55</td>
<td>0.35</td>
<td>0.15</td>
<td>72%</td>
</tr>
<tr>
<td>613</td>
<td>clay</td>
<td>2.6 (2.5)</td>
<td>2.0 (1.6)</td>
<td>0.45</td>
<td>0.3</td>
<td>0.1</td>
<td>77.7%</td>
</tr>
</tbody>
</table>

OHD: overall horizontal dimension  
IHD: internal "  
T: thickness of original plant cylinder  
MT': width of compressed plant cylinder at margins of infill  
T': thickness of compressed plant cylinder bounding upper and lower surfaces of the infill
<table>
<thead>
<tr>
<th>Experiment No.</th>
<th>Matrix</th>
<th>OHD (initial) (cms)</th>
<th>THD (initial) (cms)</th>
<th>T (cms)</th>
<th>T' (cms)</th>
<th>Compression of T' (cms)</th>
</tr>
</thead>
<tbody>
<tr>
<td>603</td>
<td>clay</td>
<td>2.7 (2.4)</td>
<td>2.5 (1.7)</td>
<td>0.35</td>
<td>0.05</td>
<td>85.7%</td>
</tr>
<tr>
<td>607</td>
<td>clay</td>
<td>3.7 (3.9)</td>
<td>2.7 (2.0)</td>
<td>0.95</td>
<td>0.1</td>
<td>89.4%</td>
</tr>
<tr>
<td>614</td>
<td>clay</td>
<td>5.2 (4.8)</td>
<td>3.6 (2.7)</td>
<td>1.05</td>
<td>0.05</td>
<td>95.2%</td>
</tr>
<tr>
<td>615</td>
<td>sand</td>
<td>3.0 (4.8)</td>
<td>2.8 (2.7)</td>
<td>1.05</td>
<td>0.15</td>
<td>85.7%</td>
</tr>
</tbody>
</table>

OHD: overall horizontal dimension
THD: thickness of original plant cylinder
T: thickness of compressed plant cylinder at margins of infill
T': thickness of compressed plant cylinder bounding upper and lower surfaces of the infill
A compression border occurs when the thickness of the original plant cylinder \(T\) equals the width of the compressed plant cylinder \(MT'\) at the margins of the infill (following Walton's definition of a compression border), and this is greater than the thickness of the compressed plant stem \(T'\) above and below the infill, i.e. \(T = MT' > T'\) (see Tables 5, 6). In one experiment (606), using rigid stems, this occurred exactly where both the compression border \(MT'\) and the original plant cylinder \(T\) measured 0.4cms, where \(T'\) was 0.01cms. The woody cylinder on the upper and lower surface of the infill had been compressed by 97.5%. In the other experiment of this type (612, 613), \(MT'\) was less than \(T\) but still greater than \(T'\). This also occurred in the non-rigid stems infilled and buried in a clay matrix \((T > MT' < T')\), but the compression borders were still obvious (Fig.3.7b; Plate3: B,D,F). In these experiments, where non-rigid stems were used, the plant cylinder is reduced to such a fine line that it is not easy to determine where it ends in the matrix.

In further experiments, the non-rigid stems were infilled and buried in a sand matrix. No compression borders were produced and the plant cylinder was reduced by 85% around the entire infill, i.e. \(MT' = T' < T\). The infill maintained its cylindrical shape and had not distorted to an ellipsoid, as was the case with the clay infills (Fig.3.7c).

(d) The effect of sediment grain size on the form of the "fossil"

The results of this experimental work have shown that the grain size of the sediment the plant stem is buried in has considerable effect on the dimensions (hence, form) of the resultant "fossil". Solid stems compressed in fine-grained sediments (clays) suffer considerable reductions in the vertical dimension of the stems (maximum of 97.5%). In contrast, stems compressed in a sand matrix undergo less reduction in the vertical dimension (40-50%), but are also reduced by 50-60% in the horizontal dimensions. The stems buried in a clay matrix retain a constant, or very slightly reduced, horizontal dimension during the compression.

In plant stems infilled and buried in a clay matrix, the internal horizontal dimension (IHD) increases substantially (averages 30%) as a result of horizontal expansion of the infill. In plant stems infilled and buried in a sand matrix, the IHD remains constant (i.e. the infill does not distort), whereas the overall horizontal dimension (OHD) is substantially reduced (by 30-40%); that is, the plant cylinder has undergone
Description of Plate 3

The results of the experimental compression of hollow plant stems infilled and buried in a clay matrix

A   T.S of a compressed, infilled, rigid plant stem (612). The infill has been compressed from a cylinder to an ellipsoid. The plant stem is slightly thicker at the margins of the infill than that bounding the upper and lower surfaces of the infill. (X 0.8)

B   T.S of a compressed, infilled, non-rigid plant stem (603). The margins of the compressed plant stem are beginning to form "compression borders". (X 1)

C   T.S of a compressed, infilled, rigid plant stem. "Compressions borders" are beginning to form at the margins of the infill as a result of the compression of the plant stem. (X 0.8)

D   T.S of a compressed, infilled, non-rigid plant stem (607). A "compression border" has formed at the right-hand margin of the infill. The entire stem has been reduced to a fine line. (X 1)

E   T.S of a compressed, infilled, rigid plant stem (606). Distinct "compression borders" have formed at the margins of the infill. (X 0.75)

F   T.S of a compressed, infilled, non-rigid plant stem (614). "Compression borders" have formed at the margins of the infill. (X 0.9)
a reduction in thickness.

The grain size of the sediment the plant stem is compressed in has a significant effect on the form of the "fossil". This must be related to the different mechanical properties of a clay sediment and a sand sediment. The clay matrix suffers considerable compaction during the compression (approximately 40%). It appears from these results that clay can also expand horizontally during compaction, i.e. has plastic properties causing an increase in the horizontal dimension of the infill. The sand matrix, though, only undergoes about 7% compaction during the compression, but the plant stems suffer a substantial reduction in the horizontal and vertical dimensions. It is postulated that this is a result of the sand grains repacking at the initial stages of compaction as a result of the compressive stress. The plant material is a very compressible structure within the sand matrix and the grains tend to move inwards, compressing the stem as repacking of the sand occurs (Fig.3.8c). This is because the stem represents a weakness with the sediment and the grains tend to migrate towards it. This is summarised in Fig.3.8.

(e) The resistance of plant tissues to compression

The rigid stems (Heracleum) used in this investigation showed considerable resistance to compression. This was clearly demonstrated when hollow stems were used. The hollow stems did not close up during the compression as was expected, but remained open (Fig.3.6a; Plate 2; C). The internal vertical dimension of the stem was reduced by up to 50%. However, the stem was not plastic enough to simply collapse into the lower surface. Instead, the stem underwent brittle failure and cracked (Plate 2; D).

Niklas (1978) showed, in his experimental work, that buckling occurred when hollow stems were compressed. This phenomena was not produced in this author's system. If the stems had been softened by degradation, the hollow would have probably closed up early in the burial due to the weight of the accruing sediment.

(f) The effect of a sediment infill on the form of the fossil

The degree to which infilling of a hollow stem occurs is dependant on several factors: the length and diameter of the stem and the flow conditions. This is demonstrated in Chapter 4. In general terms, the sediment (fine sand) infill reaches the roof of the hollow stem (Heracleum)
Description of Figure 3.8

a. Compression of a solid plant stem in a clay matrix. The principal stress axis is vertical and results in a drastic reduction of the vertical dimension of the plant stem. There is a tendency for the clay matrix to expand laterally (small arrows), but the plant stem has no plastic properties and maintains its original horizontal dimension.

b. Compression of an infilled, plant stem; infilled and buried in a clay matrix. The principal stress axis is vertical. The infill of the stem undergoes a lateral expansion during compression because of its plastic properties. The stem has few plastic properties but does deform laterally to a small extent. Therefore, the increase in the horizontal dimensions of the stem during compression results from the plastic properties of the clay matrix, but it is halted by the non-plastic properties of the stem which prevents further lateral expansion.

c. Compression of a stem in a sand matrix. The principal stress axis is vertical but, due to the incompressibility of the sand grains, the grains respond to the stress by repacking and rearranging into a tighter configuration. Since the stem represents a region of weakness within the sediment, there is a tendency for the sand grains to migrate towards the stem. This results in a reduction of the horizontal and vertical dimensions of the stem.
Fig. 3.8. The proposed difference in the mechanical behaviour of a sand and a clay matrix during compaction.
at the two ends and tapers towards the centre of the stem (Fig. 3.9a). The central part of the stem is usually unfilled, apart from 2-3mm of sediment. Once the pattern of the infill within the hollow stems had been established, the stems could be compressed and then sectioned at positions where the thickness of the infill was known (methodology described in section 3.3). Therefore, the behaviour of the plant cylinder, on compression, in relation to the degree of infilling could be determined.

At both ends of the stems, where the infill reaches the roof of the hollow stem (position A), the infill maintains its cylindrical shape after compression, e.g. 104-2A, 105-1A, 124-1A (see Table 7). The internal dimensions of the stem, i.e. the infill, suffered little change during the compression as a result of the incompressibility of the sand infill. The overall horizontal and vertical dimensions underwent some reduction; up to 30% in 124-1A. This is a reduction in the thickness of the plant cylinder around the sand infill (Fig. 3.9b, f, i; Plate 4; A, C, I).

In the centre of these stems (position C), where the infill only reached a thickness of 2-3mm during burial of the stem, the transverse-section shows a different structure than at position A. As a result of the compression process, the unsupported roof (due to the absence of infill) of the stem has begun to collapse and distort (Plate 4; D, J). The stems at this position have undergone a substantial decrease in the vertical dimensions as the plant stem collapses onto the infill, e.g. 107-1C, 116-1C. This is usually accompanied by a reduction in the horizontal dimensions of the stem. The stem collapses and is compressed towards the infill, resulting in a reduction in horizontal dimensions. It appears from these results that most of the deformation has been taken up in the collapse/compression of the plant stem towards the infill, and very little reduction of the plant tissues has occurred. In some examples, e.g. 116-1B (Plate 4; F) the hollow stem has closed up where there was an absence of infill and the IHD has been reduced by 100% and the OHD by 84%. In this case, the actual plant tissues have been compressed following closure of the hollow stem.

Longitudinal sections through the compressed plant stems demonstrate the collapse of the upper stem surface onto the infill, where the infill had not reached the roof of the stem along its entire length (Plate 2: H).

There is considerable variation in the behaviour of the rigid plant stem during the compression. This is dependent on the degree of development
TABLE 7: The results of compression of stems infilled and buried in the flume tank

<table>
<thead>
<tr>
<th>Exp. No.(Position)</th>
<th>Plant Material</th>
<th>Matrix</th>
<th>Kg/cm²</th>
<th>MR</th>
<th>OHD</th>
<th>IHD</th>
<th>OVD</th>
<th>IVD</th>
</tr>
</thead>
<tbody>
<tr>
<td>104-2 (A)</td>
<td>Heracleum</td>
<td>Fine sand</td>
<td>0.20</td>
<td>19%</td>
<td>constant</td>
<td>constant</td>
<td>R 22.7%</td>
<td>R 13.3%</td>
</tr>
<tr>
<td>104-2 (C)</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.20</td>
<td>19%</td>
<td>constant</td>
<td>constant</td>
<td>R 13.2%</td>
<td>R 92%</td>
</tr>
<tr>
<td>105-1 (A)</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.20</td>
<td>21%</td>
<td>R 10%</td>
<td>R 6.6%</td>
<td>constant</td>
<td>R 6.6%</td>
</tr>
<tr>
<td>105-1 (B)</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.20</td>
<td>21%</td>
<td>R 10%</td>
<td>R 26.6%</td>
<td>constant</td>
<td>R 26.6%</td>
</tr>
<tr>
<td>107-1 (B)</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.41</td>
<td>14%</td>
<td>R 33%</td>
<td>R 12.5%</td>
<td>R 54%</td>
<td>R 30%</td>
</tr>
<tr>
<td>107-1 (C)</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.41</td>
<td>14%</td>
<td>R 12.5%</td>
<td>R 58.3%</td>
<td>R 62.5%</td>
<td></td>
</tr>
<tr>
<td>116-1 (B)</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.35</td>
<td>13.7%</td>
<td>R 33%</td>
<td>R 40%</td>
<td>R 50%</td>
<td>R 75%</td>
</tr>
<tr>
<td>116-1 (C)</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.35</td>
<td>13.7%</td>
<td>R 26%</td>
<td>R 75%</td>
<td>R 63%</td>
<td>R 64%</td>
</tr>
<tr>
<td>124-1 (A)</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.32</td>
<td>12%</td>
<td>R 35%</td>
<td>R 15.4%</td>
<td>R 30%</td>
<td>R 20%</td>
</tr>
<tr>
<td>124-1 (C)</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.32</td>
<td>12%</td>
<td>R 10%</td>
<td>R 15.4%</td>
<td>R 10%</td>
<td>R 46%</td>
</tr>
<tr>
<td>134-1 (B)</td>
<td>&quot;</td>
<td>&quot;</td>
<td>1.3</td>
<td>26%</td>
<td>I 40%</td>
<td>I 20%</td>
<td>R 5%</td>
<td>R 33%</td>
</tr>
<tr>
<td>134-2 (A)</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.3</td>
<td>20%</td>
<td>R 8%</td>
<td>constant</td>
<td>R 16%</td>
<td>R 13%</td>
</tr>
<tr>
<td>134-2 (C)</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.3</td>
<td>20%</td>
<td>R 20%</td>
<td>R 33%</td>
<td>R 60%</td>
<td>R 66%</td>
</tr>
</tbody>
</table>

MR : matrix reduction  
OHD : overall horizontal dimension  
IHD : internal "  
OVD : overall vertical dimension  
IVD : internal "  
I : increase  
R : reduction
Description of Figure 3.9

a. The general structure of the infill, in longitudinal section, formed in a stem cavity when buried in a laboratory flume tank. A, B and C represent the positions at which the stems were sectioned after they had been compressed in the wet compression apparatus.

b. Transverse-section of the uncompressed plant stem, showing the structure of the infill. On compression, the stem has suffered little distortion as a result of the infill filling the entire, original stem cavity. (X 1)

c. T.S at the centre of the uncompressed stem. The infill only half-filled the stem cavity. On compression, the unsupported roof of the stem has collapsed and been compressed. This has resulted in a distorted stem compression being formed. (X 1).

d. T.S of the uncompressed stem, showing the cavity half-filled with sediment. On compression the stem has collapsed and been compressed around the infill (X 1).

e. T.S of the uncompressed stem in which only a fine layer of sediment occupies the base of the stem cavity. On compression, a very distorted structure is produced. (X 1).

f. T.S of the uncompressed stem in which the cavity is totally filled with sediment. On compression the infill has maintained its original structure. The plant stem has been reduced in both horizontal and vertical dimensions. (X 1).

g. T.S of the uncompressed stem where the infill has not quite reached the roof of the stem. On compression the roof collapses onto the infill. (X 1).

h. T.S. of the uncompressed stem where the infill has not quite reached the top of the stem. On compression the roof collapses onto the infill. (X 1).

i. T.S of the uncompressed stem, showing a total infilling of the hollow. On compression the shape of the infill is maintained. (X 1).

J. T.S of the uncompressed stem in which the hollow is half-filled with matrix. On compression the unsupported roof of the stem collapses and is compressed onto the infill. The stem has fractured during the compression process. (X 1).
Description of Plate 4

The results of the experimental compression of stems filled and buried in the flume tank and then compressed in the wet compression apparatus. (All stems are *Heracleum* and shown in T.S. They are all filled and buried in fine sand.)

A. 124-1A (see Fig.3.9f). The stem has compressed around an almost total infill of the stem cavity. (X 1)

B 124-1C (see Fig.3.9g). The stem is beginning to collapse and crack as there is no sediment infill supporting the stem roof. (X 1)

C 1051-1A (see Fig.3.9b). The stem has compressed around the infill of the entire stem cavity. (X 0.6)

D 105-1B (see Fig.3.9c). The unsupported roof of the stem has begun to collapse/compress. The infill of the stem base has retained the curvature of the lower surface. (X 0.6)

E 116-1B (see Fig.3.9d). The stem has collapsed and compressed onto the partial infill of the original stem cavity. (X 0.8)

F 116-1C (see Fig.3.9e). The stem has completely collapsed/compressed onto the infill and this has resulted in a very distorted "stem compression". (X 0.8)

G 107-1B. The unsupported roof of the stem is beginning to collapse and compress onto the infill. (X 0.8)

H 107-1C. The stem cavity is very reduced as the stem roof collapses onto the fine layer of infill. (X 1)

I 134-2A (see Fig.3.9i). The stem has compressed around the infill which occupies the entire stem cavity. (X 1.8)

J 134-2C (see Fig.3.9j). The stem has collapsed and compressed onto the infill, producing a very distorted stem compression. (X 2)
of the sediment infill. Where partial infilling of the stem has occurred, the sediment is obviously contained by the lower surface of the stem. This results in relatively little distortion of this surface during the compression as it is "protected" by the sediment infill. The unsupported roof, in contrast, of the stem undergoes substantial distortion, producing a very irregular upper surface collapsing around the infill. In these experiments, closure of the upper surface around the infill has not always occurred, but the pattern of this can be easily detected. The structure of the compressed stem is dictated by the degree of sedimentary infill within the original hollow stem. Therefore, along the length of the stem the structure of the "compression fossil" can show significant variation dependent on the degree of infilling of the hollow stem (Fig.3.9).

In partially infilled stems, the collapse of the unsupported stem roof appears to cause considerable distortion of the plant cylinder. This would result in a very poor impression of the internal structure of the plant stem onto the infill or adjacent matrix, e.g. internal ribs in Calamites. There would be a much better impression of the internal structure of the plant stem formed on the lower surface of the infill where distortion of the plant cylinder was negligible. This indicates a "wayupness" of the fossil infill, poor impression of internal structure on the upper surface, and good structure preserved on the lower surface. Walton (1936), in his discussion on the formation of pith casts, did not discuss "wayupness", probably because he did not consider partial infilling of hollow stems. He did consider "wayupness" in terms of the fossilisation of a leaf and stated "the shape of the resulting fossil is principally based on the form of the lower surface of the original plant fragment". This is true in the case of stem compressions where the upper surface has collapsed/compressed into the lower, forming a C-shaped structure, and also seems to occur in partially filled hollow stems.

No compression borders were produced in the experiments where the hollow stems had been completely infilled and then compressed. The plant tissues underwent a reduction in thickness in the horizontal and vertical dimensions. This occurred, to the greatest extent, in 124-1 where the plant cylinder was reduced by 30%. Compression borders may not have been formed, because the compressive stress applied to the sediment may not have been high enough to deform the plant tissues. The overall reduction in the plant tissues indicates that in this sand matrix compression borders may not be produced. This may be related to the behaviour of the
sand grains during the compression, or to the fact that very high compressive stresses are needed to deform plant stems in a sand matrix.

3.5 Comparison of the experimental results with fossil infills and compressions

(a) Stem shape

Several stem compressions and infills were sectioned to determine the nature of the transverse-section of the stem. In most cases, some matrix had entered the stem, but the upper surface of the stem had collapsed or been compressed into the lower, giving a concave-downwards or C-shaped transverse-section. This is clearly demonstrated in specimens of endocortical casts of *Lepidodendron* (GR/R/AD; GR/UN/H) (Plate 5; A,B). These are formed by the infilling of the cortical cavity with sediment. In one example the stele compression can be seen (Plate 5; B). On the upper surface of the cast there are poorly preserved leaf cushions present. The leaf cushions are well preserved on the lower surface. These are the impressions of leaf cushions through the stem cortex and not the outer surface of the stem bearing leaf cushions (see Rex & Chaloner 1983, p242-245). The collapse of the upper surface of the stem has distorted the impression of the leaf cushions. The upper surface may have collapsed as a result of decay during infilling of the stem, or it may have been compressed into the lower after burial. This cannot be determined from the fossil.

The C-shaped structure of infilled and compressed stems is well demonstrated in a *Calamites* specimen (GR/SW/M) collected in situ from the Westphalian B of the Yorkshire coalfield. Sectioning of the pith cast shows that it is distinctly C-shaped (Plate 5; C) and is infilled with a claystone matrix. The structure of the rib impressions is very different on the upper and lower surface of the cast. On the lower surface they are straight and parallel (Plate 5; D). Each rib measures approximately 0.05cms wide and there are 8-9 ribs/cm. On the upper surface of the cast the ribs are very different (Plate 5; E) forming undulating lines running along the infill. These ribs measure about 0.2cms wide and there are 4 ribs/cm. Undulating ribs are one of the main characters used in defining the species *Calamites undulatus* (Crookall 1969). In this *Calamites* specimen the upper surface of the pith cast resembles *Calamites undulatus*, whereas the lower surface resembles a species with straight ribs, probably *Calamites cisti*. This phenomenon may result from the collapse of the
Description of Plate 5

The structure of fossil stem compressions

A  T.S of an endocortical infill of a Lepidodendron (GR/UN/H). The stem has a distinct C-shaped structure. (X 1)

B  T.S of an endocortical infill of a Lepidodendron (GR/R/AD). The stem is surrounded by opaque resin. The stem has a C-shaped structure. The compression of the stele (s) has been preserved within the infill. From the Radstock coalfield. (X 1)

C  T.S of a Calamites, showing a distinct C-shaped structure. This specimen was collected in situ and shows very different rib (r) structures on the upper and lower surfaces of the stem. From the Yorkshire coalfield (GR/SW/M). (X 4)

D  View of the ribs on the lower surface of the stem shown in C. The ribs are very straight, small (in width), and parallel to each other. (X 2)

E  View of the ribs on the upper surface of the stem shown in C. The ribs are very wide and undulate along the stem. (X 2)
upper surface of the stem onto the infill. This collapse may have caused the distortion of the ribs, but this does not explain why the ribs are large and few on the upper surface, and small and numerous on the lower surface.

(b) **Compression borders**

The evidence from the experimental work indicates that compression borders form more readily when the stem is infilled and buried in a fine-grained, very compressible matrix. Evidence from fossils shows that compression borders are more commonly seen at the margins of pith casts of *Calamites* preserved in a fine-grained matrix, e.g. Gsd 6715 (Plate 6; A,B). In this specimen the compression borders measure 0.1cm wide, forming a distinct coaly line bounding the infill. In contrast, a *Calamites* preserved in a coarse, less compressible matrix does not show a distinct compression border, e.g. Gsd 18288 (Plate 6; C). It is difficult to determine whether a border formed during the compression of the woody cylinder since no organic matter is preserved. At the right-hand margin of the cast there is a faint structure on the matrix which may represent the impression of a compression border (Plate 6; C). The width of the compression border depends on the thickness of the woody cylinder in the original stem. The woody cylinder can be of very varied thickness and this is independent of the pith size (Eggert 1962); that is, a small pith may have been surrounded by a very thick woody cylinder and, therefore, a small pith cast may have a very wide compression border. The absence or presence of a very small border around a sandstone pith cast may be due to the small development of a woody cylinder in the original stem. The experimental results from this investigation have shown that there is a tendency for the plant cylinder to reduce in thickness around a sand infill. If this is applied to the fossil pith casts, the width of the compression border bounding a sandstone infill may not be a very accurate measure of the thickness of the original woody cylinder.

The most distinct compression borders encountered during the course of this work are those bounding the stele compression/infll in the cortical infills of stigmarian axes (Plate 6; D,E). The pith cavity at the centre of the stele had been infilled with a quartzitic silt (containing 80% quartz), which also infilled the cortical cavity of the Stigmaria. The compressed pith infill has an elliptical transverse-section bounded by two horizontal ribbons of coaly matter at either side of the infill (Plate 6; F). At high magnifications it can be seen that the stele compression is not simply a coaly ribbon, but is composed of many
Description of Plate 6

The structure of compression borders in and bounding fossil casts

A  Calamites (Gsd 6715). A Calamites pith cast preserved in shale. The coaly matter, representing the compression of the plant tissues, is still present on the surface of the fossil. (X 0.75)

B  Magnification of A, showing compression borders (c) bounding the pith cast. (X 2)

C  Calamites (Gsd 18288) preserved in sandstone. The pith cast has considerable topography but has lost its coaly matter. There may be an impression of a compression border (arrow) at the margin of the cast. (X 0.6)

D  T.S of an endocortical cast (ec) of Stimaria containing the compression of the stele (sc). (GR/SW/C) (X 1)

E  T.S of an endocortical cast of Stigmaria, showing the compression of the stele (sc). (GR/SW/A) (X 1)

F  Magnification of D, showing the stele compression surrounding the infill of the pith cavity. Compression borders (cb) can be seen at the margins of the pith cavity infill. The coaly matter of the stele compression is composed of many minute segments of coal. (X 2)

G  Magnification of E, showing the stele compression with slightly irregular compression borders (cb). The stele compression has a C-shaped structure as if the pith cavity was not completely infilled when the compression began. (X 2)
individual strands of coaly matter, each separated from the adjacent strand by a minute layer of sediment (Plate 6; F,G). The compression borders are composed of minute layers of the coaly matter and are not a continuous plate of coal. Evidence from permineralised Stigmaria shows that the stele of the rhizome is divided into blocks. The gaps between the blocks of the woody cylinder were termed lateral appendage gaps by Frankenburg & Eggert (1969) and are the points from which rootlet traces arose. Since the woody cylinder was not a continuous structure, matrix would have got into the lateral appendage gaps when the axis was infilled. As a result of compression, each block of the woody cylinder has formed a strand of coaly matter. Calculations ($MT' = T : T - T'$ = amount of compression of stele) show that the stele has undergone 96.4% compression in one example (GR/SW/A) and 96.8% in another example (GR/SW/C2).

In conclusion, it can be said that compression borders can be produced experimentally by the compression of infilled stems, and they are also seen at the margins of fossil pith casts. The experimental work indicates that compression borders are more likely to form where hollow stems are infilled and buried in a fine-grained, compressible sediment, rather than in a coarse-grained, incompressible sediment. This is borne out, to a certain extent, by the fossil evidence. Compression borders are more commonly seen bounding pith casts composed of fine-grained sediments.

(c) The fracturing of plant tissues

The cracking and splitting of hollow stems of Heracleum on compression, as a result of the rigidity of the plant tissues, can be seen to have occurred in some specimens of Calamites. Calamites can have a large development of secondary wood surrounding the pith cavity. The pith cavity is produced during the life of the plant by the failure of tissue at the core of the axis to keep pace with the extension growth of the peripheral tissues. The secondary wood in Calamites is composed of numerous wedges of xylem which are separated by wood rays (Plate 7; E). In many specimens of Calamites in coal balls, the secondary wood has split in the region of the rays forming wedge-shaped cracks (Plate 7; E). This cracking of the secondary wood is very similar to the classical arch failure in building construction where flying buttresses are used to prevent arches collapsing.

Many specimens of Calamites pith casts (e.g. GR/UN/A; GR/K/E) have distinct ridges of sediment running along the outer surface of the cast.
Description of Plate 7

The structure of fossil pith casts

A  Calamites pith cast (GR/UN/A), showing a ridge (r) of structureless sediment crossing the impression of the stem node. (X 0.7)

B  Calamites pith cast (GR/UN/A), showing the reverse surface as seen in A, along which there is a ridge (r) of sediment crossing the stem node. (X 0.7)

C  T.S of the Calamites pith cast shown in A and B. The ridge (r) of sediment can be seen standing above the rest of the cast. (X 1.6)

D  Artjsia pith cast (GR/UN/D), showing the impression of the transverse septations that extend into the pith cavity of the stem. Crossing these septations is a ridge (r) of sediment. (X 0.9)

E  T.S of a permineralised Calamites (D.B. coll.1), showing the radially arranged secondary xylem (sx) and the wood rays (wr) of the stem. The stem has cracked (c) along the wood rays on the upper and lower surfaces of the stem. (X 3.5)

F  T.S of a Calamites pith cast (GR/R/AH), showing the structure of the fine-grained infill. The stem has cracked during its fossilisation, producing a furrow (f) which runs along the entire length of the pith cast. (X 2)
Description of Figure 3.10

a. Transverse-section of an uncompressed Calamites, showing the radially arrangement of wood rays in the stem. The pith cavity has been partially infilled by sediment.

b. As the stem collapses and is compressed, the woody cylinder fractures along the wood rays. The sediment infill migrates into the fractures as the stem compresses around the infill.

c. Loss of the woody cylinder from the consolidated sediment infill leaves a pith cast bearing the impression of the internal surface of the woody cylinder. On the upper and lower surfaces of the pith cast are ridges of sediment representing the infill of the fractures in the woody cylinder.
Fig. 3.10. The formation of sediment ridges on a *Calamites* pith cast.
These ridges cross the nodes of the pith cast and appear to be structureless wedges of sediment. The ridges may occur on the upper or lower surface of the cast, and may run along its entire length or be discontinuous. Transverse-sections of pith casts show that these ridges have the same sediment composition as the infill and are continuous with the infill (Plate 7; C).

