

THE EXPERIMENTAL FORMATION OF PLANT COMPRESSION FOSSILS

by G. M. REX and W. G. CHALONER

ABSTRACT. Despite the common occurrence of plant compression fossils, little experimental work has been done on the processes leading to their formation and their exposure by fracture. Models of the plant (in foam rubber) and the matrix (sawdust) systems have been subjected to deformation in an apparatus constructed so that the vertical plane can be kept under observation. The process of collapse and compression observed in vertical sections of plant fossils are more closely reproduced when the compression force acts through a number of free-moving pistons applied to the matrix than when a single larger piston is employed. The processes involved in the formation of compression fossils of *Calamites*, *Lepidodendron*, *Stigmaria*, and *Sawdonia* are explored and discussed. It is shown that the topography of a plant compression is governed not only by the structures revealed on the surface exposed, but by collapse of underlying plant tissue within the matrix. It is also demonstrated in lycopod leafy shoots that the fracture plane exposing the fossil is largely controlled by the angle between the bedding planes and the plant material.

ONE of the commonest forms of fossilization by which plants have been preserved is in the condition known as 'compression fossils'. Such fossils were formed when plant organs, buried in sediment, underwent partial degradation so as to produce a much flattened version of the original structure, with its tissue represented by a layer of coalified plant material.

This paper presents an account of a simple experimental investigation of some of the processes involved in the formation of plant compression fossils. Plants showing this type of preservation are generally less informative than those preserved by permineralization (showing three-dimensional cellular structure). However, compression fossils are undoubtedly far more abundant than permineralizations, and many fossil plants are known only in this state of preservation. It is therefore important that the processes of formation of such fossils and their subsequent exposure by fracture should be understood.

We attempted in the first instance to see if we could reproduce the form of compression fossils, seen in nature, by experimentation. By doing this we hoped to determine something of the deformation that plants underwent during compression, especially by investigating whether deformation was just in the vertical dimension, as many workers have believed (Walton 1936; Schopf 1975), or whether horizontal deformation also took place. We also wished to see if we could learn more about the physical processes involved during the formation of compression fossils; for example, how collapse distorts the shape of an organ and the associated matrix and how appendages such as spines and leaf cushions reacted to the accumulation and compaction of sediment and the ensuing deformation. We believe that by making a physical model of the plant-plus-matrix system which accurately reproduces the observed form of the fossil, we could learn something about the compression process as it occurs in nature. This understanding would give us a basis for reconstructing the original form of plants known to us only in the state of compression fossils. Although there are obvious shortcomings in modelling in a 'dry' system, we believe that our model may represent an improvement on the hypothetical consideration of the compression process, suggested by some authors (Boulter 1968; Rigby 1978).

A compression-type apparatus was designed and experiments conducted using artificial materials to represent plant and matrix, to try to reproduce the kind of preservation observed in fossils of *Sawdonia*, *Calamites*, *Stigmaria*, and *Lepidodendron*. These genera were chosen as representing rather well-known plants which illustrate a range of problems relating to the processes involved in their compression.

THE FOSSILIZATION PROCESS

Degradation and collapse

Plant compression fossils formed when plant material was deposited in the sedimentary environment, and was subsequently buried. During burial the cell contents and eventually the cell walls underwent microbial breakdown; in some cases this biodegradation may well have begun before burial. Whether in any given case this process (collapse of the plant organ) occurred ahead of the compression (produced by the weight of the overlying sediment) or whether it occurred as a direct result of the compression forcing the plant to collapse is difficult to determine. It is clear, though, that the compression process and the collapse/decay process are closely linked and may well have occurred synchronously. The residual plant material was then diagenetically altered to coaly matter, and a compression fossil formed. The terminology of the diagenetic process and its products are well reviewed in Schopf (1975). Very little is known about the details of these several processes.

We have elected to study Palaeozoic, mainly Carboniferous, material, in which the alteration (diagenesis) of the plant material has generally proceeded to the state of a bituminous coal. In younger sediments of Tertiary age, for example, the coalification