It is concluded that these structureless ridges form when the secondary wood cracks during infilling of the stem or at the onset of compression. As the plant stem compresses, the sediment infill moves into the cracks in the secondary wood (Fig.3.10a,b). Subsequent loss of the organic matter from around this infill leaves a pith cast with distinct ridges running along the surface of the cast (Fig.3.10c).

This type of structure can also be seen in specimens of *Artisia* (Plate 7; D), the pith cast of *Cordaites* stems. These stems are structurally very similar to *Calamites* in having an outer woody cylinder bounding a pith cavity. In *Cordaites*, pith septations extend transversely into the outer part of the pith cavity. These are not present in *Calamites*.

Ridges of sediment do not always form on the surface of pith casts. Occasionally, furrows have formed along the surface of the pith cast. These are produced when the stem has collapsed inwards (Plate 7; F).

*Calamites* demonstrates the rigidity of certain tissues, namely, secondary wood, to the compression process and its potential for fracture. The wood splits along one or more wood rays allowing collapse of the stem around the infill. Experimental results suggest that this cracking is more likely to occur along the unsupported roof of a hollow or partially infilled stem. Observations of fossil pith casts indicate that splitting can occur on both the upper and lower surfaces of the plant cylinder.

(d) The effect of grain size

The effect of the grain size of the sediment on the form of the fossil is apparent in the topography of the fossil. Fossils infilled or preserved in a sandstone matrix have a greater topography when exposed by a fracture plane than those preserved in a fine-grained, more compressible matrix. Results from this experimental work have shown that stems compressed in an incompressible matrix, i.e. sand undergoes significant reductions in horizontal dimensions. In contrast, stems compressed in a more compressible
matrix, i.e. clay either shows an increase in horizontal dimensions (in the case of infilled and hollow stems) or the horizontal dimension remains constant. These differences in the behaviour of the plant stems in different compressibilities of sediment, obviously cannot be deduced from the fossils but should be borne in mind when determining the original shape and dimensions of a plant organ from a compression fossil.

3.6 Conclusions

By using this wet compression apparatus, considerably more has been learnt about the compression process than was possible in the dry experimental work. One of the most important factors that has been determined in this investigation is the effect of grain size of the sediment on the form of the "fossil". The nature of the sediment drastically effects the horizontal dimensions of the plant organ during the compression. This is interpreted as being directly related to the difference in mechanical behaviour of the different sediments during compacting. In the sand matrix, the sand grains react to the compressive stress by moving relative to each other and repacking into a tighter structure. This movement seems to occur inwardly in all directions because the plant stem represents an area of weakness and compressibility within the sediment. This results in a substantial reduction in the horizontal as well as vertical dimensions of the plant stem. The clay matrix behaves quite differently. The clay minerals react to the compressive stress by undergoing large degrees of vertical compaction. Where solid plant stems are buried in the matrix, the horizontal dimensions remain constant during the compression. This is interpreted as resulting from the non-plastic properties of the plant stem, i.e. the stem cannot expand laterally and the stem retains the original horizontal dimension. In experiments where the stems were left hollow or infilled with the clay matrix, horizontal expansion of the plant stem did occur. In the case of the clay infilled stem, the infill rather than the plant stem underwent horizontal expansion. This increase in the horizontal dimension of the infill seems to have been halted by the surrounding plant stem which does not have the same plastic properties as the clay matrix. When the plant stems were left hollow, they cracked during the compression, i.e. behaved as a brittle material because the stems could not deform plastically during the deformation. Therefore, the nature of the sediment the plant organ is buried in during the compression process and, to some extent, the rigidity of the tissues composing the plant organ, will determine the form of the resulting compression fossils.
Many of the structures produced during this investigation can be seen in plant compression fossils. Compression borders were formed marginally when hollow plant stems were infilled and compressed in a clay matrix. These borders can be seen developed marginally in Calamites pith casts and the stele compressions within endocortical infills of Stigmaria. The experimental work indicates that compression borders may not form in coarser, less compressible matrices.

The shape of the experimentally compressed stems, in vertical section, can be related to fossil stem compressions. The C-shaped structure, seen in transverse-sections of Calamites and Lepidodendron, were produced in the experiments. This structure is formed as a result of the upper surface of the stem being compressed (with some collapse) into the lower surface of the stem. The upper surface seems to "take up" the compressive stress, and this results in a distorted upper surface in the fossil, whereas the lower surface retains its original curvature.

It is demonstrated that the degree of infilling that has occurred of a hollow plant structure dictates the form of the fossil. Infilling and burial of stems in a laboratory flume tank, and subsequent compression in the apparatus, has allowed the natural system to be more closely modelled, and reproduction of some of the features seen in actual fossils.

This type of investigation has shown that structures can be produced during the compression which are not structurally related to the original plant. For example, "cracking" of the secondary wood in Calamites produces ridges of sediment running along the surface of the pith casts. These ridges are related to the collapse and compression of the stem, and are a "compression-product" and not a feature of the original stem.

This type of experimental modelling technique has enabled the effects of wet compacting sediments and compressing plant tissues on the form of the fossil to be determined. The form of the plant compression fossil, as seen from this investigation, is dependent on several important factors: the nature of the sediment surrounding the plant organ; the degree of infilling of the plant structure that occurred during burial and, finally, the rigidity of the plant tissues or the amount of decay/collapse that occurred of the plant tissues before the compression process began.
CHAPTER FOUR: A laboratory flume investigation of the processes involved in the formation of fossil stem infill

(see appendix B)
CHAPTER FIVE: The structure of stem infills produced in settling tank experiments
5.1 Introduction

The infilling and burial of hollow stems of varying lengths under different current velocities was investigated, using a small laboratory flume tank (this work is described in Chapter 4). This apparatus models sedimentation along a straight alluvial channel. One of the important results of this work was that total infilling of a stem cavity never occurred, regardless of the length and diameter of the stem and the flow conditions within the channel. In order to contrast the sedimentation of sands in a flume, a series of experiments was conducted using a settling tank. In the settling tank, fine clay particles were allowed to sediment from suspension in a standing body of water onto hollow plant stems placed on the floor of the settling tank. Clay-size particles had not been used in the flume tank because of the long periods of time it takes for the sediment to settle from suspension in a current. Using a settling tank it is possible to investigate whether infilling of hollow plant stems would occur in an environment with virtually no current activity. Calamites pith casts from the British Coal Measures are commonly composed of shale, and it would be interesting to see if stem infills of clay-size sediment could be produced in the settling tank, and whether they had a comparable structure with the fossil pith casts.

One of the problems of using a settling tank is that complex patterns of edge-related secondary flows may occur when the body of water is disturbed (Allen 1982). The addition of sediment to the tank did create some turbulence initially, and it must be borne in mind that this unnatural current activity may have been responsible for the formation of part of the infill within the hollow stems.

5.2 The method and materials

The settling tank was composed of glass and measured 33cms x 30cms x 35cms. A number of stems, which had been waterlogged by a stream of constantly running water for three weeks, were placed in the tank. The stems immediately sank onto the floor of the tank. A colloidal solution of clay (150mls) was added to the tank at the top of the water level. This solution was added each day for three weeks. The addition of the solution was done slowly so that the turbulence created was kept to a minimum. After three weeks the water was siphoned off and the sediment left to dry. After the clay had dried out, the structure and degree of infilling of the hollow stems could be ascertained.
Two experiments were conducted in the settling tank, and the dimensions of the stems used in each are described below:

**Experiment I**

<table>
<thead>
<tr>
<th>Stem</th>
<th>Length</th>
<th>Diameter of hollow</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stem 1 (Heracleum)</td>
<td>12cms</td>
<td>1.6cms</td>
</tr>
<tr>
<td>Stem 2 (Sonchus)</td>
<td>27cms</td>
<td>0.7cms</td>
</tr>
</tbody>
</table>

**Experiment 2**

<table>
<thead>
<tr>
<th>Stem</th>
<th>Length</th>
<th>Diameter of hollow</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stem 1 (Heracleum)</td>
<td>10cms</td>
<td>1.5cms</td>
</tr>
<tr>
<td>Stem 2 ( &quot; )</td>
<td>6.5cms</td>
<td>1.2cms</td>
</tr>
<tr>
<td>Stem 3 ( &quot; )</td>
<td>5.0cms</td>
<td>2.5cms</td>
</tr>
<tr>
<td>Stem 4 ( &quot; )</td>
<td>3.0cms</td>
<td>1.5cms</td>
</tr>
</tbody>
</table>

5.3 Results

The clay particles settled out of suspension into distinct, thin horizontal laminations, each lamina reflecting a slight change in grain size as the sediment settled out of suspension. In the first experiment, where long stems were used, the degree of infilling was not very great. In the long stem of Sonchus, there was no matrix fill along the stem apart from the first 2-5 millimetres at the two stem entrances. The shorter stem, in contrast, had a layer of sediment occupying the floor along the entire length of the stem. This had only reached a thickness of 2-3mms.

In the second experiment, the infilling had occurred to a much greater extent, as the stems used were much shorter and the colloidal solution added to the tank each day was increased from 150ml a day to 300ml a day. An infill had formed within the stem cavity of the 10cms stem. The infill was thickest at the two entrances of the stem and thinned towards the centre of the stem (Fig.5.1a). The infills of the 5.0cms and 3.0cms stems showed a uniform thickness of 0.5-0.8cms along the stem cavity (Fig.5.1b). The infills showed a structure consisting of minute laminations which were concaved downwards, following the topography of the stem cavity (Fig.5.1c). The infills of the stem had not reached the roof of the cavities and the stems had not been completely buried during the three-week sedimentation period. The drying-out of the clay, before the stems could be removed with the infill intact, had caused the infill
Fig. 5.1a. Longitudinal section of clay infilled stem.

Fig. 5.1b. Longitudinal section of the infill formed in a short stem.

Fig. 5.1c. Transverse section of the short stem showing the structure of the infill.
and the enclosing matrix to shrink considerably.

5.4 Comparison with fossil pith casts

The pith casts of Calamites, composed of shale when sectioned in longitudinal and transverse-section, show a distinct laminated structure. These laminations are approximately 2-3mm in thickness and are all parallel or sub-parallel to the long axis of the stem. The infills show very little other structure. Some may have a few microripples present within a single lamination, but generally the infill is just composed of these horizontal laminations (Plate 8; A, B, C, D).

5.5 Discussion

The main aim of these settling tank experiments was to contrast them with the alluvial channel experiments. Infills were formed within the hollow plant stems, indicating that substantial current activity is not necessarily required to transport sediment into the pith cavity. The would only occur, obviously, if there was very fine sediment in suspension. The structure of the infills produced in the stems in the settling tank is distinctly different from those formed in the flume tank. The infill has a very laminated structure in those formed in the settling tank, and this contrasts with the much more homogeneous structure of the infills formed in the flume. In the medium length stems (approximately 10cms), the infills formed in the settling tank showed a slightly wedged appearance, with the thickest layer of sediment having been deposited at each end of the stem, thinning towards the centre of the cavity. This is similar to the structure of the infills produced in the flume, where sediment is deposited at the stem entrances after the flow separates when the passage of the current through the stem is restricted. Further experimentation is required to determine whether the clay infill would reach the roof of the stem cavity before the stem was buried. From these initial results, it appears that it may, but as coarse material accrues out of suspension at the stem entrances, the passage of the finer sediment in suspension into the stem cavity becomes restricted. To produce an infill of this sediment grain size requires fairly high rates of sedimentation so that the infill can form before the stem has decayed and collapsed on the sediment surface.
Description of Plate 8

The structure of Calamites pith casts infilled with shale

A  T.S of a Calamites (GR/R/AG), showing the structure of the infill, which consists of a series of minute horizontal laminations. The margins of the infill are delineated by the fine coaly line. (X 1.2)

B  L.S of a Calamites (GR/IG/A), in which the infill consists of minute laminations. (X 2)

C  L.S of a Calamites (GR/UN/K), showing the laminated structure of the infill. (X 1)

D  L.S of a Calamites (GR/R/AH), in which small microripples are present within the structure of the infill. (X 0.6)
CHAPTER SIX: The compression state of preservation of Carboniferous lycopod leaves

(see appendix C)
CHAPTER SEVEN: The structure of pteridosperm leaf compressions and the mechanics of their fossilisation
7.1 Introduction

It has been demonstrated that apparently flat, coaly compressions, e.g. *Cyperites*, have considerable structure in the vertical dimension and are not simply "flattened" leaves. The same techniques have been applied to compression fossils of the fern-like foliage borne by the pteridosperms. These fossils are very common in the shales of the Farrington Group (Westphalian D) of the Radstock Coalfield. Most discussions of the pteridosperm leaf compressions have concentrated on the nature of the variation seen on the surface of the leaves in the recognition of species (Wagner 1968; Crookall 1955).

In this investigation, two genera have been examined - *Alethopteris* and *Neuropteris*. Specimens of *Alethopteris* have been sectioned, intact in the matrix, to determine the structure of the leaf compression. By re-assembling the part and counterpart of the leaves and then vertically sectioning them, the pathway the fracture plane took to expose the compression has been determined. The structure of the leaf compression is related to the uncompressed leaf and the factors which have dictated the form of the leaf compression fossils are discussed. These pteridosperm leaves are compared to the leaf compression/impressions of *Glossopteris* and *Cordaites*.

7.2 The nature of the part-and counterpart

(a) *Alethopteris*: two common species found in the Radstock Coalfield are *A. serli* and *A. lesquereuxii*. When these leaves are exposed by a fracture plane the part and counterpart consist of a conformable compression fossil (Plate 9; A,B). The fossil is usually in the form of one or more pinnae which are composed of numerous pinnately arranged lobes or pinnules (these are not strictly pinnules since they are not separate structures but join near the rachis; the term is used here following the usage of Crookall (1955)). Each pinna has a central rachis from which midveins branch off and extend into the pinnules. In the pinnules the midveins branch into numerous secondary veins which extend to the pinnule margin (Plate 9; C,D). It is the topography of these structures which is important, as will be demonstrated later. In the conformable compression fossil, the pinna is composed of positive pinnules, which extend above the fracture surface (Plate 9; C). The rachis and midveins are always "negative", forming deep furrows in the fossil. The secondary veins on the pinnules are in the form of positive coaly ridges.
Description of Plate 9

The part and counterpart of the Pteridosperm leaves (all specimens from the Radstock coalfield)

A. Alethopteris serli, the conformable compression (GR/R/XXXVIIB) (X 2). (r) rachis; (p) pinnule; (s) secondary veins.

B. Alethopteris serli, the conformable impression (GR/R/XXXVIIA) (X 2).

C. Alethopteris serli, detail of an individual pinnule in A (X 2.5). The topography of the pinnule from A-A' is shown in Fig.7.1a (X 2.5).

D. Alethopteris serli, the counterpart of the pinnule shown in C (X 2.5). The topography of the pinnule from B-B' is shown in Fig.7.1b.

E. Neuropteris ovata, the conformable compression (GR/R/XXXXIIIA) (X 2). (r) rachis; (p) pinnule; (s) secondary veins.

F. Neuropteris ovata, the conformable impression (GR/R/XXXXIIIB) (X 2).

G. Neuropteris ovata, detail of an individual pinnule in E (X 2.5). The topography of the pinnule from C-C' is shown in Fig.7.1e.

H. Neuropteris ovata, the counterpart of the pinnule sown in G (X 2.5). The topography of the pinnule from D-D' is shown in Fig.7.1f.
Description of Fig. 7.1

a. The topography of the *Alethopteris* pinnule compression showing positive secondary veins.

b. The topography of the conformable impression showing negative secondary veins.

c. The "burnt off" compression, now an impression, with negative secondary veins.

d. The "burnt off" impression showing negative secondary veins.

e. The topography of the *Neuropteris* pinnule compression showing positive venation.

f. The topography of the conformable impression showing negative venation.

g. The topography of the *Glossopteris* positive leaf impression.

h. The topography of the conformable negative leaf impression.

i. The topography of the cordaite leaf compression.

j. The inferred topography of the impression of the cordaite leaf.
Fig. 7.1. Diagrammatic topography of the part and counterpart of Alethopteris, Neuropteris, Glossopteris and Cordaites.

Alethopteris

b.

loss of coaly matter
d.

Neuropteris

f.

Glossopteris

h.

Cordaites

i.
In the corresponding conformable impression, these structures are topographically opposite (Fig. 7.1a,b) i.e. negative pinnules, positive rachis and midveins and negative secondary veins.

(b) *Neuropteris*: common species found at Radstock are *N. ovata* and *N. scheuchzeri*. These leaves are compound, being formed by constituent pinnae, as in *Alethopteris*, but they have a more subdued topography. The part and counterpart of these leaves consist of a conformable compression (Plate 9; E,F,G,H). The pinnules, rachis, midveins and secondary veins show the same topography on the compression and impression as *Alethopteris* (Fig. 7.1e,f).

(c) *Cordaites*: these leaf compressions differ from the pteridosperm foliage. They are strap-like leaves lacking a midrib, but are composed of numerous parallel veins (Plate 10; E,F). No part and counterpart had been preserved in the material examined. The compression fossil consisted of numerous positive coaly ridges standing above the coaly matter of the rest of the leaf. Where the coal had been lost from the surface of the fossil, the matrix exposed showed a negative impression of the veins (Fig. 7.1j) (i.e. the veins were grooves in the sediment). Therefore, it can be assumed that the counterpart of the *Cordaites* leaf was conformable, being composed of negative impressions of the parallel veins (Fig. 7.1j).

(d) *Glossopteris*: the material examined was from Natal, South Africa, and was borrowed from the British Museum (Natural History). The leaves are preserved in a fine-grained pink/buff siltstone, and are just impressions, the coaly matter having been lost. Examination of these specimens showed that in some cases both part and counterpart had been preserved (v.31192, v.31161). The leaf impressions are conformable, one negative, the other positive (Plate 10; C,D). This is not true of the venation on these leaf impressions. In both of the conformable impressions, the veins were negative, forming distinct depressions in the matrix (Fig. 7.1g,h). This is of considerable interest because it directly relates to the structure of the leaf compression (which has been lost). It appears from this simple observation that the venation in the leaf compression stood out as distinct ridges on the upper and lower surface of the leaf. Subsequent loss of the coaly matter has left impressions of the veins on the adjacent matrix.
Description of Plate 10

The part and counterpart of *Alethopteris* and *Glossopteris* (both devoid of coaly matter) and *Cordaites*.

A. *Alethopteris serli* (GR/R/XXXIVA), 'burnt off' compression - now an impression showing negative secondary veins in the pinnules (X 2). The topography of the pinnule from Al-Al' is shown in Fig.7.1c.

B. *Alethopteris serli* (GR/R/XXXIVB), the 'burnt off' counterpart of A, showing negative secondary veins in the pinnules (X 2). The topography of the pinnule from Bl-Bl' is shown in Fig.7.1d.

C. *Glossopteris* sp (v.31192), positive leaf impression showing negative venation (X 3.5). The topography of the leaf from E-E' is shown in Fig.7.1g.

D. *Glossopteris* sp (v.31192), counterpart of C showing negative venation (X 3.5). The topography of the leaf from F-F' is shown in Fig.7.1h.

E. *Cordaites* (GR/FD/A), leaf compression (X 1). The topography of the leaf from G-G' is shown in Fig.7.1i.

F. *Cordaites* (GR/FD/A), magnified view of E showing the impression of the leaf venation on the matrix underneath the compression (X 2).
7.3 The structure of the leaf impressions of Alethopteris and Neuropteris after loss of coaly matter

The phenomena described above in the Glossopteris leaf impressions were investigated in specimens of Alethopteris and Neuropteris. In these leaf compressions the secondary veins are positive structures in the compression and negative in the impression. A number of specimens of part and counterpart of these fossils were placed in a Muffle furnace at 600°C for 6 hours. This burnt off all the coaly matter, leaving the part in the form of two impressions, i.e. now in the same condition as the Glossopteris specimens. Examination of the impression fossils of Alethopteris and Neuropteris shows that the pinnules are still positive and the rachis and midveins still negative in what was the compression before removal of the coaly matter. These structures have remained topographically opposite in the impression. The secondary veins have altered their topography. They are now negative in both of the conformable impressions (Plate 10; A, B). The pteridosperm leaves exhibit the same structure as the veins on the Glossopteris impressions, that is, negative secondary veins in the conformable impressions (Fig. 7.1c, d).

7.4 The transverse-section of compressed Alethopteris pinnules

A number of specimens of Alethopteris pinnae were sectioned while intact in the matrix. Many of the fronds exposed on the rock surfaces dip into the matrix, and therefore sectioning was possible knowing the position of the leaf. These fossils occur in grey shales which are very friable if they become wet. The specimens were embedded in 'Araldite' before sectioning on a rock saw.

The transverse section of a compressed Alethopteris pinnule has considerable relief. The pinnule is composed of a fine coaly line which is strongly convex upwards (Plate 11; A). The midvein forms a U-shaped depression in the centre of the pinnule and is underlain by a small plate of coal (Plate 11; D). The margins of the pinnule are usually incurved, forming small "hooks" directed towards the midvein (Plate 11; E). At high magnifications it can be seen that the pinnule is not composed of a smooth coaly line but made up of numerous tiny "knots" of coal (Plate 11; F, G). These measure about 0.1mm in diameter and are separated from each other by a fine coaly line not thicker than 0.01mm. These coaly knots are not
Description of Plate 11

The structure of *Alethopteris* compressions in transverse-section

A. T.S of numerous *Alethopteris* pinnules (p) sectioned intact in the matrix (X 6.3).

B. T.S of the rachis of a pinna, showing the distinct coaly plate which represents the compression of the rachis (X 16).

C. T.S of the rachis of a pinna, showing the coaly plate extending into the matrix (X 20).

D. T.S of a pinnule midrib which is composed of a thick plate of coaly matter (X 20).

E. The incurved "hook" of a pinnule margin (X 20).

F. Highly magnified T.S of a pinnule, showing the "knots" in the coaly layer (X 20).

G. The coaly "knots" of the pinnule, showing that they are not preferentially arranged on any one surface (X 25).

H. T.S of a compressed pinnule that landed the right-way up in the sediment (X 6.3).

I. T.S of a compressed pinnule that landed inverted in the sediment. This pinnule shows a very similar structure to that in H (X 6.3).
arranged preferentially along the upper or lower surface of this coaly line but generally cross the line.

Transverse sections across the rachis of the pinnae show that it forms a distinct U-shaped depression between the pinnules. At the base of this depression there is a thick elongated plate of coal which extends into the matrix and from which finer coaly lines extend (Plate 11; B,C).

The distinct structure of the pinnule is maintained regardless of the orientation of the original leaf in the matrix. A leaf that landed inverted in the sediment shows the same curvature and structure of the pinnule (Plate 11; I) as a leaf that was orientated the "right-way up" in the sediment (Plate 11; H).

7.5 Pathway of the fracture plane

The pathway the fracture plane takes to expose the leaf compression _Alethopteris_ was determined by reassembling the conformable compression and impression by glueing them together with 'Araldite' and sectioning the rock vertically across the pinnules. The results of this sectioning showed that the fracture plane runs along the upper coal/matrix interface of the pinnule, leaving all of the coaly matter in the compression, the impression being devoid of coal (Plate 12; A). The fracture plane picks up the topography of the rachis and midveins, but the coaly plates at the base of these structures are left hidden in the matrix (Plate 12; B). The incurved "hooks" at the margins of the pinnules are also left in the matrix underneath the compression (Plate 12; C,D). It appears from the specimens examined that the fracture plane always runs along the upper coal/matrix interface following the convex face of the pinnule (Fig. 7.2b). It does not run along the lower coal/matrix interface, which should give a coaly compression with negative pinnules and a positive rachis and mid-vein (Fig. 7.2c); this has not been observed.

7.6 The structure of the uncompressed leaf

_Alethopteris_ is most commonly known as a compression. It was first described petrified by Lesquereux (1854) as _Callipteris sullivani_, but the leaf was transferred to _Alethopteris_ by Schimper (1869). The first anatomical description of _Alethopteris_ was by Leisman (1960), and subsequently Baxter & Willhite (1969) and Mickle & Rothwell (1982) have described
Description of Plate 12

The pathway the fracture plane takes to expose an *Alethopteris* pinnule.

A. Part and counterpart of an *Alethopteris* pinnule glued together with resin (r) and sectioned. The coaly matter is retained on the compression (c), whereas the impression (i) is devoid of coal (X 7).

B. The fracture plane has not exposed the coaly plate of the rachis and it is left hidden in the matrix (X 20).

C. The fracture plane has exposed a pinnule compression but the midrib (m) and incurved hooks (h) of the pinnule margin are left hidden in the matrix (X 6).

D. A magnification of a pinnule showing the coaly matter (cm) of the compression and the hook (h) of the pinnule margin (X 12).
Description of Fig. 7.2

a. The compressed pinnule intact in the matrix.

b. The pathway of the fracture plane, leaving a positive coaly compression and a negative impression.

c. This pathway never seems to be taken by the fracture plane, which would give a negative coaly compression and a positive impression.
Fig. 7.2. The pathway the fracture plane takes to expose an *Alethopteris* pinnule.
petrified *Alethopteris* specimens from American coal balls.

Baxter & Willhite (1969) described *A. lesquereuxi* from Pennsylvanian coal balls and their description appears to be typical of the uncompressed leaf. In transverse section the pinnules are strongly revolute with a sunken midrib on the upper surface. The central midvein is composed of numerous xylem tracheids from which the secondary veins depart (Plate 13; B). The secondary veins are very small, composed only of a few xylem tracheids (Plate 13; C). The remainder of the leaf is composed of spongy mesophyll and palisade cells. The upper epidermis is smooth, the only obvious structure being the depressed midrib. The lower epidermis is slightly ridged by the secondary veins and bears multi-cellular hairs (Plate 13; C). In some species, though, the leaves are not as strongly incurved and the lower epidermis is smooth, e.g. *A. sullivanti* (Leisman 1960) (Plate 13; A).

Petrified *Neuropteris* leaves have been described by Oestry-Stidd (1979) from American coal balls, and these show only a slight curvature of the pinnule margin (Fig.7.4a). There is no distinct midvein in the pinnule and the secondary veins are composed of a few xylem tracheids separated by mesophyll. The upper and lower epidermis are smooth, lacking any external evidence of the internal secondary veins.

7.7 The formation of the leaf compression

The structure of the leaf compression can be related to the uncompressed leaf. The overall shape of the pinnule has not been destroyed during the compression process. The "convex upwards" shape of the pinnule has been maintained, as has the depression of the midvein. The pinnule has retained much of its original shape because the matrix has completely surrounded the pinnules, getting into the depression in the upper surface of the leaf and underneath the lower surface of the pinnules. The matrix has, therefore, prevented flattening of structures such as the midvein depression and the pinnules. Obviously there has been considerable compression of the leaf tissues, reducing the leaf to a fine coaly line (Fig.7.3a-c).

It would appear that the entire midvein has been reduced to the small coaly plate at the base of the midvein depression. The rachis of the pinna has also compressed to a coaly plate underlying the rachis depression. The fine coaly lines which extend from this plate may represent coalified multi-cellular hairs, which have been described on the lower epidermis of the petrified leaves (Baxter & Willhite 1969).
Description of Plate 13

Permineralised specimens of Alethopteris, Cordaites and Sphenopteris.

A. T.S Alethopteris sullivanti from a Kansas, N. America coal ball. The leaf has a distinct midrib and slightly invurved margins (X 11).

B. T.S Alethopteris sullivanti showing the distinct midrib of the leaf with the xylem tracheids (X 16).

C. T.S Alethopteris sullivanti showing the leaf lamina with a slightly ribbed lower epidermis (X 16).

D. T.S Cordaites from a Kansas coal ball. The leaf has begun to collapse between the veins (X 35).

E. Magnification of D showing the structure of the veins and the distinctly ribbed nature of the lower and upper surface of the leaf as it collapses between the veins (X 50).

F. T.S Sphenopteris sp (DB coll. no.001); these layers have a distinct enrolled margin (X 20).

G. Magnification of one leaf in F showing the degree of enrolling of the leaf margin (X 60).
It is the structure of the pinnule which is interesting. In the compression the coaly matter of the pinnules is not smooth but composed of coaly "knots" separated by fine coaly lines. It is considered that these "knots" represent the compression of secondary veins in the pinnules of the original leaf. The finer coaly line separating these knots is the result of compression of the remainder of the leaf lamina (Fig. 7.3c). The secondary veins in the original leaf are made up of xylem tracheids. These are much more incompressible structures than the mesophyll tissue that separates them and have, therefore, been compressed to a lesser extent. This has resulted in a leaf compression being formed with secondary veins that are much more distinct than they were in the original uncompressed leaf. This is because of the contrast in rigidity of the xylem compared to the bulk of the leaf.

Fracturing of the rock, to reveal the pinnules, gives an impression showing negative impressions of the secondary veins and a compression with positive coaly secondary veins (Fig. 7.3d). Loss of the coaly matter during oxidation produces a negative impression of the secondary veins on both part and counterpart (Fig. 7.3e).

This contrasts with the rachis and midveins because they retain their original topography on the part and counterpart after removal of the coaly matter. These structures were depressions on the upper surface of the original leaf and were infilled with matrix during burial. The matrix has retained the topography of the uncompressed leaf during the fossilisation.

The "hooks" described at the pinnule margins on the transverse-section of the compression represent the compression of the incurved pinnule margins of the original leaf. These are very similar to the structures described at the tips of the "wings" on the Cyperites compression. It has been demonstrated that these structures (see Chapter 6) were formed by compression of the distorted leaf margins in Cyperites. In Alethopteris the uncompressed leaf had an incurved pinnule margin, and on compression this forms the "hook" of the compressed pinnule (Fig. 7.3a-c). The length of the "hook" gives an indication of the thickness of the original leaf lamina. For example, the "hook" is usually approximately 0.6mm long. Therefore, the leaf lamina was originally 0.6mm thick. From this, the amount of compression the leaf lamina has undergone can be determined.
Description of Fig. 7.3

A. T.S of the uncompressed pinnule. The pinnule is strongly revolute with a sunken midrib on the upper surface.

b. The pinnule is partially compressed; the leaf begins to compress around the secondary veins.

c. The compressed pinnule. The leaf lamina has been reduced to a fine coaly line and the secondary veins have formed distinct coaly "knots" within the coaly matter of the pinnule. The midrib has been compressed to a plate of coal and the leaf margins have been compressed to small "hooks".

d. The pathway of the fracture plane. This gives a distinct compression with a positive topography and an impression with a negative topography.

e. Loss of coaly matter from the compression. The compression, after loss of coal, maintains a positive topography but the secondary veins become depressions in the matrix.
Fig. 7.3. Diagrammatic account of the compression and subsequent exposure by fracture of an *Alethopteris* pinnule.
The coaly matter of each pinnule is usually 0.05mm thick; therefore, the leaf lamina has been compressed from 0.6mm to 0.05mm. This is a compression of 91.6% of the original leaf lamina.

7.8 Comparison with Neuropteris, Glossopteris and Cordaites

In the specimens of compressed Neuropteris that have been examined, the secondary variation is very prominent on the surface of the pinnules. In the uncompressed leaf the upper and lower epidermis have been described as smooth (Oestry-Stidd 1979). It appears that in these leaves, as in Alethopteris, the relative incompressibility of the xylem tracheids, compared to the remainder of the leaf, produces a much more distinct topographic venation structure on the surface of the pinnules than was present in the uncompressed leaf (Fig. 7.4a-d).

Permineralised Glossopteris leaves have been described by Schopf (1970) and Gould & Delevoryas (1977). These leaves have a smooth upper and lower epidermis. Secondary veins in the leaf are supported abaxially and adaxially by fibrous cells, giving the leaf a series of 'I'-girder structures. These are separated by spongy mesophyll and palisade cells. In the impression fossils of Glossopteris, described earlier, the leaves showed the negative impression of veins on both part and counterpart. As in the case of Alethopteris and Neuropteris the veins, probably aided by the fibrous cells above and below the vein, have resisted the compression process to a much greater extent than the mesophyll, giving the leaf impression a topography of venation that was absent in the original leaf (Fig. 7.4e-i).

Permineralised Cordaites show the 'I'-girder, described in Glossopteris, well developed. The veins are bounded on the upper and lower surface by hypodermal fibres which extend to the epidermis. The epidermis is not smooth but slightly ridged. The veins are composed of up to ten metaxylem elements (Good & Taylor 1970). Many permineralised Cordaites have been preserved in a semi-compressed or decayed state. The mesophyll between the veins has begun to collapse, giving the upper and lower leaf surfaces a distinct structure (Plate 13; D, E). This preservation state demonstrates the resistance of the veins to decay and compression compared to the bulk of the leaf, and indicates how the structure of the final leaf compression is dictated (Fig. 7.4j-m).
Description of Fig. 7.4

a. T.S of an uncompressed *Neuropteris* pinnule. The lower and upper epidermis are smooth and there is no distinct midrib.

b. The pinnule is partially compressed. The leaf has begun to compress around the rigid secondary veins.

c. The compressed pinnule composed of numerous coaly knots representing the compression of the secondary veins.

d. Pathway of the fracture plane exposing the pinnule giving a positive coaly compression and a negative impression.

e. T.S of an uncompressed *Glossopteris* leaf showing the central veins supported by fibre-like cells (from Gould & Delevoryas 1977).

f. The mesophyll between the veins begins to collapse.

g. The compressed *Glossopteris* leaf. The bulk of the leaf has formed a fine coaly line interrupted by "knots" of coal representing the compression of the veins.

h. Loss of the coaly matter of the leaf.

i. The pathway of the fracture plane exposing two leaf impressions both containing negative impressions of the veins.

j. T.S of an uncompressed cordaite leaf showing the 'I' girder structure of the veins. The upper and lower epidermis are slightly ridged.

k. The leaf begins to compress around the veins.

l. The compressed cordaite leaf composed of a fine coaly line interrupted by coaly "knots" representing the compressed veins.

m. The pathway of the fracture plane exposing a positive coaly compression and a negative impression.
Fig. 7.4. Diagrammatic account of the compression and exposure by fracture of *Neuropteris*, *Glossopteris*, and *Cordaites*.
7.9 Discussion

Walton (1936), in his paper on the factors influencing the formation of plant compression fossils, described the manner in which he considered *Alethopteris*, *Neuropteris* and *Pecopteris* were compressed. Since no per-mineralised material had been described at this time, Walton postulated the structure of the uncompressed leaf. He considered these leaves had a concavo-convex lamina. He described specimens of these leaf compressions which were surrounded by a narrow, flat carbonaceous "compression border". This structure has not been observed in the specimens examined during the course of the present investigation. Walton proposed that if the leaf fell in the sediment with the convex surface uppermost, a compression border would form as a result of the distortion of the leaf margin (Fig. 7.6a-c). If the leaf fell with the convex surface downwards, Walton considered that the compression border would not form (Fig. 7.6d-f) because the leaf margin would not distort in the same manner. He concluded that the presence of a compression border would indicate the orientation of the leaf in the matrix.

In fact, tranverse-sections of compressed *Alethopteris* pinnules have shown that the leaf compression exhibits the same structure regardless of its orientation in the matrix. The margins of the pinnule do show an inwardly directed "hook", which is a type of compression border since it gives an indication of the thickness of the original leaf lamina. This structure, though, is hidden in the matrix when the pinnule is exposed by a fracture plane, and is only revealed when the compressed leaf is sectioned.

Walton described compression borders in the enrolled leaves of *Sphenopteris*. In this example a very distinct compression border is produced, representing the thickness of the original leaf lamina (Fig. 7.7a-c). *Sphenopteris* has very enrolled leaf margins compared to *Alethopteris* (Plate 13; F, G) and may well compress to give compression borders at the margins of the leaf.

Walton (1936) also discussed the formation of *Annularia* leaf compressions, and reconstructed the uncompressed leaf using evidence from the compression. He considered that the leaf originally had a "concavo-convex leaf-lamina with a well developed midrib with overhanging sides" (Fig. 7.5a-c). During compression, he proposed, the midrib collapses inwards and finally two compression borders are produced, one surrounding the leaf and one bounding the midrib. If the leaf landed upside-down in the sediment, only the compression border bounding the midrib would be produced (Fig. 7.5d-f).
Description of Fig. 7.5

a. Hypothetical T.S of an uncompressed *Annularia* leaf orientated the right-way up in the matrix.

b. Collapse of the upper surface of the leaf into the lower.

c. The compressed leaf composed of two types of compression border (c) representing the compression border formed by the compression of the leaf margins and (c') formed from the compression of the midrib.

d. Hypothetical T.S of the uncompressed *Annularia* leaf inverted in the matrix.

e. The lower leaf surface collapses.

f. The compressed leaf which in this orientation has only formed a compression border (c') from the compression of the midrib.

Description of Fig. 7.6

a. The leaf is buried with the convex side up.

b. The effect of collapse of the soft tissues as the water in them is displaced upwards.

c. The final form of the fossil after the vertical compression of the sediment is complete. A compression border (c) is formed at the leaf margins.

d. The leaf is buried with convex side up.

e. As (b).

f. The final form of the fossil; no compression border is formed.
Fig. 7.5. Diagrams to represent the effect of vertical compression on a concavo convex leaf lamina with a well developed midrib with overhanging sides (from Walton 1936).

Fig. 7.6. Diagrams representing the vertical compression of a leaf with a concavo convex lamina (from Walton 1936).
Description of Fig. 7.7

a. Hypothetical T.S of a *Sphenopteris* leaf

b. The upper part of the leaf collapses into the lower.

c. The final form of the compressed leaf. Compressions borders (c) have formed marginally.
Fig. 7.7. Diagram to illustrate the effect of vertical compression in sediment on a leaf with an inrolled margins. (c) compression border (from Walton 1936).
This leaf reconstruction more closely resembles Alethopteris, but there is a depression on the upper surface of the original leaf, and the margins of the pinnule do not curve outwards as compression occurs but produce small "hook" structures. It is interesting to note that Walton showed the compressed vascular strand of the midrib as a small "knot" of coal distinct from the coaly matter of the remainder of the midrib.

Cridland (1968) described a compression fossil of Alethopteris ambiguа where he had investigated the vertical dimension of the leaf using the transfer method. He demonstrated that the pinnule margin was strongly incurved and that the midvein was overlain by a "prominent flattened blade-like extension"; this showed hair-like extensions. Cridland interpreted the blade-structure of the midvein as an inherent feature of the leaf and not an "artefact of compression". In the sections prepared in this investigation, the midvein shows a plate-like structure which is interpreted as resulting from the compression of the midvein in the original leaf, and therefore is a product of the compression process.

Gluchova (1972) demonstrated how the compressions (phytoleims) of Angaran cordaitе leaves became encrusted with mineral matter, and how the micro-relief of the leaf may be transmitted on to the adjacent matrix. She did not, though, consider how the leaf had compressed and the affect this may have had on the relief of the fossil.

7.10 Conclusions

The examination of vertical sections through specimens of Alethopteris compression fossils and reassembled specimens has shown the structure of the pinnules as they lay in the matrix, and the pathway the fracture plane took to expose the leaf compressions. The pinnules are in the form of convexed, fine coaly films. This film is not simple but composed of small "knots" of coal separated by a finer coaly line. By relating the compression fossil to permineralised specimens of Alethopteris, it has been demonstrated that the coaly "knots" represent the compression product of the secondary veins in the original pinnules. The xylem tracheids of the veins are much more resistant to the compression process than the softer mesophyll cells between the veins. This has resulted in a compression fossil being produced that has topographically a more distinct variation on the pinnules than was present in the original leaf. The resistance of the xylem tracheids to the compression process has influenced the structure of the compression fossil.
The midveins and rachis of the pinnules have been compressed to elongated coaly plates, which remain hidden in the matrix when the leaves are exposed by fracture. The compressed pinnule margins terminate in "hooks". These represent the compression of the incurved pinnule margin and give an indication of the original thickness of the leaf lamina. These structures also remain hidden in the matrix when the leaves are exposed.

Comparison of Alethopteris with compression fossils of Neuropteris, Glossopteris and Cordaites shows that these leaves also have a distinct topographic variation not seen in the permineralised specimens. This has also resulted from the resistance of the veins to compression compared with the remainder of the leaf. In Glossopteris and Cordaites, the veins are bounded by fibres giving an 'I'-girder structure to the vein. This structure may well have resisted the compression process to a much greater extent, giving these leaves a more distinct variation than Alethopteris and Neuropteris.
CHAPTER EIGHT: The nature of the preservation of the ovulate Glossopterid fructifications
8.1 Introduction

One of the most controversial groups of plant compression fossils is probably the fructifications borne by Glossopteris. They were first reported by Plumstead in 1952 from the Lower Permian of South Africa. Glossopteris had been known since 1822; it was first described by Brongniart, who established this genus for leaf impressions from the Permo-Carboniferous of India and Australia. Up until Plumstead's discovery of the fructifications, only the leaves and roots (Vertebraria) had been described, and the overall structure and affinities of the plant that bore them was virtually unknown. The discovery of these reproductive structures, it was hoped, would enable the affinity of the plant to be determined. In fact, since these fructifications were described, a continuing controversy has surrounded their interpretation. This is because they are known virtually only as compressions or impressions. No anatomically preserved material was available to aid the interpretation of the compressions until the publication of Gould & Delevoryas' (1977) Australian material. The uncertainties surrounding the South African impressions of Plumstead has resulted in many reconstructions being postulated to explain the structure of the fructifications, and hence, the affinities of this group of plants.

The interpretation of these fossils demonstrates well the problems that arise when only the compression state of preservation is known. In many cases our interpretation of fossil plant organs is based on evidence from both compressions and petrifications, e.g. Lepidodendron. In the case of the ovulate glossopterid fructifications, reconstructions of their uncompressed structure have been made without taking into account the deformation a complex, three-dimensional structure may undergo when it is buried in sediment.

During the course of this investigation, it has been assumed that these fructifications have a common structural arrangement, as is shown by the fructifications of other groups of fossil plants, e.g. Conifers and the Cycads. By examination of specimens of these reproductive structures, and using experimental modelling techniques, a model is postulated which is considered to probably represent the original uncompressed structure of these fructifications.
8.2 The preservation of the fructifications

The Glossopteris fructifications described by Plumstead from the South African Permian were generally found in pink or buff very fine siltstones or claystones. In most cases the fossils are devoid of coaly matter, that is to say, they are just impressions. The organic matter has presumably been lost, due to post-depositional oxidation and weathering processes (Schopf 1976). Some Indian and Australian specimens have been described (Rigby 1978; Surange & Chandra 1978) preserved as compressions. Loss of coaly matter prevents techniques such as transfers and acetate pulls being used when examining the fossils, so reducing the information that can be obtained from the fossil.

Petrified (permineralised) glossopterid fossils are very rare and only two silicified deposits containing them have been reported. Schopf (1970) reported silicified roots, leaves and associated seeds from the Permian of Antarctica, but the seed-bearing structure was not clear. Gould & Delevoryas (1977) described the first well-preserved fructifications found associated with Glossopteris from the Permian of Queensland, Australia.

8.3 Descriptions of the glossopterid fructifications

The most well-known glossopterid fructifications are the ovulate reproductive structures which will be considered here. Several of these were first described by Plumstead (1952), and she erected four genera: Scutum, Hirsutum, Cistella (now Plumsteadia, Rigby 1963) and Lanceolatus. Two further genera will be discussed: Ottokaria; this was first described by Zeiller (1902) associated with Glossopteris, and Plumstead (1956b) described Ottokaria attached to Gangamopteris (a leaf genus similar to Glossopteris). Dictyopteridium, another glossopterid fructification, was first described by Feistmantel (1881) and revised by Rigby (1972) and Surange & Chandra (1973). It has not been found attached to Glossopteris, although associated with it. Since they were first described, these genera have been subsequently reported from the Permian of Australia, India, and other parts of South Africa.

All these fructifications show the same basic structural arrangement, that is a central "head" region in which there are a series of oval "sacs". This may be surrounded by a flatter "wing" region of "fused segments", e.g. Scutum (Fig. 8.1a) and Hirsutum (Fig. 8.1b) or "free segments", e.g.
Description of Figure 8.1

a. **Scutum** showing the "fertile half", consisting of a head region containing numerous oval sacs surrounded by a wing region and the "empty veined half".

b. **Hirsutum** showing the "fertile half" of the fructification containing seeds.

c. **Plumsteadia** (previously Cistella): very similar to Scutum but has no distinct "wing" region.

d. **Lanceolatus**: this fructification is composed of two halves as in Scutum but was considered by Plumstead (1952) to be borne directly on the leaf.

e. **Ottokaria**: this fructification was borne on a longer pedicel than Scutum and the wing region consists of "free" segments.

f. **Dictyopteridium**: lacks a "wing" region and is composed of numerous small oval sacs which may be arranged in spirals.
Fig 8.1. The ovulate glossopterid fructifications.

a. Scutum

b. Hirsutum

c. Plumsteadia

d. Lanceolatus

e. Ottokaria

f. Dictyopteridium
Ottokaria (Fig. 8.1e). In Cistella (Fig. 8.1c), Lanceolatus (Fig. 8.1d) and Dictyopteridium (Fig. 8.1f), the wing region is absent. When Plumstead described these fructifications she considered that the two halves of the fossil were unconformable impressions (Introduction 1.4); that is, they were composed of completely different structures. She called one half of the fructification the "empty half" and the other the "fertile half", bearing seeds (Fig. 8.1a). Specimens which showed this structure, Plumstead termed "open cupules". Specimens, in which she considered had not "opened out" at the time of fossilisation, and hence showed the outer surface of the reproductive structure, she called "closed cupules".

8.4 Interpretations of the fructifications

Since the first descriptions of these reproductive structures by Plumstead (1952), many authors have offered very different reconstructions of the "Scutum"-type fructification. There have been four main interpretations of these fructifications:

(a) a bilateral cupule which opened out into two structurally different "valves" (Plumstead 1952, et seq);

(b) a cone or strobilus (Walton 1952; Mukherjee et al 1966);

(c) a bilateral fructification with scale leaf (Surange & Chandra 1974);

(d) a single dorsiventrail fructification (Schopf 1976; Rigby 1978).

(a) The bilateral cupule model

This model is probably the most well-known interpretation since it was postulated by Plumstead (1952) when she first described the fructifications. She described Scutum as a "bilaterally symmetrical cupule consisting of a fertile half, containing a number of sacs and an empty veined concave half (Fig. 8.2a). Plumstead based this interpretation on the fact that, when the shale was split open to reveal the fossil, the two impressions contained very different structures, representing the two halves of a cupule.

Since her original description of Scutum (1952), Plumstead only slightly modified her interpretation (Plumstead 1956a). This was due to the discovery of a Scutum specimen in which there were "filamentous, pollen bearing organs" attached to the "empty" half of the fructification. She
Description of Figure 8.2

a. Bilateral cupule model (after Plumstead 1952). The fructification is composed of two halves of a cupule borne either on a pedicel, which develops from the midrib or directly on the leaf.

b. Cone or strobilus model (after Walton 1952). The fructification is composed of numerous lamina, with seeds at their base, borne around an axis. On compression and subsequent fracturing of the fructification, the "Scutum"-type of fossil is produced.

c. The bilateral fructification with scale leaf model (after Surange & Chandra 1974). The fructification consists of a "seed-bearing" head borne on the same pedicel as a scale leaf.

d. The dorsiventral model (after Schopf 1976). The fructification is borne on a pedicel and is composed of a head bearing seeds on one surface.
Fig 8.2 Reconstructions of the ovulate glossopterid fructifications.

a. Bilateral cupule model
- Empty half
- Fertile half

b. Cone or strobilus model
- Lamina
- Axis
- Seed
- Fracture plane
- (i) Fertile half
- (ii) Empty half

(c) Bilateral fructification with scale leaf model
- Seed-head
- Scale leaf

(d) Dorsiventral model
- Seeds
concluded from this that Scutum was a hermaphrodite flower. Schopf (1976), commenting on these "pollen-organs", described them as "incidental flakes of fibrous material associated in the sedimentary matrix" and concludes, "at best they should be rated as ambiguous occurrences". What these structures in the "empty half" of the cupule actually represent is difficult to determine. Whether they are "pollen-bearing organs" cannot be proven since they have only been reported by Plumstead (1956a) from her material, and the "pollen" she removed from them is very poorly preserved.

It would appear that Plumstead's interpretation of Scutum, and the other fructifications, is based on the assumption that these structures were flat in life, and have been totally unaffected by the fossilisation mechanisms that form plant compression fossils. One important result of the fossilisation process is a drastic reduction in the original vertical dimension of the plant organ. The fructifications occur in very fine grained sediments which would have undergone significant compaction (70-80%) and are associated with other plant fossils, e.g. Cyclodendron (Plumstead 1956b; Plate 28), which appear to have undergone considerable reduction in the vertical dimension, e.g. loss of stem topography shown by the very compressed nature of the leaf cushions. In her descriptions of these fructifications, there is no discussion of the manner in which these structures were fossilised. Plumstead's interpretation of these fructifications has had very little support from other workers, but has provided a considerable area of palaeobotanical controversy (Surange & Chandra 1973, 1974; Rigby 1978; Schopf 1976).

(b) The cone or strobilus model

Published with Plumstead's original description of the glossopterid fructifications was a series of written discussions by several palaeobotanists. Of these, Walton offered a radically different explanation of the original structure of Scutum. He offered a pre- and post-fossilisation model (Fig.8.2b) and is one of the very few authors to have done so. He proposed that Scutum was originally a cone-like, radially symmetrical structure, with each seed being attached to a "projecting lamina which may have been tubular". On compression of this structure, the marginal "lamina" would produce the "wing" structure of Scutum. He concluded that "on splitting the rock, the plane of severance went over the surface of the ovules" (Fig.8.2bi). He considered, also, levels of splitting of the rock and postulated that a lower level of fracturing would
produce a fossil with the striated surface (Fig.8.2bii), Plumstead's "empty half". Walton did not consider how the "tubular appendages" on the upper and lower surfaces of the cone would have behaved during fossilisation and he omits them from his drawing. It is important to understand how these structures would have compressed so that they may be recognised in the fossil, if present.

Plumstead (1952), in her reply to the discussion, disagreed with Walton since she maintained that there was no evidence of separate appendages in the wing region, since it was "a continuous, uninterrupted structure".

Walton's theory has had some support. Mukherjee et al (1966) described a number of Scutum specimens from India. In many cases they had both halves of the fructification and stated that the "counterparts of all our specimens are mere impressions of their respective parts". They considered that the "veined upper surface is the result of flattening together of a number of separate appendages, each associated with a seed, during fossilisation". They proposed, on this evidence, that Scutum had a cone-like organisation. In fact, the plates included in this account show a number of Scutum specimens in which the two halves of the fossil appear to consist of a conformable compression and impression. These fossils differ from Plumstead's specimens in that the organic matter is still present on the surface of the fructification. Loss of coaly matter may affect the structures seen in the two halves of the fossil (see section 1.4).

Further support for Walton's "cone-hypothesis" came from Surange & Chandra (1973) in their discussion of the female fructification Dictyopteridium (Fig.8.1f). Dictyopteridium is composed of a series of "seeds" arranged in spirals; the structure lacks a wing region. It has been reported associated with Glossopteris but has not been found attached. Surange & Chandra reconstructed the fructification as a cone, composed of seeds arranged in spirals around a cone axis. They conclude that "other fructifications of the Glossopteridales, such as Scutum and Cistella, can be interpreted as having the same type of organisation. Scutum and Cistella represent a cone axis from which seeds have been shed, exposing the scars on which the seeds were attached".

This "cone-model" of Walton's, for these ovulate fructifications, has had, therefore, some support from other authors. It represents a very dynamic
interpretation, in that he reconstructed a three-dimensional structure from a flattened compression fossil.

(c) "Bilateral fructification with a scale leaf" model

This model was proposed by Surange & Chandra (1974), based on evidence from impression fossils from India. Previously (Surange & Chandra 1973), they had supported the cone model but, on examination of more material, they concluded that the two halves of the fructification showed different surface features, i.e. were unconformable. They interpreted Scutum as being composed of two organs: a seed-bearing head and a scale leaf, both borne on the same "pedicel". During fossilisation, they postulate, the "scale leaf" would have "fallen over" the seed-organ. This "falling" over the seed-head is difficult to envisage; it would be expected that sediment would have got between the two structures, keeping them apart. It also seems unlikely that the "scale leaf" would have fallen over the seed-head every time covering it entirely; sometimes it would have lain obliquely, only partially covering the head. The authors consider that during compression the marginal seeds of the fructification would have been laterally compressed, producing the wing structure described on Scutum by Plumstead (1952)(Fig.8.2c).

These Indian specimens seem to have a much greater topography than the South African specimens. In some of the published photographs the "wing" appears to be composed of distorted seeds (Plate 17; B,C).

Surange & Chandra (1978) support the above hypothesis by describing cuticle preparations from a Scutum specimen, in which the cuticles on the bract and receptacle were easily distinguished, and hence "two separate organs were involved".

This interpretation of Scutum has not had wide support, but these authors have considered something about the fossilisation process. That is, they interpret the "wing" region as resulting from the compression of outwardly directed seeds at the margin of the fructification.

(d) The dorsiventral model

This model was first proposed by Schopf (1976). He believed that the ovulate fructifications of the glossopterids had a dorsiventral structure in which the upper surface was usually striated or rugose, and the lower
Description of Figure 8.3

a. The infolded megasporophyll (m) showing seeds (s) arranged inside the envelope (x 8).

b. The opened out megasporophyll (x 9).

Description of Figure 8.4

a-b. Formation of Plumsteadia: a. the fructification (f) is orientated below the leaf (l). b. After burial the weight of sediment squeezes the fructification flat and the leaf bract is forced downwards into the space left by the fructification.

c-e. Formation of Lanceolatus: c. the fructification (f) is orientated above the leaf (l). d. The fructification is squeezed onto the leaf bract. e. The fructification is squeezed into the leaf and through its tissue.
Fig 8.3. The permineralised glossopterid fructifications
(after Gould and Delevoryas 1977)

Sediment on which the fructification fell

Sediment that buried the fructification

Fig 8.4. The burial and compression of glossopterid fructifications
(after Rigby 1978)
surface bore ovules (Fig.8.2d). He states, "the fossils unquestionably do not represent merely one visible surface of a compressed, radically symmetrical husk". He does not produce evidence for the dorsiventral model, but introduces the term "fertiliger" to describe the whole fructification, which he believed to be composed of a bract, a stalk and a capitulum.

Rigby (1978) offers a similar explanation for these glossopterid fructifications, based on his own observations and his reinterpretation of earlier work. He considers that the different structures shown on the two halves of the fossil is not because of the fracture plane running between two valves (Plumstead 1952), but through the centre of a single dorsiventral structure. He does not, though, go on to relate this to the structures observed in the fossils.

Rigby is one of the few authors who has considered the details of the fossilisation process that led to the formation of these fossils. He uses Plumsteadia RIGBY (previously Cistella PLUMSTEAD) as an example. It is similar to Scutum but has no marginal wing and was considered by Plumstead (1952) to have been borne directly on the leaf. Rigby proposes that the fructification (bearing seeds only on one surface) and the leaf fell together onto the mud. During fossilisation, "the fructification left a depression into which successive layers of sediment very gradually compressed the carbonaceous remains of the fructification and the overlying "leaf bract blade". After compression they appeared "fused" (Fig.8.4a-c). Rigby also explains Lanceolatus, also considered by Plumstead (1952) to have grown out of the leaf, as having been "squeezed" through the leaf during compression (Fig.8.4c-e).

Experimental modelling of this hypothesis, using the techniques described in Rex & Chaloner (1983), demonstrates that apparently this would not occur. The modelling shows that if sediment was present between the fructification and the "leaf bract", it prevents any "fusing" of the structures (Plate 14; A-D). If sediment had not got between the structures, which is extremely unlikely, the resulting compression fossil is still composed of two distinct structures (Plate 14; E,F).

Rigby describes the two species of Plumsteadia which he considers shows good evidence of a dorsiventral organisation. P. ampla demonstrates a definite spiral arrangement of the ovules across the fructification (Plate 18; A) and no opposite surface is described to justify a dorsiventral model.
Description of Plate 14

Experimental modelling of Rigby's (1978) hypothesis for the compression of dorsiventral fructifications.

A The fructification (f) (composed of foam rubber) is positioned under the leaf bract (1). Matrix (fine sawdust) is placed between and surrounds the two structures (x 0.4).

B After compression the leaf shows a slight distortion but the matrix separating the leaf and fructification prevents the leaf bract "sinking" towards the fructification (x 0.4).

C The fructification is positioned over the leaf bract; matrix separates the two structures (x 0.4).

D After compression the fructification remains distinct and separate from the leaf (x 0.4).

E The fructification is positioned over the leaf bract; no matrix is placed between the two structures (x 0.4).

F As a result of compression the fructification and leaf are brought close together but the fructification is not "squeezed through" the leaf (x 0.4).
The other example used by Rigby is *P. semnes*, preserved as a cast in a fine-grained sandstone. He states in his description of this species that it "shows little vertical compression although there has been some distortion by relative lateral slippage of the overlying sediments". It would be interesting to know how Rigby determines the amount of vertical compression the fossil has suffered and, also, how "lateral slippage" occurs. I conclude, from his discussion, that Rigby is trying to explain the distortion of the marginal ovules in his specimens of *P. semnes*. I would interpret their structure as a result of the marginal ovules having been orientated perpendicular to the compression direction during fossilisation and have, therefore, been flattened with their long axis orientated parallel to the bedding plane. Those ovules in the central area of the fructification were orientated with their long axis parallel to the compression direction, and so have been foreshortened. This results in the two different ovule shapes in the fossil (Plate 18; B).

Even though Rigby has considered the manner in which these fructifications may have been fossilised, the evidence from the fossils does not seem to be convincingly explained by his hypothesis.

8.5 The permineralised glossopterid fructifications

These are very rare and have only been reported from two sites, one in Antarctica and one in Australia. Schopf (1970) described silicified *Glossopteris* and *Vertebraria* from a petrified peat deposit in Antarctica. Some seeds were discovered in the deposit, but the nature of the seed-bearing structure was not discovered.

The first permineralised reproductive structures found associated with *Glossopteris* were described by Gould & Delevoryas (1978) from Queensland, Australia. The seed-bearing structure consisted of a leaf-like organ with infolded lateral margins which enclosed the seeds (Fig.8.3a). The seeds were considered by the authors to be typically gymnospermous, i.e. pollen was found in the micropyle of the seeds. Some of their specimens show the megasporophyll opened out, and they postulate that this may represent a possible dispersal stage (Fig.8.3b). Dispersal of seeds is usually indicated by the presence of an embryo in the seed. Embryos are not seen in these fossils and may indicate that this is not a dispersal stage.
8.6 Comparison of the compressed fructifications with the permineralised fructification

With the discovery of structurally preserved glossopterid fructifications, it might have been hoped that the interpretative problems surrounding the compression/impressions fossils would be solved. In fact, the infolded megasporophyll structure of the petrified fructification had not been amongst the many theories of the original structure of the ovulate fructifications.

Many factors are still unknown, such as the manner in which the seeds were attached and the arrangement of the seeds inside the megasporophyll structure. This is because only one plane of section has been described; further sections would be very informative, enabling closer comparisons to be made with the compressed fructifications.

Gould & Delevoryas (1977) state in their discussion on the relationship between the compressed and petrified fructifications, that the seeds described by authors in Scutum, Lanceolatus, Hirsutum, Plumsteadia and Ottokaria are similar to those in the silicified fructification and "are probably of the same type". They do not attempt to directly relate the structures preserved in the permineralised specimens with the compressed fructifications. The authors offer some explanation of the relationship between the megasporophyll structure and the various reconstructions that have been postulated for the Scutum-type fossils. For example, that the difference in the structures on the part and counterpart, from fracture along the megasporophyll leaving seeds on the part, while the counterpart shows a portion of the megasporophyll, which has been interpreted as a subtending bract (Surange & Chandra 1975). They explain that the cleavage passed through the flattened megasporophyll envelope so that portions (the "wing") appear on part and counterpart, and this accounts for the twin cupular valve interpretation (Plumstead 1952).

Gould & Delevoryas (1977) do not explain very clearly how they relate the compressions and the petrifactions. The manner in which the seeds were infilled, or not, is not considered, nor how the loss of organic matter would have affected the interpretation.

In order to investigate whether the infolded megasporophyll structure would, on compression, produce the Scutum-type of fructification, to determine
if the common plan of these impression fossils formed, models were constructed, based closely on the described permineralised specimens. Two types of model were used to represent:

(i) The infolded fructification bearing seeds (Fig.8.3a).

(ii) The opened out megasporophyll envelope bearing seeds (Fig.8.3b).

Rigby considered that the Scutum structure could only have been produced from the opened-out megasporophyll structure, representing a "dessication" of the fructification, allowing the seeds to disperse.

When reconstructing the models, it had to be considered whether the seeds became infilled with sediment during burial. Evidence from previously described specimens and observations on some of Plumstead's fossils (borrowed from the British Museum, Natural History) showed that the seeds in the impressions were not depressions in the matrix but positive structures and were, in fact, seed casts (Plate16;C). Seed casts are able to form because the outer wall of the seed (the sclerotesta) is rigid enough to maintain its shape and prevent collapse of the structure while the seed contents decay. The seed cavity is then infilled by sediment which forms a cast of the internal structure of the seed. Therefore, in the models described below, the seeds were all infilled with sediment.

Models were first constructed of the infolded megasporophyll. Matrix was placed between the seeds, since the fructification was an open structure sediment would have easily infilled it, and infilling the seeds. The models were surrounded by the same matrix, since in the fossils the matrix in and around the specimens is the same. On compression the fructification was considerably reduced in vertical dimension. The seeds showed some distortion and the megasporophyll wall became much thinner. The overall shape of the compressed form retained much of the structure of the uncompressed form (Plate15;A). It is difficult to envisage, after loss of the organic matter, how fracturing of the fructification would produce any of the ovulate glossopterid fructifications that have been described (Plate 15; C,D).

Further models were constructed, this time of the unfolded megasporophyll bearing seeds (Plate15;E). The seeds were infilled and surrounded by matrix. On compression, the seeds foreshortened considerably but retained a topography distinct from the megasporophyll envelope (Plate15;F). Loss
Description of Plate 15

Experimental modelling demonstrating the compression of enrolled fructifications

A  Model, constructed of foam rubber, representing the infolded megasporophyll envelope. The seeds and fructifications are infilled with matrix (fine sawdust) ( x 0.3).

B  After compression, the megasporophyll has been reduced in vertical dimension but the overall shape of the original structure has been maintained (x 0.3).

C  Loss of coaly matter from the fossil.

D  Possible pathway of the fracture plane; the "Scutum-type of structure is not revealed.

E  Model representing the opened out megasporophyll envelope; the seeds are infilled with matrix (x 0.3).

F  After compression, the seeds are distorted and the megasporophyll envelope reduced to a thin line (x 0.3).

G  Loss of coaly matter from the fossil.

H  Pathway of the fracture plane to expose the seed casts. The resulting part and counterpart are conformable.
of coaly matter from this type of compression would leave the seeds as positive structures. To expose the seed structure of this compressed model, a fracture plane would have to run along the upper surface of the seeds (Plate 15; G,H). This would result in two conformable impressions being exposed. If the fructification fractured along the line of the compressed metasporophyll envelope the seeds would not be exposed.

One of Rigby's (1978) arguments for the unrolled fructification producing Scutum is that a "wing" region would be present representing the margins of the megasporophyll. The "wing" region, that would be produced from the margins of the megasporophyll, should be a distinct structure showing no gradation or connection with the seeds (this is discussed in detail later), and this does not appear to be the case in the compressed fructifications.

Experimental modelling of these silicified glossopterid fructifications has shown that the infolded form does not appear to produce a "Scutum" type structure on compression. The resulting form cannot be related to any previously described compression fossils of Glossopteris fructifications. The unfolded form of the structure does produce a form much more closely resembling Scutum, but fracturing of this structure would not result in the exposure of two unconformable impressions. It is also difficult to relate the "wing" region in the compressed unfolded form to the structure seen in the fossils. It is very apparent that it is not easy to relate the silicified seed-bearing organ to the structures seen in the compression/impression fossils. These permineralised fossils do not appear to show a structure which can be used as a common uncompressed structural plan for the "Scutum"-type of fossils.

8.7 Lines of evidence for the structure of the ovulate glossopterid fructifications

The following sources of information have been explored in an attempt to determine the original nature of the uncompressed reproductive structure of the glossopterids:

1. Specimens of these fructifications deposited in the British Museum (Natural History) by Plumstead. (Many of them are described in the catalogue in Plumstead (1952)).

2. Other previously described specimens.
3. Comparison with other types of compressed fructifications.

4. Experimental modelling.

(a) The nature of the part and counterpart in glossopterid fructifications

Examination of the specimens of these fructifications from the British Museum (Natural History) revealed that there were a number of specimens in which both part and counterpart of the fructification were preserved. *Scutum stowanum* (v.31210, LV2, 2A) demonstrates that while both the "wing" regions are conformable in impression A and B, the "head" regions are unconformable. Impression A shows the arrangement of positive (sediment-infilled) seeds, in the head region, whereas impression B is striated, lacking any evidence of the impression of seeds (Plate 16; A,B).

This is also demonstrated in "Scutum" sp (v.31161); in this specimen the seed infills show considerable structure (Plate16;C,D). Each seed has a central depression with a raised centre. This structure is totally absent in the unconformable impression B. The leaf on which the fructification is situated shows numerous negative impressions of veins. These are also negative in impression B.

In a specimen of another genus of ovulate fructifications, *Lanceolatus lerouxides* (v.31192, LV1, 1A) the part and counterpart are conformable impressions. Impression A is positive (Plate16;E,F) and impression B is negative but has a very rough surface in the area of the fructification. As in the specimen described above, the veins on the leaf surfaces are negative in both impression A and B. The negative nature of the veins on both surfaces of the fossil is related to the structure of the leaf compression which has not been preserved. The veins have suffered less compression than the remainder of the leaf, giving the leaf impression a distinct topography. This is described in detail in Chapter 7).

A close examination of published figures of parts and counterparts of these ovulate fructifications show that there is no consistency amongst these fossils. Some show conformable part and counterparts, whereas others are obviously conformable. However, Scutum specimens, when clearly seen, show a seed arrangement in the head region on one impression
Description of Plate 16

Specimens of impression fossils of the ovulate glossopterid fructifications

A  **Scutum stowanum** (v.31210, LV2). Unconformable impression A, composed of a number of seed casts surrounded by a wing (x 2).

B  **Scutum stowanum** (v.31210, LV2A). Unconformable impression B, showing a striated "head" region surrounded by the wing (x 2).

C  **Scutum sp** (v.31161). Unconformable impression A, showing positive seeds (x 2.6).

D  **Scutum sp** (v.31161). Unconformable impression B, showing the "striated empty half" of the fructification (x 2.6).

E  **Lanceolatus lerouxides** (v.31192, LV1). Conformable impression A, showing part of the lanceolate cupule as a positive structure (x 2.5).

F  **Lanceolatus lerouxides** (v.31192, LV1A). Conformable impression B, showing the cupule as a depression in the leaf surface. In A and B the veins on the leaf impression are negative (x 2.5).
and a striated head region in the opposite unconformable impression.

(b) Distinction between head and wing region

Plumstead's (1952) main arguments for her two-valved model for these fructifications was that the "wing" region was a distinct and separate structure from the "head" region. Examination of specimens of Scutum shows that the "wing" region may have considerable structure to it, e.g. Scutum rubridgeum (v.31205) and Scutum leslium (v.31195) show a segmented structure in the "wing". Each segment has a rounded base which merges into the seeds in the "head" region (Plate 17; E, F). This phenomena is also demonstrated in Scutum sp (v.31161) where the base of the "wing" segments shows the same structure as the seeds in the head region, i.e. a central depression possibly representing the micropyle (Plate 17; D). These examples appear to indicate that the "wing" and "head" regions are not as separate as Plumstead maintained, but rather that the wing is made up of units which seem to represent lateral views of the distal parts of the seeds.

In some of the Indian specimens, illustrated by Surange & Chandra (1974), the fructifications have a considerable topography. In these examples the wing region has considerable structure and is deeply segmented (Plate 17; B, C). The segments have the appearance of representing elongated seeds, possibly resulting from lateral compression. This phenomena can also be seen in some specimens of Cistella illustrated by Plumstead (1958), where the wing segments show the same structure as the seeds, but have suffered lateral compression (Plate 17; A).

(c) Evidence of spiral arrangement of seeds

If the "cone-hypothesis" of Walton (in discussion, Plumstead 1952) fits for these fructifications, then a spiral arrangement of seeds should be seen in the compression fossils if the units in the cone are helically arranged. This has been described and illustrated in Dictyopteridium sporiferum by Surange & Chandra (1973). Rigby (1978) describes a number of glossopterid fructifications which show some spiral arrangement of seeds, e.g. Plumsteadia ampla (Plate 18; A) and Plumsteadia microstacca (Rigby 1978, fig.3).

Some of the specimens examined showed a spiral arrangement of seeds on
Description of Plate 17

The structure of the wing region in the ovulate glossopterid fructifications.

A. **Plumsteadia** (from Plumstead 1958). The wing region is composed of distorted seeds showing the same structure as the seeds in the head region (x 3).

B. **Scutum indicum** (from Surange & Chandra 1974). The wing region is composed of distorted seeds (x 5).

C. **Scutum elongatum** (from Surange & Chandra 1974). The fructification has considerable topography and the wing region appears to be composed of distorted seeds (x 5).

D. **Scutum sp** (v.31161). The base of the wing segments show the same structure as the seeds in the head region (x 14).

E. **Scutum leslium** (v.31195). The wing segments show rounded bases and extend into the head region (x 7).

F. **Scutum rubridgeum** (v.31205). The wing shows a distinctly segmented structure and these segments have rounded bases (x 7).
Description of Plate 18

The arrangement of seeds in the impression fossils of ovulate glossopterid fructifications.

A  *Plumsteadia ampla* (from Rigby 1978) showing a spiral arrangement of seeds (x 2).

B  *Plumsteadia semnes* (from Rigby 1978); the seeds "fan" away from the centre of the fructification (x 1\(\frac{1}{2}\)).

C  *Scutum dutoitides* (v.31201) showing a faint spiral arrangement of seeds (x 4).

D  *Scutum rubridgeum* (v.31207), the veined structure of the "empty" half of the fructification (x 2.5).
the impression fossils, e.g. Scutum dutoitides (v.31201) (Plate 18; C). Many of the specimens, though, do not show spirality but the seeds appear to show a "fanning" arrangement away from the central, rather indistinct, area of the fructification, e.g. Plumsteadia semnes (Plate 18; B).

It would appear that there is no consistent distribution of seeds in these ovulate glossopterid fructifications. A few show a spiral structure, but there is no conclusive proof for the "cone-hypothesis" from the seed arrangement in these fossil fructifications.

(d) Comparison with other fructifications

It is important to relate the glossopterid fructifications to other reproductive structures described for other groups of fossil plants, to determine whether there are any comparable structures which may aid the interpretation of the "Scutum-type" of compressions.

One of the well known reproductive structures preserved as a compression and organised as a cone is Lepidostrobus. The distinctive features of Lepidostrobus are:

(i) Spiral arrangement or sporophylls;
(ii) Distinct cone axis;
(iii) Sporangium borne on sporophylls.

The cone may be exposed by two different fracture planes. The fracture plane may take a pathway over the outer surface of the cone exposing the lamina of the sporophylls (Fig.8.5b), or it may run through the centre of cone exposing the cone axis and the sporangium (Fig.8.5a). When the cone is fractured open the part and counterpart are conformable.

Comparing Lepidostrobus with the ovulate glossopterid fructifications, in Scutum:

(i) A spiral arrangement of seeds may or may not be present;
(ii) No distinct cone axis;
(iii) No distinct sporophylls present bearing the seeds;
(iv) Part and counterpart may be unconformable or conformable.

It would appear that sporophylls are not present in Scutum since specimens have not been described showing an obvious outer surface bearing the
Description of Figure 8.5

a. *Lepidostrobus variabilis* (from the Radstock Coalfield, Westphalian D). The fracture plane has exposed the cone axis (c), which shows "false" scars (sc) where the sporophylls have been lost in the counterpart. The sporophylls (sp) are exposed at the margins of the axis (x 2).

b. *Lepidostrobus variabilis* (from the Radstock Coalfield, Westphalian D). The outer surface of the cone has been exposed by a fracture plane running over the lamina (l) of the sporophylls (x 1.5).

c. *Lacoea* (from Leary 1973). When exposed in this manner, the fructification has features in common with *Scutum*, a seed-bearing region and a wing region (x 1.5).

d. Reconstruction of *Lacoea* (after Leary 1973) showing the cone-like organisation of the fructification. The sporophylls (s) bear a number of disks (d), scars (sc) are left when these are shed (x 7).

e. *Scutum rubridgeum* (v.31205) preserved as an impression showing the central seed area bounded by the wing (x 2.3).
Fig 8.5. Comparison of Scutum with Lepidostrobus and Lacoea.
lamina of sporophylls. Since these structures are commonly exposed in *Lepidostrobus*, and the fructification appears to easily fracture along the lamina, it would seem that they were not present in *Scutum*.

Another fructification that has been described as a cone is *Lacoea*, a Noeggerathialean cone (Leary 1973; Beck 1981) from the Lower Pennsylvanian of Illinois. This fructification is found preserved as a compression and has a very similar appearance to *Scutum* (Fig. 8.5c). It consists of a central "head" region exposing a fan-like arrangement of disks, and a "wing" region composed of a number of sporophylls. The sporophylls are clearly separate and do not show the close arrangement of structures as seen in the wing region of *Scutum*. Well preserved 3-D specimens of *Lacoea* have shown that these disks are spirally arranged around a cone axis (Fig. 8.5d).

Even though the similarity between *Lacoea* and *Scutum* is striking when *Lacoea* is exposed in this manner (Fig. 8.5c) there is no implication that *Scutum* is related to the Noeggerathiales. The similar structures seen in the two fossils may possibly support the "cone-hypothesis" for *Scutum*.

(e) **Experimental modelling**

A number of experiments have been described earlier in which models were made of Rigby's (1978) hypothesis of the fossilisation of *Plumsteadia* and *Lanceolatus*, and of the megasporophyll reproductive structures described by Gould & Delevoryas (1977). Results of these experiments have shown that those original uncompressed structures do not appear to produce the features observed in the "Scutum"-type of fossil. Further experimental modelling was conducted to test a number of hypotheses that arose as a result of the evidence described above.

Firstly, a model was made to represent Walton's cone hypothesis. In his discussion on these fructifications (Plumstead 1952), Walton considered that the seed was borne at the base of a lamina, "which may have been tubular", although in normal usage a lamina is, by definition, a flat structure, and so could not be tubular. A model was constructed consisting of an axis around which tubular appendages were arranged (Plate 19; A). At the base of each of these there would be a seed. The appendages and seeds were infilled with matrix; since the appendages were open structures, matrix would have entered them. On compression, the appendages
Description of Plate 39

Experimental Modelling of "Scutum"

A. Model of Walton's cone hypothesis consisting of numbers of tubular appendages, with seeds at the base, borne around a central axis. The model is constructed of foam rubber and the matrix is fine sawdust (x 0.3).

B. On compression the appendages on the upper and lower surface of the structure foreshortened while the marginal appendages became very thin (x 0.3).

C. Model of Walton's cone hypothesis consisting of a number of sporophylls, with seeds at the base, borne around a central, solid axis (x 0.3).

D. On compression the sporophylls on the upper and lower surface foreshorten, while the marginal sporophylls become very thin but retain their original length (x 0.3).

E. Model in which a number of large naked ovoid seeds are arranged around a solid axis and infilled with matrix (x 0.3).

F. On compression the marginal seeds retain their length but become thinner, whereas the seeds on the upper and lower surface have foreshortened (x 0.3).
on the upper and lower surfaces foreshortened, the marginal appendages became thinner. The matrix infilling the appendages prevented closure of these structures (Plate 19; B). A fracture plane exposing this compressed fructification would probably run over or under the seeds, leaving the appendages in the counterpart.

This type of model does produce some of the features observed in Scutum when deformed in the compression apparatus. The flattening of the marginal structures produces a "wing-like" structure and seeds are present in the central part of the compression. If Scutum did have this type of structure it would be expected that a fracture plane would run over the outer surface of the fructification, exposing the appendages on the outer surface of the fossil, since the infilling of them would have given them an obvious topography.

As no appendages are seen in these fructifications it may be that they were not tubular but, in fact, laminae. A further model was built with lamina at the base of which were seeds. The lamina, being a planar structure, would not be infilled with matrix but the seeds may well have been (Plate 19; C). Compression of this type of structure resulted in loss of the topography of the upper and lower surfaces of the fructification as the laminae were easily compressed. Marginally the laminae were reduced in thickness but maintained their length, giving the "wing" structure of the compression fossil. Fracturing of this compression may occur along the seeds, leaving the compressed lamina in the counterpart. This might result in two unconformable impressions, one covered in seed casts, the other the impression of the compressed lamina (Fig. 8.6i,j).

This type of model fits the evidence from some of Plumstead's specimens where it appears that there are seeds at the base of some of the wing segments. The vein-like structures described on the surface of some of the specimens may represent the impression of sporophylls, i.e. a possible external surface of the fructification, e.g. Scutum rubridgeum (v.31207) (Plate 18; D).

This model does not fit all the specimens described. In some of the Indian and Australian specimens, the wing regions have a considerable topography to them and appear to be composed of distorted seeds. A further model was designed consisting of naked ovoid seeds borne around an axis (Plate 19; E). The seeds were infilled with and embedded in the same matrix. The central axis was not infilled and, since this structure
is indistinct in the fossils, it probably never got infilled and was totally flattened during the compression. On deformation of this model the seeds on the upper and lower surface maintained a topography but were considerably reduced in vertical dimension (Plate 19; F). The marginal seeds underwent significant flattening, giving a "wing" structure to the compression. The seeds would have been packed much more tightly than in the model, giving the appearance of a continuous wing structure. Adjacent to the "wing" would be the undistorted seeds of the "head" region. A fracture plane exposing the fructification would take a pathway over the "wing" and then over the seed infills at the centre of the fructification. This would give a part and counterpart composed of two conformable impressions. If the coaly matter was very thick on the "seed" area of the structure, the seed topography may not have been transmitted onto the adjacent matrix giving two unconformable impressions (Fig.8.6d,e).

8.8 Proposed model for glossopterid fructifications

It would be expected, as a result of this investigation of the ovulate glossopterid fructifications, that a definite model could be postulated. One of the limitations of this work has been the restrictions on availability of material and the inability to do sectioning or replicas on the fossils, due to the small number of specimens held at the BMNH and their status as cited specimens.

One of the problems encountered during this investigation is the apparent conflicting evidence from the fossils. Some show evidence of spirality, or the "wing" area representing laterally compressed seeds, or composed of numerous sporophylls with seeds at their base. Some specimens show conformable part and counterpart, whereas in other specimens they are unconformable.

As a result of these factors, it is impossible to produce a model which satisfies all the structures seen in this group of fossils, that is, a single common structural plan cannot be postulated. This author considers that there are two possible models which may have produced the "Scutum"-type compression fossil. Both are strobilar structures, one in which naked seeds are borne around a small axis (Fig.8.6a) or a structure in which the seeds are borne at the base of sporophylls of Lamina (Fig.8.6f). Both these models will produce on compression "wing" structures, in the first case as a result of lateral compression of the seeds and, in the second as a result of the flattening of microsporophylls. Also, both
Description of Figure 8.6

a. The uncompressed fructification consisted of a number of ovoid seeds arranged around a solid axis. The seeds are infilled with matrix during burial.

b. On compression the seeds distort marginally, becoming very thin but retaining their original length. The seeds on the upper and lower surfaces foreshorten but retain their original diameter. Coaly matter is very thick on the upper and lower surfaces and may drape across the seeds, preventing the seed structure being impressed on the adjacent matrix.

c. Loss of coaly matter leaves a cast of the fructification; the matrix above and below the seed casts shows little structure.

d. Pathway of the fracture plane producing an unconformable part and counterpart.

e. The exposed surface of the fossil showing a veined part and the seed-bearing counterpart. The wing region is produced by the distorted marginal seeds.

f. The uncompressed fructification consisting of a number of sporophylls, each with a seed at the base, arranged around a solid axis.

g. On compression the sporophylls on the upper and lower surface foreshorten and become very thin but retain their original length at the margins of the structure.

h. Loss of coaly matter leaves an impression where the lamina were and seeds in the form of casts.

i. Pathway of the fracture plane exposing an unconformable part (bearing the impression of sporophylls) and an unconformable counterpart (bearing positive seed casts). The marginal sporophylls form the wing region.

j. The exposed surface of the fossil showing the structure of the unconformable part and counterpart.
Fig 8.6. Diagrammatic account of the compression and exposure by fracture of the two proposed models for the Scutum type of fructification.
will show "seeds" present in the "head" region of the compression. In both cases the seeds would have been infilled with matrix, but the central axis would have been a solid structure and been flattened during compression.

It is postulated that the difference between Scutum, Hirsutum, Plumsteadia, Ottokaira and Dictyopteridium may be a result of size difference in the original seeds or the seeds and sporophylls. In Plumsteadia, the seeds in the "head" region are much smaller and would produce on distortion a very small wing region or be attached to small sporophylls. Conversely, in Ottokaria the seeds are much larger and would produce a more distinct wing region on compression. Lanceolatus is not as easily explained as it is not well reported in the literature and does not appear to show the same structural arrangement as the other ovulate fructifications.

The one feature shown by the compression fossils that is difficult to explain is the different structures in the part and counterpart. Most of these fossils are just impressions, all the organic matter having been lost. It is possible that this loss of organic matter has produced this phenomena. In all cases examined the wing regions were conformable in the part and counterpart, and it is only the "head" regions which are unconformable. This may result from the thickness of the organic matter preventing the seed topography being impressed onto the adjacent sediment (Fig.8.6). In the proposed model, where there are sporophylls present, these would have been compressed to fine coaly protrusions; loss of the coaly matter would have left the seed casts on one surface and the impression of the sporophylls on the other, resulting in different structures on the part and counterpart.

8.9 Discussion
The ovulate glossopterid fructifications provide a very good example of the difficulties encountered when only the compression state of preservation is known. This has resulted in many interpretations being offered to explain the uncompressed structures of these fructifications. The discovery of the permineralised reproductive structures (Gould & Delevoryas 1977) has not resolved the controversy. Experimental modelling of the enrolled megasporophyll structure has shown that the "Scutum"-type of fossil is not produced. The unrolled structure produces a compression, when modelled, much more closely resembling Scutum. As with
the dorsiventral model postulated by Schopf (1976) and Rigby (1978), it is difficult to explain the wing structure (which is not considered by Rigby and Schopf). This should be very different from the head region and not show structure, such as deformed seeds or seeds at the base of the wing segments, as has been described from the fossils. This model would not produce an unconformable part and counterpart when fractured, as has been postulated by Gould & Delevoryas (1977). It is very desirable that more material be investigated to enable closer comparison of these two preservation states.

The bilateral cupule hypothesis (Plumstead 1952) and the seed-bearing head with scale leaf model (Surange & Chandra 1974) are not accepted here. There is no evidence of a "foliar leaf" or "empty cupule" falling over the seed head. It would be expected that matrix would keep the two structures apart in some instances, or that overlap or mismatch would occur during transport and burial to indicate the presence of two components.

Two models are postulated here to explain the "Scutum"-structure. Both fit parts of the evidence described from the fossils. They are both strobilar structures. One consists of naked seeds arranged around an axis; the other consists of seeds situated at the base of small sporophylls which are arranged around an axis. Both these structures will produce wing and head regions on compression, but satisfy different structures observed in the fossils. The first proposed that the wing region is composed of laterally compressed seeds. This is based on evidence from Indian and Australian material which has more topography than the South African fossils. The second model proposes that the wing is composed of sporophylls with seeds at their base. This is based on evidence from the South African material.

This investigation is necessarily inconclusive due to the unavailability of material. The specimens need to be examined using sectioning and reconstructing the part and counterpart to determine the thickness of original organic matter and the pathway the fracture plane has taken to expose the fructification. Information of this nature would allow closer comparison with the permineralised specimens and to support or disprove the models proposed in this investigation.
CHAPTER NINE: The structure of cone compressions (c.f. *Lepidostrobus*) as revealed by vertical sectioning
9.1 Introduction

Brongniart (1828) described the cone Lepidostrobus, which is now generally believed to represent the reproductive structure of the Lepidodendrids. Lepidostrobus, unlike some of the compression fossils examined during this study, e.g. Alethopteris, Cyperites, Stigmaria, represented an original three-dimensional structure of some complexity into which sediment had penetrated. This has resulted in the formation of a complex 3-D compression. The fracture plane may take several different pathways through the cone compression. Lepidostrobus is found preserved as a permineralisation as well as a compression, and its structure has been elucidated from studies of permineralised specimens (Arber 1914; Brack 1970). This cone genus, therefore, is well known in the uncompressed state. Most studies of the compressed cones have concentrated on the extraction of the megaspores and microspores from the cone (Arnold 1933; Chaloner 1953; Felix 1954) to improve the definition of species, and to relate dispersed spores to their parent cones. In this study the cone compressions have been cut in longitudinal and transverse sections and these have demonstrated that the cones have retained a three-dimensional structure during the compression. A similar technique was used by Selling (1944) in an investigation of Calamitean cones. He, though, ground down the compressed cones and photographed the structures at various levels through the compression. In the present study the cones were coated in resin ('Araldite') to prevent the cones collapsing during sectioning. They were then cut at various positions along the cone on a rock saw. The cone compressions examined during this work were collected from the Radstock and Kent coalfields.

This type of investigation of a compressed fructification, which is also known as a petrification, is a useful model for understanding how complex 3-D structures behave on compression. Information of this type is extremely helpful in understanding how other fossil fructifications, such as the Glossopteris fructifications, may have responded to the compression process.

9.2 The basic organisation of Lepidostrobus

Lepidostrobus is composed of numbers of sporophylls which are arranged helically around a cone axis. The sporophylls consist of two structures: the pedicel, which extend from the cone axis, and this joins an upturned lamina at about 90° to the pedicel (Fig.9.1). The sporangia are
Description of Figure 9.1

Longitudinal section of *Lepidostrobus*, showing the main structural features of the cone. The distal part of the cone is microsporangiate, the basal part is megasporangiate, and the central region is heterosporous.
Fig. 9.1. Longitudinal section of *Lepidostrobus* showing the representative portions of the cone (after Andrews 1961).
borne on the adaxial surfaces of the pedicels. These sporongia may contain megaspores or microspores.

9.3 The external structure of the cone compression

The cone compressions are most commonly exposed by a fracture plane which runs over the outer surface of the sporophyll laminae. The tip of each lamina is usually left in the counterpart, so that a truncated lamina is seen on the surface of the fossil cone (Plate 20; A). At the margins of the cone the entire length of the lamina is preserved (see arrows on Plate 20; B). Two fine veins are present on the surface of the lamina. These widen towards the base of the structure and taper towards the apex.

The fracture plane does not always take a pathway over the outer surface of the cone but may pass through the centre of the compression. This fracture plane reveals a central cone axis with marginally arranged sporophylls (Plate 20; C). Sediment can be seen separating the sporophylls. The cone axis may not be well defined when the cone is exposed by this fracture plane. This seems to be directly related to the fact that very little or no sediment entered the cone axis during burial of the fructification. In specimens where sediment did get into the axis, it has considerable structure and topography (Plate 20; C). A spiral arrangement of small diamond-shaped structures can be seen across the axis. These are the sporophyll "scars" (Plate 20; C). They represent the points of attachment of the sporophylls for the cone axis. They are probably not true abscission surfaces, but are formed as a result of the fracture plane removing the sporophylls in the counterpart, i.e. similar to the "false leaf scars" on some Lepidodendron species (Chaloner & Boureau 1967). Sediment can be seen exposed within the sporophyll "false scars", indicating the sediment infill of the cone axis. The sediment may have infilled a small portion of the sporophyll base.

9.4 The internal structure of the cone compression

The cone compressions were sectioned at/or near the base, apex and centre of the cone. Other specimens were cut in longitudinal section. The cones that were collected from the Radstock coalfield have a considerable topography when they are exposed by a fracture plane which has run along the outer surface of the cone. Sectioning of these cones has shown that this topography is a result of the infiltration of very fine sediment (now shale) into the entire cone structure. The presence of the sediment has
Description of Plate 20

The external structure of the cone compression

A. Cone compression (GR/R/W) from the Radstock coalfield. The fracture plane has run over the surface of the sporophyll laminae (s1), exposing the outer surface of the cone. The tips of the laminae have been left in the counterpart (X 1.5).

B. Cone compression (GR/R/U) from the Radstock coalfield. The fracture plane has passed over the surface of the sporophyll lamina. The entire length of the lamina (l) can be seen preserved at the margins of the cone (X 1).

C. Cone compression (GR/R/X) from the Radstock coalfield. The fracture plane has taken a pathway through the centre of the cone, revealing the central cone axis (ca) and marginal sporophylls (sp). "Sporophyll scars" (sc) can be seen arranged spirally on the cone axis (X 2.3).

D. Cone compression (GR/K/D) from the Kent coalfield. The fracture plane has passed over the outer surface of the cone. The cone is very compressed and indistinct due to the absence of a sediment infill (X 1.2).
prevented flattening of the cone and allowed the retention of a significant three-dimensional structure. Many features that have been reported from the permineralised specimens of *Lepidostrobus* can be identified in these compressions:

(a) Cone axis
(b) Sporangium
(c) Pedicels of sporophylls
(d) Lamina of sporophylls

(a) Cone axis

The longest cone sectioned was 7.4cms long, and none of the cones exceeded 2.0cms in diameter. Usually, the apices and bases were not preserved, but the cones tapered towards the distal end.

Transverse sections of the cone compressions show a central distinct structure of thick coaly matter (Plate 21; A). This is interpreted as being the compressed cone axis. The structure of the axis varies along the length of the cone and there is some variation between cones. In some specimens (GR/R/W; GR/R/V), the axis is composed of small plates of coaly matter forming a discontinuous structure surrounding a central core of sediment. In these examples the cone axis has a diameter of 2.5-5.0mms. The shape of the axis is not consistent between specimens. In GR/R/W the axis is subcircular, whereas in GR/R/V the axis is concaved downwards or C-shaped (Plate 21; A,C). The coaly matter forming the compressed axis is about 1-2mms thick, and small protrusions of coal extend from it into the adjacent matrix.

Towards the apex of the cone the axis changes in shape. In GR/R/V the axis becomes a distinct horizontal plate of coal from a C-shaped structure at the centre of the cone (Plate 21; B). In this example the upper and lower surfaces of the compressed axis are separated by a very fine layer of sediment. In the other example, GR/R/W, the axis becomes much more disrupted and fragmented towards the cone apex (Plate 21; D).

This variation in the cone axis also occurs between cones, all of which can be assigned to the same species, *Lepidostrobus variabilis* Lindley & Hutton. In some specimens, e.g. GR/R/U, the compressed cone axis is in
Description of Plate 21

Transverse-sections of cone compressions, showing the variation in the structure of the cone axis (all specimens from the Radstock coalfield).

A. Median T.S. of a cone compression (GR/R/W). The cone axis (ca) forms a distinct concave-downwards structure of thick coal in the centre of the field of view (X 10).

B. T.S near the apex of the cone compression (GR/R/W). The cone axis (ca) has been compressed to a horizontal plate of coal in which the two surfaces of the axis are separated by a fine layer of sediment (X 10).

C. Median T.S of a cone compression (GR/R/V). The cone axis (ca) is sub-circular and composed of numerous separate plates of coal (X 8).

D. T.S near the apex of the cone compression (GR/R/V). The cone axis (ca) has become disrupted and lost its sub-circular structure (X 8).

E. Median T.S of a cone compression (GR/R/Z). The cone axis (ca) is composed of two horizontal layers of coal separated by a layer of matrix (X 6).

F. T.S near the apex of the cone compression (GR/R/Z). The cone axis (ca) has a more reduced topography.

G. Median T.S of a cone compression (GR/R/U). The cone axis (ca) is in the form of a single horizontal plate of coal (X 10).

H. T.S near the apex of the cone compression (GR/R/U). The cone axis consists of a single plate of coal as in the median section (X 10).
the form of a small irregular plate of coaly matter measuring 3.0mm in length and 0.5mm thick (Plate 21; G). This structure shows little variation along the cone (Plate 21; H). In another example, GR/R/Z, the cone axis is a flat, plate structure in which the two surfaces are separated by the matrix (Plate 21; E). This separation of the surfaces can be seen clearly in longitudinal section (Plate 22; E). Further up the cone, towards the apex, these two surfaces have almost completely closed up (Plate 21; F). Longitudinal sections through the cone, where the axis is simply a solid plate of coal (e.g. GR/R/U), shows the axis as a continuous fine coaly line running through the centre of the cone (Plate 22; D).

The structure of the cone axis appears to be dictated by the degree of sedimentary infilling of the axis that occurred during the burial of the fructification. Where a substantial sediment infill of the axis formed, the axis has retained a three-dimensional structure. Some fragmentation of the axis seems to have occurred during the compression, resulting in the compressed axis being composed of separate small plates of coal. In the specimens where the compressed axis is in the form of a plate structure, it is concluded that virtually no, or very little, sediment entered the axis during the burial of the cone. In the example where the cone axis is in the form of a C-shaped structure (GR/R/W), it appears that the axis was only partially infilled with sediment, resulting in the upper surface being compressed (or it collapsed) into the lower.

(b) Sporangium

In most cases the sporangium walls have been preserved as very fine coaly lines occupying most of the compressed cone. These fine coaly lines are separated by matrix. In some specimens the sporangium walls have been left intact during the fossilisation process, and the structure of the individual sporangia has been preserved (Plate 22; A,B). In most of the specimens, though, the compressed sporangium walls are very distorted, forming a mass of irregular coaly lines extending through the matrix infill of the cone (Plate 22; C). In longitudinal section, the remnants of the sporangium wall can be seen lying within the compressed sporophylls (Plate 22; D,E). Slightly oblique sections show the contorted, fine coaly lines of the sporangium underlain by the thicker coaly base of the compressed pedicels (Plate 22; F).
Description of Plate 22

The structure of the sporangium and pedicels in cone compressions (all specimens from the Radstock coalfield)

A. T.S of a cone compression (GR/R/W), showing numerous coaly lines within the infill of the cone. These represent the compression of the sporangium walls (sp) (X 12).

B. T.S of a cone compression (GR/R/Z), showing the fine coaly lines of the compressed sporangium (sp) walls. The cone axis (ca) can be seen at the right-hand margin of the photograph (X 12).

C. T.S of a cone compression (GR/R/V), showing a much more distorted arrangement of the fine coaly lines of the compressed sporangium (sp) walls (X 12).

D. L.S of a cone compression (GR/R/U), showing the compressed cone axis (ca) with fine coaly projections; these are the compressed pedicels (p) of the sporophylls. Within the matrix of the cone compression, can be seen the fine coaly lines of the compressed sporangium walls (sp) (X 12).

E. L.S of a cone compression (GR/R/V). The cone axis (ca) consists of two layers of coal separated by matrix. (sp) compressed sporangium walls (X 12).

F. L.S of a compressed cone (GR/R/V). The section is slightly oblique and shows the compressed sporangia (sp), each of which is underlain by an angular piece of coal representing the compression of the pedicels (p) (X 12).
(c) **Pedicels of sporophylls**

These are not very well preserved in the transverse-sections of the cones and can only be seen as short, coaly extensions from the coaly matter of the cone axis. Their structure is seen much more clearly in longitudinal section. The pedicels branch off from the cone axis and extend away from it as a finer coaly line joining the upturned lamina at the core margin (Plate 23; F). Often, this feature is not picked up in the plane of section and the pedicel is just seen as a short, coaly extension (1-2mm) from the cone axis (Plate 22; D).

(d) **Sporophyll lamina**

One of the easily distinguished structures in these cone sections is the lamina of the sporophylls. In transverse-section they bound the entire margin of the cone in the form of many fine coaly lines approximately 1-1.5mm in length. The compressed lamina are in the form of slightly V-shaped structures. At the margins of the cone, where the lamina were orientated in the plane of the compressive stress, the lamina have, as a consequence of this, a slightly more "closed" structure compared to the lamina on the upper and lower surfaces of the cone (Plate 23; B). The two sides of the lamina, though, have been kept apart by the sediment that infiltrated the cone structure. The structure of the lamina borne on the upper and lower surface of the cone shows little variation (Plate 23; C,D). On the upper surface they V-upwards, and on the lower they V-downwards. The lamina fan around the compressed cone as they change orientation slightly around the axis (Plate 23; A,E). In longitudinal section, the fine coaly lamina can be seen running parallel with the axis, providing a distinct surface (parallel to bedding) along which the fracture plane can run (Plate 23; F).

9.5 **Comparison of the compressed cone structure with permineralised Lepidostrobus.**

The general structure of a number of species of *Lepidostrobus* has been determined from American and British Coal Balls (Arber 1914; Brack 1970). Transverse sections of fertile permineralised specimens of *Lepidostrobus* show a central cone axis around which sporophylls are arranged radially. The sporangia are borne on the sporophylls and these may contain megaspores or microspores, or frequently they are found to be empty (Plate 24; A).

The cone axis in *Lepidostrobus* is usually composed of three layers (Brack 1970): a small stele with a central pith; a zone of parenchymatous cells.
Description of Plate 23

The structure of the lamina of the sporophylls in the cone compression (all specimens from the Radstock coalfield)

A. T.S of a cone compression (GR/R/W), showing the lamina of the sporophylls (sh) fanning around the compression (X 4).

B. Magnification of A, showing the "closed" structure of the marginal sporophylls (sh) (X 8).

C. T.S of a cone compression (GR/R/U). The sporophyll (sh) laminae show a slight V-structure on the lower surface of the cone (X 15).

D. The sporophyll lamina show a similar V-structure on the upper surface of the cone compression (X 15).

E. T.S of a cone compression (GR/R/Z), showing the fracture plane migrating over the sporophyll (sh) lamina (X 6).

F. L.S of a cone compression (GR/R/V), showing the sporophyll (sh) lamina providing a surface parallel to the bedding plane over which the fracture plane can run (X 10).
which are not often preserved; and a distinct cortex composed in part of (Plate 24; B) fibrous elements. In the cone compression, the cone axes are composed of a single layer of thick coal surrounding a core of sediment. No stele structures are seen preserved within the cone axis infill. It is concluded that the fibrous cells of the cortex probably produced the compression structure, the stele and parenchyma zone of the axis having decayed away before infilling with matrix.

The sporangium walls in the permineralised specimens are very thin, consisting of a single layer of palisade cells (Plate 24; D). On compression, these have formed the fine coaly lines occupying the bulk of the cone compression. In the permineralised Lepidostrobus, where the sporangia have dehisced, the sporangium walls have been completely disrupted, forming a mass of contorted structures (Plate 24; C). It can be envisaged that this type of arrangement of the sporangium walls would, when separated by matrix and compressed, produce the structure observed in the sectioned cone compression.

Transverse-sections of the sporophyll laminae, in the permineralised cones (Plate 24; E,F), show them to have a lanceolate shape, tapering to a point at the margins of the structure. The lamina has a slightly V-shaped abaxial face and a flat adaxial face. Each lamina has a central midvein, the remainder being composed of thin-walled mesophyll cells. This V-shaped structure has been retained in the compressions of the laminae. The centre of the lamina compression, in transverse-section, may be slightly thicker than the rest of the lamina, probably resulting from the compression of the midrib.

The pedicels of the sporophylls can be seen forming distinct extensions from the cone in the longitudinal sections of permineralised Lepidostrobus (Plate 24; G,H). In the cone compressions, small projections of coaly matter are seen branching from the cone axis, representing the compression of the pedicels.

The structure of these compressed cones, therefore, can be related to the permineralised Lepidostrobus. The four major anatomical features of the uncompressed fructification, the cone axis, the sporangium walls, the pedicel and the lamina of the sporophylls, can be recognised in the compressed cone. These structures, in the compressions, are composed of different thicknesses of coaly matter, and this can be directly related to the original anatomy of the cone. For example, in the compressions the
Description of Plate 24

Sections of permineralised Lepidostrobus (from the Kansas coalfield) (W.G.C. coll.)

A. T.S. of an entire cone, showing the central cone axis (ca) and the distorted walls of sporangia (sp). Bounding the cone are the lamina of sporophylls (sh) (X 2).

B. Magnification of A, showing the cone axis. The axis is composed of three layers: a fibrous outer cortex (co); a middle parenchymatous layer (pa), and a central pith (ph) (X 8).

C. T.S of an entire cone, showing the distorted walls of the sporangia (sp) (X 1.75).

D. Magnification of C, showing the single layer of cells that form the sporangium (sp) walls (X 7).

E. T.S of the lamina of the sporophylls (X 7).

F. T.S of the lamina of the sporophylls (X 7).

G. Oblique longitudinal section of Lepidostrobus, showing the cone axis (ca), pedicels (p), and the sporangium walls (sp) (X 5).

H. Oblique longitudinal section of Lepidostrobus, showing the cone axis (ca) with short projections representing the pedicels (p) of the sporophylls (X 5).
sporangium walls are represented by very fine coaly lines. In the permineralised specimens the sporangium walls are only one cell thick. In contrast, the uncompressed cone axis consists of a very thick cortical layer, and in the compression the axis is composed of a thick coaly layer.

The original three-dimensional detail of these cones has been preserved during the fossilisation process as a result of the infilling of the cones with very fine sediment during burial. The fine sediment infiltrated all the spaces within the cone structure, into the sporangium from which the spores had been dispersed, and in between the individual sporophylls. Sediment did not always infill the cone axis, and in many cases only partial infilling of the cavity occurred. This is probably related to the axis remaining a solid structure or that it had collapsed as a result of decay; both of these would prevent infilling. Obviously the cone is closed at the apex and sediment would only have been able to enter the cone from the basal end, and this may well have restricted the passage of sediment into the axis. The degree of sediment infill that formed in the axis dictated the structure of the compressed axis. Where no sediment had entered the axis the compression process closed the empty axis, forming a thick, flat plate of coal. If substantial infilling of the axis occurred, the compressed axis retained the 3-D structure of the original axis forming a semi-circular compression.

The infilling of these cones during burial has prevented the collapse/compression of the internal structure of these fructifications. In cone compression from the Kent coalfield, no internal structure has been preserved since, apparently, no sediment entered the cone as it was being buried. These cones consist of a single, flat layer of coal with only the external details of the cone having been preserved (Plate 20; D).

9.6 Conclusions

Sectioning of cone compressions from the Radstock coalfield has shown that the basic structural features have been preserved. The anatomical structure described from permineralised Lepidostrobus (Arber 1914; Brack 1970) can be recognised in transverse and longitudinal sections of the cone compressions. The cone axis, sporangium, pedicel and lamina of the sporophylls can all be identified in the sections of the compressions. This three-dimensional detail has been preserved during the fossilisation process as a result of fine sediment infilling the cones during burial.
The sediment, because it is less compressible than the plant organ, has prevented the internal detail of the cone being destroyed during the compression. The matrix has "protected" the cone structure during fossilisation and maintained the three-dimensional structure of the uncompressed fructification (obviously there has been some reduction in the vertical dimensions of the cones as the fine sediment would have been very compressible).

This investigation has demonstrated how a complex structure, such as a fructification, reacts to the compression process. Having permineralised material available has enabled a close comparison of the uncompressed and compressed structures in the cones. A knowledge of the configuration of these structures in the compressed state, and the factors which have dictated their form, should enable interpretations to be made of complex structures, such as fructifications, when only the compression state of preservation is known. It is interesting to note that the radial symmetry of the original cone survives the compression and is immediately evident when the cones are sectioned. Therefore, when material is available for sectioning, the problem of the Glossopteris fructifications could be resolved, at least in some of the basic elements, such as whether the fructifications were bilateral or radial.

9.7 Discussion of the nomenclature of Lepidostrobus

Brongniart (1828) erected the genus Lepidostrobus for a cone preserved as a compression. Subsequently, this generic name has been applied to cones preserved as petrifactions as well as compressions. The main character that has been used in defining species of Lepidostrobus is the type of spores present in the cones. This was well demonstrated by Chaloner (1953) and Felix (1954). In this work, cone compressions have been examined in which no spores are present. The absence of spores, i.e. empty cones, presents difficulties in applying a specific or even generic name to the fossil. Other criteria have been used in defining species of Lepidostrobus. Crookall (1966) described numerous species in terms of cone size and the arrangement and size of the sporophylls, but he also used spore characters. He did not consider the nature of the preservation of the cones and the different types of information that can be determined from a petrified cone versus a compressed cone. Chaloner (1967) did consider the different preservation states present within the genus Lepidostrobus. He separated Lepidostrobus into permineralised species
(and then into microspore-bearing and heterosporous) and compressed species, which he also divided into heterosporous cones and microsporangiate and empty cones.

Recent work by Brack-Hanes & Thomas (1983) on the type specimen of Lepidostrobus has shown that the cone was microsporangiate. They have, as a result of this, revised Lepidostrobus and it is now a microsporangiate cone genus. Chaloner (1953) had already demonstrated that another cone genus, Flemingites Carruthers 1865, contained mega- and microspores. Brack-Hanes & Thomas (1983) have placed all bisporangiate cones (formerly Lepidostrobus) into Flemingites. The authors, though, have left all cones in which no spores are present in Lepidostrobus. In their emended diagnosis of the two genera, many of the features are based on data available only from permineralised specimens, e.g. "Axis with exarch vascular bundle", "Sporangium with narrow attachment along its length to adaxial surface of sporophyll pedicel". If empty permineralised cones are preserved, it is possible to assign them to a genus on the basis of anatomical features of the cone. This is not possible with empty compressed cones where frequently only the outer surface is exposed. Even where internal structural detail is preserved in compressed cones, the configuration of the structures is dependent on the degree of sediment infill. Therefore, it is these types of cones, i.e. compressions lacking spores, that are difficult to classify. It may be useful to have a third genus of lycopod cones for compressions (and possibly petrifactions) without spores. This would further limit the application of the genus Lepidostrobus. Alternatively, we need to decide which characters of the cone compressions, i.e. sporophyll size etc, should be used in specific diagnosis. In this discussion of the empty compressed cones, the only name that can be applied to them is "c.f. Lepidostrobus" as not enough data, i.e. spore content, is available to classify them further.
CHAPTER TEN: The preservation of the Carboniferous seed cast *Trigonocarpus*
10.1 Introduction

The formation of stem casts has been investigated experimentally using a laboratory flume. The results of this work were closely compared to fossil stem infills (see Chapter 4). Another type of cast which is common in Carboniferous sediments is the seed cast. Some of these seed casts were called *Trigonocarpus* by Brongniart (1828), and are now considered to be the infills of seeds borne by the medullosan pteridosperms (Taylor 1981). The infilling of a seed represents a very different process from the infilling of a hollow stem. A seed is a sealed structure, i.e. it has a continuous wall or integument which protects the nucellus enclosing the megaspore. There is only one small opening in the seed at the apex, called the micropyle. Through this aperture the ovule is fertilised.

It was demonstrated in the experimental flume work that a stem lying horizontally on the sediment surface is only infilled substantially when both ends of the stem are open. This allows the current to flow through the stem, depositing sediment within the pith cavity. In the case of the seed, there is no large entrance or exit for the current to flow through. Discussions of these seed casts have neither considered how these seeds were infilled nor the conditions under which infilling could have occurred (Salisbury 1914; Arnold 1938). In this investigation, a number of specimens of *Trigonocarpus* were examined in the sediment they were buried in. Isolated specimens of the seed casts were sectioned in longitudinal and transverse-section in order to determine the nature and structure of the infill. Information of this type gives an indication of how these seed casts were formed and the factors which dictated their structure.

10.2 Brief description of *Trigonocarpus* and *Pachytesta*.

Brongniart (1828) erected *Trigonocarpus* as a genus representing seeds preserved as casts. He also erected the genus *Pachytesta* for structurally preserved (permineralised) ovules.

The term ovule is probably more appropriate than seed when discussing these fossils, since evidence of an embryo is very rare in fossil seeds. The term seed cast is used here only as a descriptive term and does not imply that an embryo had formed within the seed wall. The genus, *Pachytesta*, was not well defined and some authors placed permineralised
Description of Figure 10.1

a. Longitudinal section of Pachytesta showing the general structure of the seed (X 1).

b. Transverse-section, at point 1, of Pachytesta showing the micropyle and the three primary ribs (X 1).

c. Transverse-section, at point 2, of Pachytesta showing the median section of the seed with the distinct layers of the seed wall bounding the nucellus (X 1).
Fig. 10.1. The general structure of *Pachytesta* (after Hoskins and Cross 1946).
Description of Figure 10.2

a. *Trigonocarpus*; the presence of the three primary ribs indicates that the sarcotesta had been lost or compressed during fossilisation (X 2).

b. *Trigonocarpus*; the surface of the seed cast is smooth, indicating the sarcotesta was present during fossilisation (X 2).

c. *Trigonocarpus*; the surface of the seed cast is smooth, apart from three ridges of sediment which represent the infill of the three primary ribs of the sclerotesta (X 2).
Fig. 10.2. The structure of *Trigonocarpus* (after Hoskins and Cross 1946)
seeds in *Trigonocarpus*, e.g. *T. shorensis* (Salisbury 1914), whereas other authors used *Pachytesta* for permineralised seeds, e.g. *P. gigantea* (Reed 1939). These two genera were revised by Hoskins & Cross (1946), since seeds had been assigned to a genus in which some species were well preserved (anatomically), whereas other species were only known as casts. They re-established *Trigonocarpus* as a genus for seeds preserved as casts and compressions, and placed similar but anatomically preserved seeds in *Pachytesta*.

The basic structure of *Pachytesta* is shown in Fig.10.1. The seed is radially symmetrical, has a stalked nucellus, except at the chalaza (base), free from the integument, has a multilayered integument consisting of an inner fleshy layer, a middle sclerotic or stony layer (the sclerotesta), and an outer fleshy layer (the sarcotesta). The integument is divided into three equal valves by three primary ribs which extend from the base of the seed to the micropylar opening (Plate 26; F,G).

*Trigonocarpus*, shown in Fig.10.2a & c, is usually ovoid in shape with a rounded base and a pointed apex. The surface of the seed cast is usually smooth with three prominent ridges extending from the apex to near the base. Hoskins & Cross (1946) were some of the few authors to consider the possible variation in the structure of the seed cast. They demonstrated that the outer surface of the seed cast may have a different structure depending on the degree of "decortification" or compression the seed suffered during its fossilisation. For example, the seed may be smooth, indicating that the outer fleshy layer (the sarcotesta) was present when the seed was fossilised (Fig.10.2b). Sometimes the seed cast may show strongly developed ridges, indicating that the outer layer (sarcotesta) had been lost (Fig.10.2a, c) before fossilisation. These authors have indicated the various states of preservation the seed casts may represent, but they did not consider how the actual cast was formed.

10.3 Descriptions of specimens of *Trigonocarpus*.

A number of specimens of *Trigonocarpus* were examined in situ in the sediment that buried them. These specimens were borrowed from the British Museum (Natural History). In one specimen, (v.198), many seeds were present, orientated at various angles in a fine-grained, quartzitic sandstone (Plate 25; A). In some cases the seed casts are partially embedded in the sediment, where in others all that is left is a mould of the seed
Description of Plate 25

The structure of Trigonocarpus

A. Specimen of fine-grained sandstone containing Trigonocarpus parkinsonii (v.198) from the Coal Measures of Lancashire (X 1).

B. A seed mould on A, showing the compressed sarcotesta surrounding the mould. The mould is lined with a thick layer of coal, representing the compression of the sclerotesta and the sarcotesta of the seed wall (X 1.75).

C. The base of a seed cast from the specimen shown in A. The coaly layer (1) represents the compression of the seed wall (X 1.6).

D. A fractured seed cast from specimen A, showing the internal structure of the cast composed of concentric layers of sediment (X 2).

E. Trigonocarpus parkinsonii (v.40583) from the British Coal Measures. The seed cast has a split (sp), which has infilled with sediment, along one of the primary ribs (X 2).

F. Trigonocarpus parkinsonii (v.40582) from the British Coal Measures. The seed cast is bounded by a compression border (cb), resulting from the compression of the sarcotesta. There is a distinct ridge (r) of sediment on the surface of the cast, which is continuous with the adjacent sediment (X 1.6).

G. Trigonocarpus sp (v.40583); the apex of the seed cast is not pointed but has a triangular shape as a result of splitting along the primary ribs (X 3.5).
cast. In one example of a mould, a distinct coaly line can be seen extending around the margins of the seed mould into the matrix at the apical end of the cavity (Plate 25; B). The coaly lines do not meet at the apex but end in the matrix. The area between the coaly lines and the seed mould is occupied by matrix. This seed mould is lined with a thick layer of coal. The coaly lines surrounding the mould are interpreted as representing the compression of the sarcotesta (the outer fleshy layer of the integument). The coaly layer lining the mould is interpreted as representing the compression of the sclerotesta. This seed was compressed with its long axis orientated perpendicular to the compressive stress.

The sarcotesta was compressed at the margins of the seed cast, forming the flat coaly layer exposed in the sediment at the margins of the seed mould. The sarcotesta, on the upper and lower surfaces of the seed, was compressed with the sclerotesta, forming the thick coaly layer lining the seed mould. Therefore, the compressed sarcotesta forms "compression borders" at the margins of the seed cavity (Fig.10.3). These compression borders, bounding the margins of the infill, would only be produced when the seed fell onto the sediment surface with its long axis parallel to the bedding plane and had an intact sarcotesta. The seeds seem to have generally taken up this position on the sediment.

Specimens of permineralised seeds show that the sclerotesta is composed of thickened fibres, whereas the sarcotesta is composed of much thinner-walled parenchymatous cells. During this course of this work on the compression process, it has been demonstrated that fibrous, or thickened regions of cells in the original plant organ, form the thickest regions of coal in the compression fossil because these cells are relatively incompressible, e.g. the cone axis in *Lepidostrobus*, the venation in pteridosperm leaves. Therefore, the original, rigid sclerotesta of the seed wall in these seeds would produce, on compression, the thickest layer of coal. This thick layer of coal can be seen in a specimen where the base of a seed cast is exposed, the remainder of the seed being buried in matrix (Plate 25; C). Sediment has infilled the original, primary ribs of the seed. As a result, the ribs are in the form of ridges of sediment standing above the surface of the seed cast. Between these structures is a layer of coal (approximately 1mm thick) which thins over the infilled rib structures. This coaly layer is interpreted as being formed mainly from the sclerotesta. The sarcotesta may have been present when the seed was fossilised, but it is more likely to have been lost or decayed during transport of the seed due to the fleshy nature of
Description of Figure 10.3

a. Transverse-section of the seed, showing the intact seed wall surrounding the infill of the nucellar cavity. The seed is lying with its long axis parallel to the bedding plane.

b. On compression, the seed wall is reduced to a thick layer of coal on the upper and lower surface of the seed infill. The sarcotesta forms compression borders (c) at the margins of the seed infill.

c. View of the seed infill exposed on the bedding surface, showing the compression border produced by the deformation and coalification of the sarcotesta bounding the seed infill.
a. sclerotesta

b. sarcotesta

sclerotesta

sarcotesta

sediment infill of nucellar cavity

c. coaly layer produced as a result compression of the sclerotesta and the sarcotesta.

compression border formed from the compression of the sarcotesta.

matrix

seed infill

Fig. 10.3. The formation of compression borders during the fossilization of a seed which has been infilled and in which the sarcotesta is intact.
of this part of the seed wall. It is more likely that the tough, fibrous sclerotesta would have withstand the transport processes and retained its rigidity, so that the nucellar cavity remained open and allowed infilling to occur.

Another seed on the same specimen has been fractured so that the inside of the seed cast is revealed. This shows that the cast is composed of a series of concentric layers of sediment (Plate 25; D). These layers appear to indicate that infilling was episodic; that is, sediment was washed into the cavity, forming a layer, and then there was a time interval before the next layer of sediment was deposited.

Other specimens of seed casts still attached to the sediment they were buried in, e.g. v.40583, show that the seed has split along one of the (Plate 25; E) primary ribs at the seed apex. This split is occupied by matrix, and it seems that the seed split open at the apex, giving a larger aperture for sediment to enter the seed cavity. In a second example, v.40582, an infilled, primary rib can be seen running along the seed surface. This ridge of sediment has an uneven, fractured surface, as if it was continuous with the matrix before the seed was exposed (Plate 25; F); that is, the rib was split during infilling of the seed cavity and not separated from the adjacent matrix by the integument. Bounding this specimen of a seed cast is a thin coaly layer about 2mm wide. This is a compression border formed from the compression of the sarcotesta.

10.4 The transverse and longitudinal section of Trigonocarpus

A number of isolated specimens of Trigonocarpus casts were sectioned; some in longitudinal, others in transverse-section. Many of the casts examined did not show a sharp point at the seed apex where the three primary ribs meet, but the apices were fractured off, exposing the infill of the seed cavity (Plate 25; G). This irregular structure may represent a fracture surface where the pointed apex has been left in the matrix. It is possible that it represents an opening in the seed through which matrix entered. The seed seems to have split a short distance along the three primary ribs at its apical end.

When these seeds are sectioned (on a rock saw), the infill in T.S and L.S shows no structure at all. The matrix is very homogeneous, consisting of small, subrounded grains of quartz and feldspar (0.20-0.5mm in diameter).
Description of Plate 26

The internal structure of *Trigonocarpus* and *Pachytesta*

A. L.S of *Trigonocarpus* (v.40583), showing the homogeneous nature of the fine-grained infill (X 2).

B. L.S of *Trigonocarpus* (v.6006), showing the structure of the infill. The infill contains a curved line of clay particles which may have accrued on a remnant of the nucellus (X 2.5).

C. Magnification of B, showing the nature of the sediment. The sediment is composed of sub-rounded grains of quartz and feldspar in a clay matrix (X 8).

D. T.S of *Trigonocarpus* (GR/UN/E). The infills of the three primary (pr) ribs can be seen as distinct ridges on the surface of the cast (X 4).

E. Magnification of D, showing the homogeneous nature of the sediment infill (X 24).


G. T.S. of *Pachytesta*, showing the sclerotesta (sc) and the three primary ribs. The sarcotesta has been lost (X 3.6) (W.G.C. coll. 85).
included in a fine clay matrix (Plate 26; A). There are no sedimentary structures, such as grading or microbedding in the infill. In T.S the infills of the primary ribs can be seen standing as positive structures away from the seed surface (Plate 26; D,E). These structures are composed of the same matrix as the main seed infill. In L.S the matrix is as structureless; only in one example, (v.6006), is there any change in composition within the infill. Within this seed cast there is a faint, curved line which is composed of fine clay particles. This may represent the position of part of the nucellus when the seed was infilled (Plate 26; B,C).

The sectioning of these casts has not indicated the direction of infilling or indicated where the sediment entered the seed cavity. The uniform nature of the matrix and lack of sedimentary structures seems to indicate that infilling occurred in very quiescent conditions in which there was little current activity. Sediment settled out of suspension and slowly infilled and buried the seed. There appears to have been a constant sediment supply, since any fluctuations would have resulted in the formation of microbedding or grading.

10.5 The formation of Trigonocarpus.

The only opening in the living seed is the micropyle. Studies of Pachytesta have shown that there is considerable variation in the length and transverse-section of the micropyle between species (Taylor 1965). Hoskins & Cross (1946) demonstrated, in their discussion of Pachytesta vera, that the micropyle at the distal end is about 350 \( \mu \)m in diameter, increasing to 1mm at midway down the micropyle. It enlarges abruptly to 1cm at the top of the nucellar dome (Fig.10.4). The nucellus, in this species, is about 2.5-3.0cms in diameter. Hence, it is larger than the seed casts examined in this study, which range from 0.7-1.5cms in diameter.

The nucellus, in permineralised specimens, is bounded by a fibrous (Plate 26; G). sclerotesta and an outer sarcotesta, and this indicates that the integument would generally be impermeable to any infill, unless the seed wall had been damaged during transport or by the activity of boring organisms. The only other area of the seed through which sediment may have entered would be the chalaza. At the chalaza, the nucellus is attached to the integument on a stalk. The sclerotesta extends into this region, forming
Description of Figure 10.4

Diagrammatic reconstruction of an L.S through the micropyle of *Pachytesta vera*, showing the enlargement of the micropyle at the top of the nucellar dome.
Fig 10.4. Longitudinal section through the micropyle and upper part of the nucellus in *Pachytesta vera* (after Hoskins and Cross 1946).
a thickened cone structure. The integument is slightly thinner in this region. The chalaza does not appear to provide a distinct opening which would allow the movement of sediment into or out of the seed cavity. The stalk of the nucellus is composed of the same fibrous cells as the sclerotesta and would not give an area of weakness in the integument. Examination of the seed casts does not give any indication of infilling from the chalaza.

It is concluded that infilling of these seeds would have occurred through the micropyle. The micropyle, though, represents a very minute opening in the seed apex, and would easily have been blocked by sediment, even by a grain size of 0.2-0.5mms. Some of these casts are composed of much coarser sediments. It is indicated from the casts that the micropyle area was enlarged to about 2-3mms diameter at the seed apex by the splitting of the three primary ribs at the apical area of the seed. This would give a larger aperture for the passage of sediment into the seed cavity.

The fossilisation of these seeds seems to have proceeded by the splitting of the three primary ribs at the micropyle. This splitting may have occurred as a result of: dessication of the seed after it had been shed from the tree, as a result of germination of the seed; or the splitting may have occurred during transport of the seed.

After the apical region of the seed had been enlarged, the nucellus rotted away leaving a seed cavity. The outer layer of the integument, the sarcotesta, may well have decayed or been removed during transport processes. Whether the seed was transported or was buried (near where it was shed from the tree) is not easy to determine. However, the seed was buried and infilled by sediment percolating into the seed cavity, or being gently washed in through the enlarged micropylar area. Infilling seems to have occurred under very quiet conditions with low current activity. There are no sedimentary structures preserved in the infill, and this seems to indicate that there was little change in current conditions during infilling. In order for the infill to have formed in these fossils, the seed must have been orientated with its long axis parallel to the bedding, or upright, or at an angle to the bedding. If the seed had landed with its micropyle down in the sediment, infilling would have been prevented.
Once the seed had been infilled and buried, the compression would have begun. The degree to which the cast is compressed is a function of the compressibility of the matrix forming the infill, and the degree to which infilling occurred. The usual orientation of infilled seed casts is with their long axes parallel to the bedding plane, and any remaining sarcotesta is preserved as coaly compression borders at the margins of the casts. Where only the sclerotesta was present bounding the infill, this has formed a distinct coaly layer borne on the surface of the seed cast. These fossils, unless the coaly matter has been lost are, therefore, casts and compressions. The sclerotesta did not form compression borders as the sarcotesta did, probably because it was much thinner in the original seed (only about 400-500μm, compared to the 4.5mm diameter of the sarcotesta (from Hoskin & Cross 1946) and was very fibrous.

Gastaldo & Matten (1978), in their discussion of Trigonocarpus leeanus, considered that "the invading sediments filled not only the nucellus, but also the entire seed cavity inside the integument". They concluded that the morphological features of the cast represented the structure of the inner integment, probably the sclerotesta, and not the nucellus. They also considered that the secondary ridge structures on the casts of their species may have been the "manifestation of the compressed integumentary vascularisation". Thus, the ridge structures were produced from the compression of vascular bundles in the integument, i.e. very similar to the behaviour of the venation in the pteridosperm leaves (Chapter 7) and were not ribs in the original seed wall.

Taylor (1981) stated that in some instances "it is difficult to determine whether the seed cast was formed from the outer surface of the integument (sarcotesta) or the inner surface". Considering the great differences in the rigidity of these two layers, it is difficult to envisage how the tough, fibrous sclerotesta could have been lost and the parenchymatous sarcotesta remained. The sarcotesta would have collapsed and not provided a rigid, open cavity in which sediment could have accrued. Therefore, it is considered that, to form the cast, the sclerotesta had to be present in order for there to be a seed cavity, and that these fossils are generally the casts of the inner wall of the sclerotesta. The formation of Trigonocarpus is summarised in Fig.10.5.
Description of Figure 10.5

a. The original seed with its entire seed wall intact.

b. As a result of transport and decay of the seed, the sarcotesta has been lost, and the contents of the seed rotted away leaving a seed cavity. The micropyle area at the seed apex has been enlarged by splitting of the three primary ribs.

c. The seed settles on the sediment surface, probably with its long axis parallel to the bedding surface. The seed cavity is infilled by fine sediment entering the seed via the enlarged micropyle.

d. After compression, and subsequent exposure by fracture, the fossil is in the form of a seed cast composed of the same sediment it was buried in. The sclerotesta has formed a layer of coal surrounding the infill.
Fig. 10.5. The formation of *Trigonocarpus*.

- **a.** transport, loss of sarcotesta, formation of seed cavity, splitting of the three primary ribs at seed apex.
- **b.** split
- **c.** infill and burial
- **d.** coaly layer representing the compression of the sclerotesta.

**T.S.**
- *sclerotesta*
- *sclerotesta*

**T.S.**
- *sclerotesta*
- nucellar cavity

**Seed cast**
- compression
- coalification
- sediment washing into seed cavity

**Sediment seed**
- buried in.
10.6 Conclusions

Examination of specimens of *Trigonocarpus*, and sectioning of some of these seed casts, seems to indicate that the seeds were infilled through the micropyle. The micropyle was enlarged during dessication, germination or, possibly, transport, by splitting along the three primary ribs of the sclerotesta near the seed apex. This produced a larger aperture through which infilling could occur. It is postulated that the micropyle, before this enlargement, was too small a structure in the seed apex to allow infilling, especially when the seeds were infilled by fine- medium-grained sands (0.125-0.50mm). Many of these casts have been infilled by sands of this grain-size.

The sediment infilled the seed cavity and the three primary ribs of the sclerotesta. This produced a cast with three prominent ridges running along it. The sclerotesta was compressed and coalified around the infill. This part of the seed wall was rigid in the original seed and would have withstood decay and transportation. It is this structure that would have maintained a cavity and allowed infilling to occur.

Having considered the formation of *Trigonocarpus*, it seems that the interpretation of Hoskins & Cross (1946) of the different forms of the seed cast is not entirely correct (Fig.10.2). They proposed that the smooth, slightly striated cast (Fig.10.2a) represents the fossilisation of a seed which still contained the outer fleshy sarcotesta. In order to produce a seed cast in this form, the entire internal structure of the seed up to the sarcotesta must have been lost before infilling; that is, the sclerotesta, (composed of much more rigid tissues than the sarcotesta), decayed, leaving the soft parenchymontous layer of the sarcotesta. It cannot be envisaged how this could occur. If it did, the seed would have collapsed before it was infilled, as the sarcotesta would not have had enough rigidity to maintain a seed cavity. The authors' other interpretation of the ridged seed cast, representing a seed which had lost its sarcotesta before fossilisation, or that the sclerotesta showed through a compressed layer of the sarcotesta, seems to be a more adequate explanation for this type of cast (Fig.10.2a, c).

Hoskins & Cross (1946) proposed that some casts are casts of the nucellus. This type of cast may have formed, but only detailed examination of the structure of the infill would give any information on this. Gastaldo &
Matten (1978) seem to be convinced that a "nucellar cast" is actually a cast of the sclerotesta.

The formation of a seed cast is very similar in some aspects to that of the formation of a pith cast; that is, the stem or seed wall has to be rigid enough to withstand decay and collapse to maintain a cavity in which the sediment can accrue. In many of the stem infills, the cavities were formed during the life of the plant. In the seed, the cavity formed as a result of decay of the nucellus as the seed was transported and waterlogged. The infilling of the seed cavity occurred only through the small, but slightly enlarged, micropyle. It is the rigidity of the sclerotesta and the structure of its internal wall that dictates the form of the cast. The sarcotesta is only preserved as a compression border, bounding the seed cast when the seed was compressed perpendicular to the compressive stress.

The formation of *Trigonocarpus* is related to the decay of parts of the original seed. It is also related to the seed being transported into an area where it could be infilled by fine sediment with a grain-size smaller than the enlarged aperture at the micropyle. The seed also had to be orientated on the sediment surface, so that the micropyle was orientated in such a way as to allow infilling of the seed cavity. Therefore, formation of these casts seems to have required much more exact conditions than was necessary to form a pith cast.
CHAPTER ELEVEN: Computer modelling of the compression process
11.1 Introduction

This computer modelling work was carried out in the Department of Strength of Materials at Stockholm Royal Technical College during March 1982 with Dr Nils Gunnar-Ohlson. In this Department they are concerned with the deformations that occur in metals when they are subjected to large stresses. The metals respond to the deformation by fracturing. Minute hair fractures form, which can usually only be seen with a microscope. These deformations are very small and are less than a millimetre in width. Much of the work in the Department involves computer modelling of the stresses and deformations involved in the fracturing process. These are calculated using the NONSAP program.

It was hoped that, during my visit to Stockholm, this computer program could be adapted to produce much larger deformations. The system we wished to model on the computer was the dry compression apparatus work (see Rex & Chaloner 1983), to see if the results that had been determined experimentally could be produced on the computer. This involved adapting the program to calculate vertical deformations of the order of 50-60%. These deformations were produced experimentally in the compression apparatus.

11.2 The NONSAP program

The NONSAP program was used, in this instance, for calculating plane strain. This is the type of strain where shortening and extension occur parallel to the strain axes \( \lambda_3 \) and \( \lambda_1 \), respectively (Fig.11.1a). The strain was assumed to be only in two-dimensions \( \lambda_3 \) and \( \lambda_1 \), the intermediate strain axis \( \lambda_2 \) equalling zero; that is, deformation would only occur along the vertical axis (z) and the horizontal axis (y). The other horizontal axis (x) is unchanged during the deformation (Fig.11.1b). This is the case in the experimental compression apparatus, where the matrix and plant material can deform along the vertical and horizontal axes, but deformation is prevented in the x direction by the back and front of the loading box.

In the computer program, the loading box of the compression apparatus is expressed as a nodal quadrat. The quadrat used in this work was the upper right-hand side of the loading box. This quadrat is subdivided into a series of nodes, 1-82. Each node has a co-ordinate expressed in terms of y (the horizontal axis) and z (the vertical axis). For example,
Fig. 11.1b. The strain axes used in the NONSAP program; $z$ the (vertical axis) = $\lambda_1$ and $y$ (horizontal axis) = $\lambda_3$

Fig. 11.1a. A plane strain $\lambda_1 > \lambda_2 > \lambda_3$

Fig. 11.1c. Components of stress
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Fig 11.2 The Nodal quadrat.

* = matrix; • = plant cylinder; 18 = node point; ® = nodes bounding plant cylinder and upper surface of quadrat; ④ = element number.
Description of Plate 27

The hydraulic press apparatus

The hydraulic press used to make determinations of the elastic and viscous properties of the materials used in the computer modelling. The loading box (1) can be seen on the base plate of the apparatus, with the piston (p) extending into the column of the press.
node point 2 is (0, 2.0) (see Table 1). The nodes are situated along the bounding edge of the quadrat, and along and within the position the foam rubber cylinder occupies within the loading box; that is, the bottom, left-hand side of the quadrat (Fig.11.2). The co-ordinates of these nodes are fed into the computer, and this gives their position at the beginning of the deformation. The entire quadrat is then subjected to a uniform load. The computer calculates the displacement that occurs at each nodal point in terms of y (the horizontal axis) and z (the vertical axis) for that load. The load is then increased at a uniform rate in a series of time or deformation steps. This continues until the deformation loses convergence; that is, the time steps cannot be increased at the dictated rate.

As can be seen in Fig.11.2, the quadrat is sub-divided into a series of elements. Each element has a number and there are 25 elements within the quadrat. Within each element there are four points; these are marked by crosses in the "matrix" and dots in the "plant cylinder". The computer calculates the stresses in terms of sigma-X\(_1\) (the horizontal stress axis), sigma-X\(_3\) (the vertical stress axis), and sigma-X\(_2\) (the horizontal intermediate stress axis) (Fig.11.1c) at these four points during the deformations. Therefore, it can be determined where the greatest stresses are being produced during the compression.

11.3 The method

The first values, that had to be calculated before the program could be run, were the elastic and viscous properties of the materials used in the experimental work. This involved determining the Young's modulus (E):

\[ \sigma = E\varepsilon \]

where \( \sigma \) is the stress and \( \varepsilon \) is the strain. Also, the Poisson's ratio \( (\nu) \) had to be calculated, where \( \nu \) is the ratio of lateral contraction of a rod to longitudinal extension. These were determined for both sawdust and foam rubber. These values were calculated, using a large hydraulic press (Plate 27), which exerted a vertical pressure onto a loading box in which the materials had been placed. The pressure was increased (in kgs) onto the materials until they reached maximum compaction. The results of this work are shown in Fig.11.3. In can be seen, that the foam rubber is more compressible than the sawdust, but neither material undergoes any significant lateral expansion. The calculated Young's modulus
node point 2 is (0, 2.0) (see Table 1). The nodes are situated along the bounding edge of the quadrat, and along and within the position the foam rubber cylinder occupies within the loading box; that is, the bottom, left-hand side of the quadrat (Fig.11.2). The co-ordinates of these nodes are fed into the computer, and this gives their position at the beginning of the deformation. The entire quadrat is then subjected to a uniform load. The computer calculates the displacement that occurs at each nodal point in terms of y (the horizontal axis) and z (the vertical axis) for that load. The load is then increased at a uniform rate in a series of time or deformation steps. This continues until the deformation loses convergence; that is, the time steps cannot be increased at the dictated rate.

As can be seen in Fig.11.2, the quadrat is sub-divided into a series of elements. Each element has a number and there are 25 elements within the quadrat. Within each element there are four points; these are marked by crosses in the "matrix" and dots in the "plant cylinder". The computer calculates the stresses in terms of sigma-X₁ (the horizontal stress axis), sigma-X₂ (the vertical stress axis), and sigma-X₃ (the horizontal intermediate stress axis) (Fig.11.1c) at these four points during the deformations. Therefore, it can be determined where the greatest stresses are being produced during the compression.

11.3 The method

The first values, that had to be calculated before the program could be run, were the elastic and viscous properties of the materials used in the experimental work. This involved determining the Young's modulus (E):

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where \( \sigma \) is the stress and \( \varepsilon \) is the strain. Also, the Poisson's ratio (\( \nu \)) had to be calculated, where \( \nu \) is the ratio of lateral contraction of a rod to longitudinal extension. These were determined for both sawdust and foam rubber. These values were calculated, using a large hydraulic press (Plate 27), which exerted a vertical pressure onto a loading box in which the materials had been placed. The pressure was increased (in kgs) onto the materials until they reached maximum compaction. The results of this work are shown in Fig.11.3. In can be seen, that the foam rubber is more compressible than the sawdust, but neither material undergoes any significant lateral expansion. The calculated Young's modulus
Fig 11.3a. Graph showing the vertical compression of foam rubber (---△--) and sawdust (----■--).

Fig 11.3b. Graph showing the vertical contraction and horizontal extension of foam rubber and sawdust.
and Poisson's ratio for sawdust and foam rubber are:

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<th>Poisson's ratio</th>
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<tr>
<td>Sawdust</td>
<td>0.0047 kp/mm²</td>
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These values could then be inserted into the computer program. Material 1 was foam rubber, and material 2 was the sawdust. Each nodal point was assigned a 1 or a 2, depending on where the "matrix" and the "plant material" were positioned within the quadrat. The program could now be run, and the displacements of each nodal point along the y and z axes were calculated. The displacements were then plotted onto a deformation map, and it could be seen how the "matrix" and "plant" had responded to the deformation.

11.4 The results

The first runs that were made using the NONSAP program used the simplest experimental design; that is, the solid foam rubber cylinder in the surrounding sawdust matrix. Initial runs were not very successful, as the loads applied were too great to maintain equilibrium. Further runs were made using smaller loads but a larger number of time (deformation) steps. This produced the hoped-for results. The deformations for a solid foam rubber cylinder in a sawdust matrix are given in Table 2 and are illustrated on Fig.11.4. It can be seen that the nodal points at the upper limit of the quadrat have not been displaced equally. Nodes 50 and 53 have been displaced to a much greater extent than nodes 35 and 38. This indicates that the load is increasing from node 50 to node 35, and that there is not a uniform load across the quadrat. This fits extremely well with the experimental compression apparatus, where the individual pistons respond differently along the loading box, even though they have the same initial load exerted on them. The pistons, at the centre of the loading box, move considerably further than those at the margins of the box (Plate 28; H). This is a result of the compressibility of the materials present. The foam rubber cylinder, occupying the centre of the box, is much more compressible than the sawdust at the margins of the box. Therefore, the variation in the load in the computer model is very similar to the variation in the load across the pistons of the compression apparatus, and indicates that the results of the deformations may well be comparable.
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**TABLE 2**: The displacement (in mms) of each node along the horizontal (y) and vertical (z) axes with each time step (RUN 1).
Description of Figure 11.4

Deformation map showing the successive deformations of a solid cylinder composed of a compressible material in a less compressible matrix. Each of the arrows indicates the successive positions of the nodal point for the 8 time steps. The upper margin of the quadrat has not been deformed equally. The distortion is greatest above the cylinder, decreasing towards nodal point 35.
Fig 11.4. Deformation map showing the behaviour of a solid cylinder bounded by matrix after loading in the NONSAP program (RUN 1).
Description of Plate 28

The compression of a solid cylinder of foam rubber in a sawdust matrix in the dry compression apparatus.

A  Initial, before the beginning of the deformation. (X 0.2)

B-G  The compression of the cylinder. (X 0.2)

H  The final form of the "compression", showing a C-shaped structure. The central pistons have moved further than the marginal pistons, due to the compressibility of the foam rubber compared to that of the sawdust. (X 0.2)
In this first run, the displacement at node 50 was 14.7%, whereas at node 35 the displacement was only 2.8%. These are displacements of the sawdust matrix. The "plant cylinder" responded to the load by shortening along the z axis (vertical) on the upper surface of the cylinder. This shortening reached a maximum of 21.4% at node 55. The degree of shortening along the z axis reduces around the cylinder until, at node 24, it is only 12%. After this node, the shortening occurs along the y axis (horizontal) but this is much less than the vertical deformation. For example, at node 7, the horizontal dimension has been reduced by 3%. The resulting deformed cylinder has maintained its curvature but has a lower relief.

In the experimental work, compression of this model did not produce any change in the horizontal dimensions (Plate 28). As compression proceeded, the upper surface of the foam rubber cylinder began to deform, and the outline of the upper surface at D (Plate 28) is not unlike the resultant deformation in the computer model. In the experimentally compressed cylinder, the vertical dimension at D has been reduced by 37.5%. This is greater than the deformation produced in the computer model after 8 time steps.

The run was repeated, using the same model of foam rubber and sawdust, but the number of time steps was increased to 10. The results of this run are given in Table 3 and illustrated on Fig.11.5. The upper nodes of the quadrat have not been displaced equally as in the previous run. Again, the load is increasing outwards from node 50 to node 35. The final displacement of node 50 is slightly greater than in RUN 1, having undergone a vertical reduction of 17.7%. At the upper left margin of the quadrat, node 35, the vertical reduction is much less, only 5%. As in RUN 1, the cylinder has retained a curvature during the deformation with some lowering of relief. At node 55, the vertical displacement was 26.8%, and 24.4% at node 60. At node 7, the horizontal displacement was 4%. It was not possible to increase the time steps beyond 10 and therefore, it could not be seen whether the c-shaped structure, produced in the experimentally compressed cylinder (Plate 28; H), would have been produced in the computer model. One would expect, with the same load conditions present as in the compression apparatus, that the same structure would be produced.
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**TABLE 3:** The displacement (in mms) of each node along the horizontal (y) and vertical (z) axes with each time step (RUN 2)
Description of Figure 11.5

This run has the same components as those in Fig.11.4, but the number of time steps used has been increased to 10. This has resulted in considerable reduction in the vertical dimension and a small reduction in the horizontal dimension of the cylinder.
Fig. 11.5. Deformation map showing the behaviour of a solid cylinder bounded by matrix after loading in the NONSAP program (RUN 2).
The other computer model that produced good results during this work was of a hollow cylinder of foam rubber infilled and surrounded by sawdust. In this run only 7 time steps could be performed. The deformations that occurred were quite different than in RUNS 1 and 2, as would be expected. The displacements for this run are given in Table 4. The resulting deformation map is shown in Fig.11.6. The "plant cylinder" at node 55 underwent a large vertical displacement of 53.3%, where at node 7 it remained unchanged. The relatively incompressible infill of the "plant cylinder" resulted in the vertical displacement of the lower surface of the "plant cylinder" of only 4.9% at node 60, and a horizontal displacement of 3.9% at node 7. This resistance to compression of the infill is transmitted to the upper nodes of the quadrat, where the maximum vertical displacement is only 7.8% at node 50, compared to 17.7% displacement at this node in RUN 2.

The experimental compression of this hollow, infilled model is shown in Plate 29. The deformation in the computer model is about equivalent to C on this plate. At this stage of the compression, the foam rubber cylinder on the upper surface of the model has been reduced by 50% along the vertical axis, the horizontal dimensions of the cylinder being unchanged. The computer model has responded to the load in the same manner as the experimental model but, as in the case of the two runs described previously, the computer model cannot be deformed to the same extent as the experimental model.

11.5 Behaviour of the stress axes during the deformation

At each time step the computer calculated the stress in terms of sigma \( X_1, X_2 \) and \( X_3 \) within the element numbers. By plotting the values of these stresses (Tables 5 & 6) against the time steps, the maximum stress can be determined and the areas in the quadrat, where the stresses are greatest, can be seen. This has been done for RUNS I and 3 for certain element numbers in the quadrat.

In RUN I (solid foam rubber cylinder in sawdust matrix), the graphs show that sigma \( X_1 \) and \( X_3 \) are almost equal, where sigma \( X_2 \) is slightly larger for each element number (Fig.11.7). Therefore, the stresses in the vertical (z) and horizontal (y) directions, as the deformation proceeds, are about equal. The stresses are highest in the element numbers 16, 20 and 25; that is, in the matrix. Whereas the lowest are in the foam rubber
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**TABLE 4**: The displacement (in mms) of each node along the horizontal (y) and vertical (z) axes with each time stem (RUN 3)
Description of Figure 11.6

In this run, matrix has been introduced into the centre of the cylinder and occupies an area from nodal point 60 through 80 to nodal point 12. This matrix has the same properties as the matrix surrounding the cylinder. After 7 time steps the plant cylinder has been reduced by about 50% at node 55, but has suffered no horizontal distortion. The matrix infill of the cylinder has suffered little deformation.
Fig 11.6. Deformation map showing the behaviour of a hollow matrix infilled cylinder, bounded by the same matrix, after loading in the NONSAP program (RUN 3).
Description of Plate 29

The compression of a hollow cylinder of foam rubber, infilled and buried, in a sawdust matrix in the dry compression apparatus.

A Initial. (X 0.2)

B-H The compression of the infilled cylinder. (X 0.2)

I The final form of the "compression". The cylinder on the upper and lower surfaces of the infill has been reduced by 87%. "Compression borders" have formed at the margins of the infill from the compression of the cylinder. (X 0.2)
cylinders (element numbers 10, 11, 13 and 15). This indicates the contrast in compressibility of the materials in the quadrant. The foam rubber responds to the load, and deforms to a much greater extent than the relatively incompressible sawdust matrix. This results in the stresses within the sawdust being greater, as it has not the capacity to deform, than in the foam rubber which can continue to deform as the load increases.

The plots of the stresses in RUN 3 (Fig.11.8) show that they are generally higher than in RUN 1. As in the previous cases, sigma X₁ and X₂ are almost equal and slightly lower than sigma X₃. The stresses are lower overall in the plant cylinder (element numbers 11, 13, and 15) than in the surrounding matrix (element numbers 16, 20, 25). In the matrix infill of the hollow cylinder, the stresses are also higher (6, 8 and 10), but not quite as high as those in the surrounding matrix.

In the experimental models the parts of the cylinder, which are under the greatest stress, are depicted by the distortion of the squares that were marked on the uncompressed cylinder. Those squares nearest the outer surface of the cylinder have been compressed more (Plate 29) than those towards the centre of the cylinder. In these experimental models there is no indication of the stresses that form in the matrix, or where the greatest stresses are. This computer modelling has indicated where these are, and shows the contrast in the stresses present in the sawdust and in the foam rubber as the deformation proceeds.

11.6 Conclusions

One of the unavoidable problems of this work was the short time that was spent in Stockholm, and this obviously restricted the amount of runs that could be made. Further runs, using smaller increments of load but increasing the number of time steps, may have produced the larger displacement that were formed in the experimental load.

The results that have been obtained show that the same load conditions, i.e. that were produced by the series of pistons in the compression apparatus of the greatest load being exerted at the margins of the loading box decreasing towards the centre, were formed in the computer model. This similar pattern of the load in the two models indicates that the response
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**TABLE 5:** The changes in stress values at each element number during successive time steps (RUN 1)
Description of Figure 11.7

A series of graphs showing the changes in stress values at each time step for certain key element numbers within the nodal quadrat for Run 1 (solid cylinder). $X_1$ (dots) and $X_3$ (triangles) are generally equal and have slightly lower values than $X_2$ (squares).
Fig. 11.7 The change in stress values during each time step for RUN 1 for certain element numbers.
Position of the element numbers shown in Fig. 11.7.
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TABLE 6: The changes in stress values at each element number during successive time steps (RUN 3)
Description of Figure 11.8

A series of graphs showing the changes in stress values at each time step for certain key element numbers within the nodal quadrat for Run 3 (infilled cylinder). As in the previous figure, $X_1$ (dots) and $X_3$ (triangles) are generally equal and have slightly lower values than $X_2$ (squares).
Fig. 11.8. The change in stress values during each time step for RUN 3 for certain element numbers.
Position of the element numbers shown in Fig. 11.8.
of the materials to the load would be similar in both cases. In fact, the deformations of the "plant" cylinder produced in the computer model compared with the initial stages of compression of the foam rubber cylinder in the experimental apparatus. It would have been very interesting to see how the deformations continued, using the NONSAP program, and also to have conducted some runs, using a lower quadrat, to see if the lower surface of the plant cylinder behaved differently to the upper surface during the deformation. This occurred in the experimental compression apparatus.

This work has demonstrated an alternative method for studying the compression process, and it is encouraging to see the results from the experimental work compare quite closely with the results of the computer modelling. Obviously, further work on improving the NONSAP program to tolerate larger deformations would produce very interesting results, but this would involve a great deal of expensive computer time.
CHAPTER TWELVE: Conclusions
CONCLUSIONS

This research has concentrated on examining the processes that affect a plant organ when it is buried in sediment and on the factors that dictate the final form of a plant compression fossil. The investigation has used a combination of techniques: firstly, experimental modelling of the compression process and, accompanying this, a detailed examination of plant compression fossils.

Initial experimental modelling used the simplest system possible: a dry compression apparatus in which artificial materials representing plant and matrix were subjected to vertical deformation. Models were constructed, which represented uncompressed plant organs, using information from permineralisations, and on compression produced forms which closely resembled known vertical sections of plant compression fossils. Using this apparatus, several lines of investigation were pursued:

(a) The deformation of simple cylinders, representing plant stems.

(b) The behaviour of appendages borne on stems during compression, e.g. spines and leaf cushions.

(c) The transmission of structures onto an opposite surface during compression, e.g. leaf cushions in the Lepidodendrids appearing on an endocortical cast, and the collapse and compression of the stele in Stigmaria producing "groove structures" on the outer surface of the fossil.

A second compression apparatus was designed and built, in which wet sediment and actual plant material could be compressed. This apparatus more closely reproduced the system of natural compaction: sediment, and enabled further investigation of the results obtained from the first apparatus. It also allowed further factors involved in the compression process, such as the effect of the nature of the matrix the plant organ was buried in on the form of the "fossil", and the behaviour of plant tissues during collapse and compression, to be ascertained.

During the course of the wet compression work it became apparent that little was known about the degree to which infilling of cavities within plant organs occurred and the structure of the infills that were formed. A small, recirculating laboratory flume tank was used, in which the flow
conditions, that led to the formation of a sedimentary infill of a stem cavity, were investigated. This apparatus enabled the effect of stem length, diameter and orientation on the structure of the infill to be demonstrated. The results of the experimentally produced infills were closely comparable to the structures observed in fossil pith casts. A technique was developed by which plant stems buried in the flume tank could be removed within a core of adjacent sediment and placed in the wet compression apparatus. This enabled the entire process of infill, burial and compression to be replicated, and indicated the affect of varying degrees of sediment infill on the structure of the compressed plant cylinder.

Closely associated with the experimental work has been a detailed examination of plant compression fossils. This has mainly used vertical sectioning techniques. This gives a section of the fossil that has a similar orientation as the "fossils" produced in the experimental compression apparatus; therefore, allowing close comparison of the actual fossil and the structure produced under experimental conditions. Vertical sectioning and reassembling the part and counterpart of a fossil, and then sectioning, has revealed the entire structure of the compression and the factors that dictated the pathway the fracture plane took to expose the fossil. A number of compression fossils were examined in this manner, e.g. *Cyperites*, *Alethopteris*, *Lepidostrobus* and *Trigonocarpus*.

An understanding of the factors that effect the form of a plant compression, using the techniques described above, gives a new insight into the fossilisation process. This is of potential value in reconstructing plants from fossils that are only known in the compression state of preservation. An example of a group of fossils to which this can be applied, is the Permian ovulate glossopterid fructifications, which are almost only known as impressions, though some permineralisations have now been described. By conducting experimental modelling of some of the proposed original forms for these fructifications, and examining a number of specimens in detail, the structure and preservation of these fossils is discussed. A basic model of their uncompressed structure is proposed, based on the evidence observed.

Since each chapter in this thesis has its own conclusion section, only general conclusions will be given here, in order to avoid repetition.
The general conclusions of this research are:

(1) Experimental modelling enables us to interpret the events leading to the formation of a plant compression fossil and allows the behaviour of the uncompressed plant organ during the compression process to be reconstructed.

(2) The dimensions of a plant organ change differentially during the compression process. Not only does the plant organ suffer vertical flattening as the overburden increases, and the sediment compacts, but there is also a change in the horizontal dimensions of the plant organ.

(3) The changes in the dimensions of the plant organ are dependent on the compressibility of the sediment the plant organ is buried in, as well as in the plant tissue itself. Experimental results in the wet compression apparatus indicate that, in an incompressible matrix, e.g. sandstone, the plant organ undergoes a reduction in both horizontal and vertical dimensions. In contrast, a plant organ incorporated in a compressible matrix undergoes a reduction in vertical dimension but an increase in horizontal dimensions. This difference is attributed to the different mechanical behaviour of the sediments during compaction.

(4) The form of the compression fossil is affected to a considerable extent by the degree of infilling of any cavities within the plant organ that occurred during burial. For example, a hollow stem devoid of a sedimentary infill will, on compression, suffer closure of the cavity, resulting in a drastic loss of stem topography. If, in contrast, the hollow stem was infilled to the roof, the stem on compression would retain a vertical dimension. The degree to which this occurs is dependent on the compressibility of the matrix that composes the sediment infill.

The effect of an infill on the structure of the compression was illustrated by Lepidostrobus. The fine-grained infill of some specimens of members of this cone genus, during burial, enabled the detailed structure of the cone to be preserved during the compression process. Absence of an infill or collapse of the cone during burial resulted in the cone being compressed to a single coaly layer, devoid of evident internal detail.

The structure of the sedimentary infill of a fossil, revealed by sectioning, indicates the flow conditions under which the plant organ was infilled
and buried. This is possible, due to stem infills being produced experimentally in a laboratory flume tank, and the flow conditions that produce the structure of the infills having been ascertained. This, therefore, enables interpretations to be made of the sedimentary environment in which the plant became buried.

(5) The experimental compression work has indicated that a "way-up-ness" is produced in the fossil during compression. This occurs when, for example, a hollow stem is only partially infilled and there is collapse and compression of the upper unsupported stem roof. This results in the formation of a C-shaped compression, the lower surface retaining a curvature reflecting the shape of the original stem, whereas the upper surface suffers loss of topography and distortion of structure. This "way-up-ness" to the compression can be applied to the fossils and can sometimes be supported by evidence from sedimentary structures.

Structures, such as leaves or sporophyll laminae, when supported by matrix, do not produce different forms of compression whether orientated the "right-way up" or inverted in the matrix. The matrix "protects" the structure, preventing it flattening or losing its topography.

(6) Compression borders (Walton 1936) were produced experimentally in both the dry and the wet compression apparatus. The results, using the wet compression apparatus, indicated that compression borders were more readily formed when the stems were infilled and buried in a fine-grained compressible matrix. This may be related to the difference in mechanical behaviour of sediments of different grain sizes or a function of the experimental conditions. Compression border formation was accompanied by a change in the horizontal dimensions of the plant organ. Compression borders can be recognised in fossil material.

(7) The nature of the tissues within the plant stem may affect the structure of the compression. Rigid, incompressible tissues, such as fibres (sclerenchyma) and secondary xylem, commonly form the thickest layer of coal in a compression, and may give an accentuated topography to the fossil. For example, the secondary venation in some pteridosperm leaves may show enhanced topography in the compression which is absent in the permineralised specimens, where the upper and lower epiderms are flat or only slightly ridged. The mesophyll tissue separating the veins is much more compressible than the veins, and is reduced to a fine coaly
line. The incompressible veins on compression form coaly "knots", which are seen as distinct ridges on the surface of the leaf compression when it is exposed by a fracture plane.

(8) In large stems, for example, Calamites, the rigidity of the woody cylinder caused it to respond to the compressive stress by fracturing radially ("arch-failure"), producing a sedimentary feature on the pith cast that is unrelated to the structure of the original stem.

(9) Vertical sectioning of the plant compression fossils has proved to be the most useful technique for examining them in the present context. Sectioning of the intact fossil in the matrix enables the vertical dimension and the entire structure of the compression to be seen. One of the fossils which illustrates this clearly is Cyperites. Sectioning of this apparently flat lycopod leaf revealed a complex three-dimensional fossil of previously unknown character. By combining this information with experimental modelling, the uncompressed leaf structure was reconstructed.

(10) The pathway the fracture plane takes to expose the fossil, governs the extent to which the structure of the compression is revealed. This is a function of the relationship between the bedding plane and the orientation of incipient fracture surfaces (planes of weakness) represented by coaly layers. False structures, such as "false leaf scars", may be produced on the surface of the fossil when parts of the fossil are removed in the counterpart. Reassembling the part and counterpart of the compression, and then vertically sectioning, shows the pathway the fracture plane took over/through the fossil, and indicates the extent to which parts of the compression remain hidden in the matrix, and how far they have governed the pathway of the fracture plane.

The main factors that dictate the form of a plant compression fossil, as indicated by the results of this work, are summarised below:

(a) The nature of the sediment in which the plant organ was incorporated.

(b) The extent to which infilling of cavities within the plant organ occurred during burial.

(c) The rigidity of plant tissues within the plant organ and the extent to which decay, collapse or fracture of the plant organ occurred
before or during the onset of the deformation.

(d) The pathway the fracture plane takes to reveal the plant compression fossil.
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APPENDIX B
A LABORATORY FLUME INVESTIGATION OF THE PROCESSES INVOLVED IN THE FORMATION OF FOSSIL STEM INFILLS

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ABSTRACT

The mechanism of formation of fossil plant "pith casts" has been investigated experimentally using a small laboratory flume tank. The extent to which infilling occurs is dependent on stem length and diameter and on the current velocity. Stem infills produced by sediment carried in suspension show a distinct structure. This consists of two wedges of sediment deposited at either end of the stem cavity. These wedges are deposited from eddy currents which form when the flow around the stem separates, as flow through the stem becomes restricted. Stems infilled by traction currents do not show such a uniform structure. The experimentally produced stem infills are comparable with fossil pith casts. This investigation of the mechanics of infilling of hollow plant organs, and the structure of the infill produced, offers a basis for interpreting the sedimentary environment in which the fossil infills have formed, and leads to a fuller understanding of the mode of formation of such fossils.
A. Introduction

Plant remains, that have been incorporated in clastic sediments and deformed as the sediment compacts, are known as plant compression fossils. The fossil formed as a result of collapse, compression, and coalification of the original plant organ has a drastically reduced vertical dimension. The plant tissues are commonly diagenetically altered to coal in typical Carboniferous fossils, but in younger fossils the plant tissues may not have reached that stage of coalification and may be in the form of lignite or brown coal. Plant compression fossils are probably the most common form of preservation of plant organs in the fossil record.

Preliminary investigations on the effect of the compression process on plant organs have been made using experimental modelling techniques. Initially, artificial materials were used to represent plant and matrix in a dry compression apparatus (Rex & Chaloner 1983). Subsequently, a system closer to the natural process using wet sands and clays and plant in a more elaborate compression apparatus was used. During the course of modelling in the second apparatus, it became obvious that little was known about how sediment accrued around plant organs and filled cavities within them.

The object of the present work has been to investigate how sedimentary infills form in hollows within plant stems. This has involved the use of a small laboratory flume tank to determine the flow conditions under which infilling occurs and the structure of the infills formed. The results of this experimental work have been compared with fossil "pith casts" and similar structures. An understanding of the mechanisms and extent to which sediment accumulates within hollow plant stems has led to a more accurate modelling of the compression process. It is shown that the structure of the infills is dependent on the flow conditions the infill formed in. Information of this type will lead to a more accurate interpretation of fossil casts, especially when little is known about the environment they formed in.

Three types of plant fossil can be recognised as having an origin basically similar to the conventional "compression fossil":

(a) Compression fossils sensu stricto: no infilling of the plant structure has occurred and the plant organ has deformed as the sediment compacts.
(b) Pith casts (and other casts): these are fossils in the form of sedimentary infills of parts of the plant structure, and from which the organic matter has been removed during weathering, e.g. infill of the pith cavity in Calamites and of the seed cavity in Trigonocarpus.

(c) Combination of (a) and (b): composed of an infill containing or surrounded by a "compression fossil", e.g. in Calamites, the pith cast may have a compression of the woody cylinder at the margins of the casts, or the cortical infill (endocortical cast) of Stigmaria, which may contain within it a compression of the stele.

This investigation concentrates on the formation of (b) and (c). The topography of these infills is governed by the compressibility of the sediment forming the infill, e.g. a sandstone infill will have suffered less vertical distortion than a claystone infill, due to the relative incompressibility of sand grains compared to clay minerals.

B. Previous research

Laboratory flumes have been used primarily to determine the mechanisms by which sediments are moved along a stream bed. This was first demonstrated by the classic work of Gilbert (1914), and subsequently by Simons et al (1965) and many other workers. As a result of this work, much is now known about bedforms and their relation to flow regimes. In this investigation, the flume tank has been used for a slightly different purpose; namely, to study the manner in which sediment accrues around and infills plant material under varying current conditions.

Several investigations have been undertaken to examine the processes and effect of transport of plant material along alluvial systems, and the subsequent formation of plant beds. Ferguson (1971), examining Miocene leaves from Kreuzau, West Germany, conducted a series of experiments to determine the attrition suffered by thick and thin leaves when transported along fast to moderate-flowing rivers. He used a number of revolving cylinders filled with sand and water to represent the river, and circulated them, with leaves, for a time interval equivalent to 80kms transport. After this treatment none of the leaves showed any perceptible damage from this attrition. Ferguson concluded that both mesomorphic (thin) and xeromorphic (thick) leaves had an equal chance of entering the fossil record. This rather surprising outcome may have been
because his apparatus was not closely reproducing the effects of transport on leaves along a river system, or perhaps the combined effect of biodegradation and transport on the leaves had not been taken into account.

Spicer (1981) examined the formation of plant beds by sampling sediments and buried vegetation (using coring methods) in a modern fluvio-lacustrine environment. He showed that two plant beds had formed in association with delta formation: one, as a result of burial of leaf matter on the lake bottom by the advancing delta front; and the other, formed at the top of the foreset slope, as a result of settling of the stream bed load material. Referring to depositional sorting of plant remains, Spicer (1980) demonstrated that low-energy systems, such as fluvio-lacustrine environments, in which the resulting plant beds consisted only of leaves, gave a biased sample of the surrounding vegetation. In contrast, flood deposits yielded a wide variety of plant organs, e.g. twigs, fruits, seeds, giving a fuller representation of the diversity of taxa present in the environment.

The only investigation, which has involved the use of a flume tank in the study of the preservation of plant remains, was by Harris (1976). He was considering the environment in which the Wealden lycopod, Lycopodites hannahensis, had grown. Harris concluded that the plant had actually rooted in and lived on the river sands in which it was found preserved, becoming progressively buried during its period of growth. He showed that the plant could have withstood the current activity in a river channel, by using a laboratory flume tank to determine the resistance of erect (living) rush stems to current activity.

Some palaeobotanists have considered the mechanisms by which plants became infilled with sediment, but this has mainly been concerned with upright trunks. Arnold (1956) postulated how a large Calamites cast might have been formed. The cast was orientated at a high angle to the bedding. He considered that it might have been buried in the upright position it had grown in, but it was more likely that it had been upended during a flood. Arnold (1956) proposed that the trunk was infilled as the plant tissues gradually decayed. In contrast, MacGregor & Walton (1948) considered how the "tree stumps" of the Fossil Grove, Victoria Park, Glasgow, had formed. The base of the Lepidodendron trees are preserved as casts formed, as MacGregor & Walton believed, by sand and
mud washing into the hollow stumps after the upper part of the tree had been removed. The sediment had then "worked its way down into the roots". The "root" systems of these trees are almost all that has been preserved, apart from less than a metre of the (upright) base of the trunk.

Dawson (1891) described how tree stumps of the early Pennsylvanian from Joggins, Nova Scotia, became infilled. This is one of the earliest accounts of a tree infill. These fossil tree stumps were of great interest to vertebrate palaeontologists, since they contained the bones of the earliest known reptiles. Dawson considered that the forest of Sigillariae was buried by inundations of muddy waters. This resulted in the tree trunks being buried by several feet of sediment. The projecting tops of these trees decayed, according to Dawson, and the buried stumps became hollow with their outer bark remaining intact. The surface of the sediment during this time had become dry land covered with vegetation, and Dawson proposed that small quadrupeds fell into the open holes (of the hollow tree stumps) and could not extricate themselves. Eventually, the hollow stumps were infilled by successive inundations of sediment.

B. The apparatus
A small, recirculating flume tank was used in this study. The flume consisted of a narrow, straight channel measuring 1.5 metres long, 30cms deep, and 30cms wide. The channel sides were constructed of thick perspex so that sedimentation could be continuously observed (Fig.1). The perspex channel sides were attached and sealed to a metal base forming the floor of the channel. Water was circulated through an electric pump (this had a maximum discharge rate of 8 l/sec) into the feeder tank from which it flowed into the channel. At the end of the tank there was a sluice-gate which controlled the height of the water in the channel. The water flowed over the sluice-gate and into the receiver tank, through a sediment trap, and was then recirculated through the pump. Wet sediment was fed into the system from a hopper situated at the entrance of the channel, and extending across its full width. Measurements of the current velocity were made using a Stream-Flo Probe.

C. Materials and methods
A number of varying grain sizes were used during this investigation. The principal sediment used was a sand with a grain size not exceeding 0.1mm; that is, a "fine sand" on Wentworth's grain size scale. Coarser sands were also used with a grain size of about 1.0mm.
The plant material used during this work was mainly the stems of *Heracleum sphondylium* (Hogweed) and species of *Sonchus* (Sowthistle). The stems of these plants are hollow and do not collapse when waterlogged, i.e. they retain their rigidity and so allow the passage of currents carrying suspended sediment through the stem. The plant material was waterlogged (i.e. intercellular spaces were flooded) by leaving it submerged in running water for 2-3 weeks before it was used in the flume tank. Following this treatment, the plant material settled onto the sediment surface when placed in the flow in the flume tank.

Each run in the flume tank began by depositing a layer of sediment over the floor of the channel. The plant material was then added to the flow and allowed to settle onto the sediment surface. Sediment was then added to the flow, and the burial of the plant material observed and photographed. When the run was finished the flume was drained and the sediment left to dry for 24-36 hours. After this time the sand had dried out sufficiently for the plant material to be cored out without the sand fluidising when it was removed. In order to prevent disruption of the buried plant material and adjacent sediment, a metal plate was slid along the floor of the channel and positioned under the plant material. A hollow metal cylinder was then forced through the sediment and onto the metal plate. The core, containing the buried plant material, was then frozen in a deep-freeze. The core was then removed from the cylinder and sectioned with a hack-saw while still frozen. This method of freezing the cores was adopted because it allowed the plant material and sediment to be sectioned with the minimum of disruption.

D. Results

In a river channel, sediment grains can be transported in three ways: rolling, bouncing, or in suspension. Gravel will roll along the bottom, sand will saltate, and silt and clay are carried in suspension (Selley 1982). The sands form a traction carpet or channel bed load, and the silt and clay form the suspended load. In this investigation, two types of deposits were modelled: traction deposits and suspension deposits. Plant material may be incorporated in either of these two deposits. A number of experiments were conducted to investigate the infilling of stems, set at various angles to the flow, by sediment deposited from suspension, and also infilling by sediment moved in the traction carpet.
Burial by a suspended load

(a) Stems parallel to the flow

In this series of experiments, plant material was dropped into the lower part of the flume tank where fine sands and silts were dropping out of suspension. The sedimentary structures, associated with the deposition of very fine-grained sediments, are horizontal laminations (Selley 1982), reflecting slight vertical changes in grain size. It was predicted that hollow plant stems would infill by the formation of a succession of minute laminations within the stem cavity. To test this hypothesis, a number of stems of varied length, but with a constant diameter (1.5cms), were placed in the lower part of the flume tank. Very low current speeds (4-5cms/sec) were used in these runs. As burial of the stem began, sediment accrued on the exposed upper surface of stem and built up to a ridge. When the slope of the accrued sediment reached a critical angle, the sediment avalanched down the sides and open ends of the stem. This process continued until the stem was completely buried. When the stems were sectioned in a vertical, longitudinal plane, the stem infills did not show the anticipated laminated structure. The structure of the infill formed within the hollow was found to be dependent on the length of the stem.

In short stems (5-6cms long), the hollow stem had become almost totally infilled (Figs.2A, 5A), but the infill did not reach the roof in the centre of the hollow stem. In longer stems (10-12cms long), infilling had occurred to a lesser extent (Fig.2B). The infill had a distinct structure, consisting of two wedges of sediment extending into the stem from either end (Fig.5B). The wedges had not met and were separated by a region in which no sediment had accumulated. It appeared, from the structure of the infill, that sediment was being transported into both ends of the stem. Hollow glass tubes, exactly the same length and diameter as the plant stems, were placed in the flume tank in the same position and subjected to the same flow conditions as the plant stems. Dye was used to monitor the behaviour of the flow in and around the glass tubes, and this enabled the current activity involved in the formation of the infill to be observed.

At the beginning of the formation of the infill, the current flowed straight through the hollow stem, depositing sediment in a horizontal layer along the floor of the pith cavity (Fig.3A). This layer was built
up to a greater thickness in the short stems than in the longer stems. This is because a short stem does not reduce the velocity of the current passing through the stem to the same extent as a longer stem. Therefore, transport of sediment along the entire length of the stem can continue for a longer period, forming a thicker horizontal layer in short stems than in longer stems of the same diameter. Eventually, the horizontal layer of sediment reaches a thickness that so restricts the flow of water that the current passing through the stem effectively ceases. At this stage, "eddy" currents form at either end of the stem, transporting sediment only into the two open ends (Fig.3B). These currents are relatively weak, and sediment is "dumped" at the entrances to the stem. The sediment forms two wedges which build up, extending into the stem by the avalanching of sediment down the slope of the wedge. As infilling continues, the current at the downstream end of the stem becomes dominant, and there is flow up the stem and out of the upstream entrance. This results in the sedimentary wedge, at the downstream end, building up the stem faster and becoming much larger than the wedge at the upstream end (Fig.3C). The "eddy" current, at the upstream end of the stem, ceases to function and eventually the stem is buried by the accruing sediment. The downstream sedimentary wedge reaches the roof of the hollow stem before it meets the upstream wedge, and this prevents total infilling of the pith cavity (Fig.3.D). It is the transport of sediment into the stem from current activity at both stem entrances that produces the structure of the infill observed in these stems.

In the shorter stems, the eddy currents form at the stem entrances when the horizontal layer of sediment reaches a thickness which restricts the current flow (about 1.0cms). In this case, though, the upstream and downstream eddy currents have the same strength, and this results in two sediment wedges of equal size being produced within the stem cavity.

In very long stems (20-30cms), very little infilling occurs (Figs.2.C, 5E). Two small wedges of sediment form at either end of the stem, reaching in about 2cms into the cavity. This low degree of infilling is related to the length of the stem restricting the current flow through the stem. The only current activity occurs at the entrances to the stem where eddy currents form, depositing wedges of sediment. There is no current movement within the remainder of the stem. The resulting relationship between stem length and the degree of infilling is shown in Fig.4.
The runs described above were all repeated, but at higher current velocities (10-20cms/sec) to determine how flow rate affected the formation of the infills. At these velocities, the stems were infilled to a less extent in the short (5cms) and medium (10cms) length stems, with a diameter of 1.5cms. At higher flow rates, more sediment is carried in suspension and, as a result, burial of the stems is rapid. This rapid burial prevents the migration of the sedimentary wedges, at the stem entrances, as far down the stem cavity as the "wedges" in the stems buried at lower current velocities (Fig.4). The accruing sediment quickly restricts the passage of currents at the stem entrance.

(b) The effect of the diameter of the stem cavity on the infill

Stems, with a diameter of less than 1.0cms, did not infill to a great extent regardless of the stem length or current velocity. The small diameter restricted the current flow through the stem. Eddy current formed at either end of the stem immediately it settled onto the sediment surface, i.e. there was no initial current flow through the stem. This resulted in the formation of sediment wedges which extended approximately 1-2cms into the stem cavity. The remainder of the stem cavity was unfilled (Fig.4).

Stems, with large diameters (2.5cms), were infilled to a considerable extent. Due to the large diameter of the stem, the current could flow through the stem, depositing sediment in horizontal laminations until a considerable thickness had formed (1.0-1.5cms). Eventually, this build up of sediment restricted the passage of the current and eddy currents formed at either end of the stem, depositing sediment in wedges at both ends. As in the previous experiments described, total infilling of the stem cavity did not occur (of lengths 5 and 10cms). Higher current velocities did not substantially effect the degree of infilling of these large diameter stems. Slightly more infilling occurred at higher flow rates (10-12cms/sec) than at lower flow rates (4-5cms/sec). The infills had more structure than those produced in the small diameter stems. Micro-ripples had formed between the wedges of sediment, probably resulting from stronger current activity in the hollow stem during the formation of the infill (Fig.5G).

(c) Stems in which the entrance or exit was sealed

A number of experiments were conducted to determine the effect of sealing up of either end of the stem on the formation of the infill. This was
to simulate some structural feature, (e.g. a nodal diaphragm), a pebble, or collapse of one end of the stem preventing current movement in that direction. The effect of sealing up of the downstream end or the upstream end of the stem was the same in both cases. A small wedge of sediment formed at the open end but it only extended about 2cms into the hollow stem (Fig.5F). It appears, from these results, that both ends of the stem need to be open to allow the transport of sediment into the hollow and hence, the formation of a substantial sedimentary infill.

(d) Stems lying at right-angles to the flow

A number of runs were made in which the stems were orientated at right-angles to the flow. This had to be done at very low current velocities (4.4cms/sec) because, at higher flow rates, the stems moved to become aligned with the flow. In nature, stems will only be orientated at right-angles to the flow in very quiet current conditions, e.g. a lake bottom. Only short stems could be used in these runs, so that they were not near the walls of the channel; this would have affected the flow conditions. The nature of the infill produced in these runs was very similar to those in which the stems were orientated parallel to the flow. A horizontal layer of sediment had built up on the floor of the hollow stem, and then two "wedges" of sediment had built out into the hollow from both ends of the stem.

(e) Upright stems

The infilling of upright stems would probably only occur when the stem was rooted in the sediment, as for example in the Lepidodendron bases in the Fossil Grove, Victoria Park, Glasgow (MacGregor & Walton 1948). It is difficult to envisage flow conditions where isolated stems would become orientated upright on the sediment surface. It does, though, seem to occur in nature. Calamites (Fig.6), collected in situ from Swillington Quarry, Yorkshire, are orientated more or less perpendicular or at steep angles to the bedding planes. Jefferson (1982) described large fern fronds from Antarctica which crossed bedding planes, and attributed this phenomenon to a low current regime.

Runs in the flume tank were conducted in which upright stems were pushed into the sediment layer. It was found that, even at moderate flow rates, rapid scouring occurred around the base of the stem and it was quickly excavated. Only at very low current speeds (4.4cms/sec) was the scouring
reduced to an extent that allowed sedimentation to occur on the downstream side of the stem, and this prevented its excavation. Infilling of the hollow stem occurred by the building up of minute horizontal laminations of sediment within the cavity (Fig.5D).

From these results it would seem that burial of upright plant material, within the conditions of this author's experiments, only occurs in very low current conditions. Slight increases in the current velocity results in the rapid excavation of the plant stem by scouring activity at the upstream side of the stem. Obviously, infill of much larger hollow structures, i.e. Stigmaria rooted in a submerged soil surface, would not have been disturbed by excavation at high flow rates.

**Burial by a traction carpet**

In this part of the investigation, stems were dropped onto the sediment surface when current ripple formation had been reached (38cms/sec). The current conditions producing this type of bedform are very different from those involved in the formation of the suspension deposits. The current velocities are much greater and the flow is unidirectional. In the formation of the suspension deposits, the current velocities were much lower and the current very erratic.

The stems used in these runs had small diameters (approximately 1.0cms) so that burial occurred fairly rapidly. Large diameter stems took considerable time before burial of the entire stem occurred. This is due to the small amplitude (1-2cms) of the ripples formed on the channel floor. Hollow glass tubes were used to determine the mechanisms by which stems would infill in the traction carpet. Plant stems were also used, and these were cored out and sectioned after burial.

Burial of the stems occurred as the current ripples migrated downstream, burying the stems in a cross-laminated bed. Total infilling of stems in these current conditions did not occur. The structure and formation of the infills produced in this flow regime were not as consistent as the infills formed in the suspension deposits. The nature of the infill, and the degree of infilling of these hollow stems, depended on the position the stems took up on the stream bed and on the length of the stem. If, for example, the stem becomes wedged up against the stoss side of a ripple, this restricts movement of sediment into the stem. The downstream end of the stem becomes blocked due to contact with the
ripple, and this prevents flow of the current through the stem. As a result of this, an eddy current forms at the upstream end of the stem, depositing sediment at the stem entrance. Eventually, a small wedge (2cms long) builds up, extending down the hollow stem. The next approaching ripple covers the stem, completely burying it. Under these circumstances very little infilling of the stem occurs.

In other cases the stem may be orientated on the channel bed so that the current can flow through it. Sediment is transported into the stem as a ripple approaches. This forms a thin wedge extending into the hollow. The distance and thickness of the "wedge" is dependent on the length of the stem. In short stems (4-6cms), the "wedge" builds up right down the stem and may be washed out of the stem completely as the ripple migrates over the stem. In longer stems (9-11cms), the "wedge" usually extends half-way down the stem, whereas in longer stems (17-22cms), the wedge reaches only a few centimetres into the stem entrance. This build up of the wedge is a function of the effect of the stem length on the current, as in suspension flow, with the shorter stem producing less friction slowing of the current. A relatively long stem, though, reduces the velocity considerably, so that it lacks the energy to transport sediment any distance along the hollow stem.

In medium length stems (approximately 10cms long), infilling begins with the formation of the "wedge", which reaches about 5-6cms down the stem (Fig.3E). As the next ripple reaches the stem it covers it completely. The stem is exposed again as the stoss side of the ripple migrates over it. The "wedge" of sediment, which thins down the stem, is then moved down the stem by the current flow, and a wedge is formed at the downstream end of the stem; this thins up the stem (Fig.3F). As the next ripple approaches the stem, sediment is supplied from the lee slope of the ripple, and this builds up as a second wedge formed at the upstream end of the stem. This builds out down the stem, while some sediment is also added to the wedge at the downstream end of the stem (Fig.3G, H).

Eventually, the wedges reach the roof at the openings at either end of the hollow stem without having met, and no further sediment enters the cavity (Figs. 3I, 5C).

Infilling, burial and excavation of the stems may occur several times before the stem is incorporated into the bed. This results in a variety of structures being produced in the infills and a variation in the degree
of infilling of the stems. At higher current velocities, i.e. greater than 38cms/sec, the stems do not become incorporated into the traction deposit. The stems are transported along the channel floor by the fast current and are washed out of the flume tank.

E. Discussion of experimental results

The presence of a solid object on the boundary layer results in a change in the flow conditions around that object. This occurs when the current flows into a region of high pressure or encounters changes in shape boundaries, e.g. steps up and down, bluff bodies, and sharp bends. As fluid piles up around the structure, it forces the main flow away from the boundary while forming a backflow itself. This process is termed flow separation. Experimental studies of flow separation have shown that the flow separates in front of the bluff object or step (the separation point), and reattaches beyond it (the attachment point). These two points divide up a region of rotating flow known as a separation bubble. Separated flow has been associated with many sedimentary structures, e.g. ripples, dunes, flute marks and obstacle marks.

Studies on step-ups across the boundary layer (Kiya & Arie 1972; Bradshaw & Wong 1972) have shown that a large roller forms in the flow in front of the step. At downstream facing steps, separation bubbles also form and may be accompanied by secondary bubbles. The length of the separation bubble depends on the angle and height of the step (Allen 1968, 1969). These separation bubbles form when impermeable bluff bodies or steps are present on the boundary layer, e.g. they would be produced where pebbles or solid stems were present.

Permeable bluff bodies, such as clumps of weed or hollow stems, will divert some of the flow around the body, and some of it will be passed through it. Castro (1971) experimented with perforated plates placed in a uniform stream. He demonstrated that when the apertures in the plate exceeded a third of the total area of the plate, then the separation bubble disappeared as the current could flow freely through the plate. Reductions in the numbers of apertures in the plates caused the formation of small separation bubbles when the plates were "semi-permeable", and large bubbles formed when the plates were impermeable.

Castro's (1971) experimental work can be related to the infill structures formed in the hollow stems in the present investigation. At the
Formation of the stem infill: The current could flow freely through it, resulting in the deposition of fine, horizontal laminations of sand along the length of the stem. As these layers built up, they restricted the flow of the current, and small separation bubbles or eddy currents formed at either end of the stem as a result of the now "semi-permeable" nature of the stem. The separation of the flow, in front and behind the stem, increased as the stem infilled and eventually became "impermeable". The backflow, within the separation bubbles at both ends of the stem, transported sand grains into the stem entrances and formed the sedimentary wedges seen in the sectioned stems.

Flow separation also occurs around vertical bluff bodies, e.g. vertical stems, pier and bridge supports. In these cases, the flow separation around the body produces a down-flow in front of the object. This results in a scouring of the sediment surface in this area. This occurred in the experiments in the flume tank described earlier, where vertical stems were excavated from the bed at current velocities greater than 4.4 cms/sec. Allen (1982) describes the sedimentary structures produced when suspended sediment is deposited from flow around these vertical bodies. A crescentic furrow forms in front of the body, as a result of the scouring activity of the current, and a tail of sediment is produced on the leeward side, due to the lack of current activity in this area. These types of structures were produced in this experimental work when vertical stems were placed in the flow.

F. Comparison with fossil infills

One of the main objects of this work was to compare the structure of the experimentally produced infills with fossil infills. The most well-known Coal Measure stem infill is Calamites, and it is mainly specimens of this genus that have been used in this comparison. Other infills that have been used are infills of cordaites, Artisia, and cortical infills ("endocortical casts") of Lepidodendron and Stigmaria. A range of infills with different grain sizes have been examined from coarse sandstones (0.5 mm) to fine sands (0.1 mm) to silt/claystones (0.05 mm). The infills have been sectioned in longitudinal and transverse-section to compare with the stem infills formed in the flume tank.

(a) Coarse-grained infills

Stem infills, with a grain size of 0.5 mm (coarse sand) to 0.2 mm (medium sand) in diameter, are considered in this section. These sandstones
are usually composed of irregular quartz and feldspar grains, cemented together with very little matrix. Some of the infills are very homogeneous, showing virtually no structure (Fig. 7A). Others have large clay clasts included in the sandstone (Fig. 7C). The coarse-grained nature of the sandstones indicates that these sediments would have been moved by traction currents, and not in suspension. The absence of structures in these infills, such as graded bedding or cross-laminations, may indicate that these infills were formed by rapid infilling and burial of the stem; that is, they were formed in consistent flow conditions which did not fluctuate during the burial of these stems. Alternatively, they may have formed under current conditions which were stable for long periods. Scott (1979), in his discussion on the ecology of the British Coal Measure floras, shows that *Calamites* is usually associated with a marginal lake habitat (poorly laminated shaley silts), and also formed reed swamps on the delta surface. *Calamites* is also found in the medium-fine sands of point bars of the meandering rivers of the coal swamp.

The medium-grained sandstone infills (approximately 0.2mm grain-size), show considerably more structure. Graded bedding is very common. The bottom of the infill has usually a very fine-grained layer, indicating initially quiet current conditions, and this is followed by a much coarser sand, indicating higher current velocities. There may be several layers of graded bedding within the infill (Fig. 7B). Very often, the coarser layers in these infills show cross-laminations which have formed at one or both ends of the stem (Fig. 7B). Some of these cross-laminations may be quite substantial and have built out down the stem.

The coarse-grained infills may show considerable structure, reflecting minute changes in the current conditions, or they may be very homogeneous, showing no structure at all. These structureless infills are interpreted as having been formed very quickly as a result of rapid burial of the stem during a single deposition episode. Those with structures present in the infill, especially if showing graded bedding, are interpreted as having been infilled and buried slowly in conditions where the current velocity fluctuated.

The structures produced in the stems, infilled by the traction currents in the flume and the fossils, are comparable. The cross-laminations observed in the fossil infills formed in the experimentally infilled stems
within the sediment wedges that built up and down the stem cavity. Graded bedding can also be seen in the flume infills where the current fluctuated as the ripples migrated over the stems.

One of the problems involved in comparing the fossil infills with those formed in the flume tank, is that it is not easy to determine from the fossil whether the pith cast represents the infill of the entire cavity of the original stem. If it is assumed that the diameter of the original pith cavity of the stem corresponds to the horizontal diameter of the pith cast, then it is relatively easy to estimate the original height of the infill within the stem cavity. For example, if the infill had a diameter of 4.0cms, and the height of the fossil infill was 2.0cms, this would seem to indicate that the sandstone infill had compressed by 50%. Measurements of sandstone fossils infills indicate that the height of the infill is usually half the value of the diameter of the infill. However, experimental work on the compaction of sands (Chilingarian & Wolf 1975) has indicated that sands do not undergo such large degrees of compaction but generally only compact by 10-12%. Applying this figure to the sandstone pith cast indicates that the height of the infill was originally only 2.2cms and, therefore, the infill only half-filled the stem cavity. Total infilling of the pith cast does not appear to have occurred in the fossil infills (formed of sandstone) and, in the experimentally formed infills, total infilling of the stems was never produced. This reasoning assumes that the stem had not decayed to the extent of causing appreciable collapse before infilling, so that during burial the stem maintained a circular cross-section. Calamites had a thick layer of secondary xylem surrounding the pith cavity, which would have been rigid and resistant to decay. The possibility must be acknowledged that the stems, in a few cases, may have collapsed, developing an ellipsoidal profile before infilling had occurred.

(b) Fine-grained infills

Infills, described in this section, are composed of finesand and silt particle size. These infills have considerably more structure than the coarse-grained infills. Calamites, composed of fine sand to silt size grains, when sectioned in longitudinal section, show small-scale cross-laminations dipping steeply towards the centre of the infill from either end (Fig.7E). Some of the stem infills show a change in current conditions, having a coarse sand formed at the base of the infill, with the remainder being composed of a fine clay. The clay contains minute sandstone laminations
(1-2mm thick) which dip towards the centre of the stem from either end (Fig.7D).

Many of the very fine-grained infills contain distinct horizontal laminations and minute ripples (1-2mm in amplitude). These infills are composed of claystone sediments. This type of sediment has not been used in the flume tank, since it is so fine-grained it would be carried in suspension and not deposited for a considerable period of time.

The Calamites pith casts, composed of very fine sands and silts, show a structure very similar to those produced by infilling of stems from suspension currents in the flume tank; that is, two distinct cross-laminated structures formed at either end of the stem, indicating movement of sediment into the stem from both ends.

G. "The typical case of Stigmaria"

A very different situation occurs in Stigmaria compared with the infilling of isolated stems discussed previously. Stigmaria is the underground rhizophore of large arborescent Coal Measure trees (principally Lepidodendron and Sigillaria). The rhizophore is composed of numerous axes which may reach up to two metres in length. They do not taper to a fine point, but end in a relatively blunt termination (Frankenburg & Eggert 1969). These Stigmarian axes were hollow in life, as a result of a schizogenous cavity forming between the stele and outer cortex of the axis. This cavity may have been enlarged by degradation of some of the cortical parenchyma. In any event, the large cortical cavity contains the small stele which comes to rest against the side, roof or floor of the Stigmaria.

Numerous specimens of Stigmaria were collected in situ from Swillington Brick Works, West Yorkshire (Westphalian B). These were buried, or rather grew, in a fine-grained grey mudstone, which Scott (1978) interpreted as part of a freshwater lake sequence. The mudstone is very homogeneous, lacking distinct bedding, and contains abundant Stigmaria.

In contrast, the cortical infill of the Stigmaria is composed of a fine-grained siltstone consisting of 75% anhedral quartz (maximum grain-size 0.05mm). The remainder of the sediment is composed of white mica (15%), organic matter (8%), and feldspar (2%). The sediment shows distinct
horizontal laminations, ripples, and minute washout channels. Sectioning of the infill along the length of a Stigmaria indicates that the composition of the infill is uniform.

It was postulated (MacGregor & Walton 1948) that the cortical cavity of the Stigmaria was infilled by sediment being "washed down" into the rhizophore. Models of a simple Stigmaria were constructed, consisting of a hollow trunk, with two hollow axes extending horizontally from its base. Such a model was placed in the flume, with one axis directed upstream and the other downstream. The axes were sealed distally (i.e. at the ends of the rhizophore branches), as they would have been in life. Very low current velocities (4.0cms/sec) were used in these experiments and sediment settled out of suspension, falling into the open upright stem. Sectioning of the models after burial showed that very little sediment had penetrated any great distance along the horizontal axes. Modelling of this type of situation presents a scale problem; that is, reproducing the environment in which the infilling of a large underground root system would have occurred in relatively quiescent conditions is not really possible in the flume tank.

The infill of the fossil Stigmaria is very uniform, and indicates that there must have been a continuous supply of fine sediment being carried in suspension into the area in which the Stigmaria were being infilled. One of the problems that is difficult to answer in the case of these cortical infills, is how did the sediment work its way along the entire length of the Stigmaria? The ends of the rhizophore were closed and buried in the mudstone, so there could have been no current movement or flow through the Stigmaria allowing transport of sediment along the axis.

The sediment surrounding the Stigmaria is very similar to that of a seat-earth. These are characterised by being non-bedded, containing plant material in the form of rootlets, and being composed of a uniform grain-size (Huddle & Patterson 1961). Very often, seatearths show slicken-sides, and this has been attributed to the effect of dewatering and compaction in argillaceous rocks (Schultz 1958). The formation of seatearths is a very controversial subject, largely because of differing views of the origins of the kaolinite which forms a large fraction of most seatearths. Some workers argue that the kaolinite was a weathering product of the hinterland that was washed into the swamps (Schultz 1958), while others consider that the kaolinite was formed more or less in situ.
by a complex leaching process in the soil (Huddle & Patterson 1961), or as a result of fluctuations in aerobic and anaerobic conditions in the region of accumulation (Moore 1968).

If seatearth formation was a complex process, as it would seem to be, involving complex chemical changes in the soil, this may have affected the plant remains buried in the sediment; that is, that the infilling of the rhizophore may not have been a simple process of sediment being "washed down" the axes. The infills contain 15% white mica, and this may be in the form of kaolinites or illites. This cannot be determined optically due to the fine-grained nature of the grains. These kaolinites and illites may have crystallised out of solution, having been formed by leaching processes within or above the soil, while the quartz grains were transported in suspension. This solution would have infilled the stigmatic axes, with the kaolinites forming from solution during diagenesis; that is, the Stigmaria may not have been infilled simply by the movement of clastic grains along the axes, but rather that an appreciable faction of the infill (the kaolinites) were formed diagenetically in situ.

It is envisaged that a solution, or gel containing clastic quartz, would have reached along the entire system of the rhizophore relatively easily. It is more difficult to understand how clastic grains, with no associated current activity, could have infilled the axes as uniformly, as appears to be the case in these fossils, as suggested by MacGregor & Walton (1948).

H. Conclusions

By using a small laboratory flume tank the infilling of hollow plant stems has been investigated. It has been demonstrated that the infilling of these stems is not a straightforward process, but is related to stem length and diameter and current velocity. Stem infills, formed by sediment carried in suspension, show a distinct structure. This consists of two wedges of sediment formed at either end of the stem cavity, and these migrate along the stem. The extent to which these wedges develop is dependent on the length and diameter of the stem. The wedges are produced by sediment being deposited from small eddy currents which form at the stem entrances. These are produced when the flow separates in front and behind the stem when the flow of the current is restricted through the stem cavity.
Infilling of stems by traction currents is not as uniform as in the suspension currents because of the variation in the positions the stems can take up on the traction carpet. This results in a variation in the structure of the infills produced. Comparisons of the experimentally formed infills with fossil infills, has shown that the structure of the infills are comparable. This throws light on the flow conditions under which the fossil infill formed. Applying the information obtained from this experimental study has indicated that the formation of some fossil infills, e.g. Stigmaria, may not be as simple as has been assumed, and that diagenetically formed kaolinite may have contributed to the sedimentary infill.

An understanding of the extent to which infilling of hollow plant occurs using controlled conditions, and the structures produced during infilling, leads both to a fuller understanding of the fossil and of the nature of the environment in which infilling and burial occurred.
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REFERENCES


Description of Figure 1

The flume tank used in this study (X 0.05). Feeder tank (f); receiver tank (r); sluice gate (s); pump (p).
Description of Figure 2

The structure of the sediment infill produced in stems of varying length, but with a constant diameter (1.5cms), under the same flow conditions (5cms/sec). A. Short stem (5cms) in which the infill occupies most of the stem cavity (X 0.5). B. Medium stem (10cms) in which the infill consists of two distinct wedges of sediment (X 0.5). C. Long stem (35cms) in which the main part of the stem cavity is devoid of sediment. Infilling has only occurred at the two entrances of the stem (X 0.5). (c) current direction.
Description of Figure 3

A-D. The formation of the infill in a stem (10cm long, 1.5cms diameter) from sediment being carried in suspension (at 5cms/sec).

A. The current flows through the stem, depositing a layer of sediment along the floor of the stem. (c) the overall current direction.

B. The flow of the current is restricted and two small eddy currents form at either end of the stem. These deposit sediment in two small wedges at the stem entrances.

C. The downstream eddy current becomes dominate, and the wedge at the downstream end of the stem migrates up the stem cavity by the avalanching of sediment down the slope of the wedge. The upstream eddy current loses velocity.

D. The structure of the infill formed in the stem cavity.

E-I. The formation of the infill in a stem (length 10cms, diameter 1.0cms) buried in the traction carpet.

E. The current flows through the stem cavity, depositing a wedge of sediment which thins down the cavity. (c) overall current direction (38cms/sec).

F. The stem is exposed as the ripple migrates over the stem. The sediment is washed down the stem, forming a wedge of sediment which thins up the stem cavity.

G. As the next ripple approaches the stem, sediment is supplied from the lee slope of the ripple. The sediment forms a wedge at the upstream end of the stem, and some sediment accrues on the downstream wedge as the current flows through the stem cavity.

H. Eventually, the downstream wedge blocks the current flow through the stem, and an eddy current forms at the upstream end of the stem which deposits sediment adding to the wedge.

I. The structure of the infill formed in the stem cavity.
Description of Figure 4

Graph showing the relationship between stem length (L) and diameter (d), and the thickness of the infill formed in the central part of the stem cavity (E) with varying current velocity (c).
Description of Figure 5

Longitudinal sections of stems of varying dimensions that were infilled and buried in the flume tank. Arrow gives the current direction.

A. L.S of a stem (5cms long and 1.5cm diameter). The infill has almost filled the stem cavity. The stem was buried by sediment carried in suspension (X 1).

B. L.S of a stem (10cms long and 1.5cms diameter). The infill is composed of two wedges of sediment, the downstream wedge being larger than the upstream wedge (X 0.6).

C. L.S of a stem (5cms long and 1.5cms diameter) which was buried in the traction carpet. Most of the stem cavity has been infilled (X 1).

D. L.S of a stem placed upright in the flow. The stem has been infilled by sediment settling out of suspension and forming horizontal laminations within the pith cavity (X 1).

E. L.S of a stem (22cms long and 1.5cms in diameter). The stem cavity is devoid of infill, apart from a wedge of sediment formed at either end of the stem (X 1.5).

F. L.S of a stem (10.0cms long, 1.5cms in diameter) in which the exit was sealed. The formation of an infill was restricted, and only a small wedge of sediment formed in the stem cavity at the entrance to the stem (X 1.4).

G. L.S of a stem (10.0cms long, 2.0cms diameter) in which a substantial infill has formed as a result of the large diameter of the stem. The infill has some structure to it; a small ripple has formed within the sediment of the stem cavity (X 1.4).
Description of Figure 6

A block of sandstone containing a *Calamites* pith cast orientated almost perpendicular to the bedding plane (bp) (X 0.5). From the Westphalian B of the Yorkshire Coalfield.
Description of Figure 7

Longitudinal sections of Calamites pith casts.

A. Coarse-grained infill showing virtually no sedimentary structures (X 0.5).

B. Medium-grained infill showing distinct laminations and grading. At the top of the cast the laminations are gently dipping towards the tapered end of the infill (X 0.5).

C. Coarse-grained infill of sandstone containing large clay clasts (X 1).

D. Fine-grained infill consisting of lower layer of fairly coarse sand which grades into silt-size sediment. The silt contains fine sandy layers which dip into the centre of the infill from both ends (see arrows) (X 0.5).

E. Fine-grained infill composed of distinct laminations which dip towards the centre of the stem infill (see arrows) (X 0.75).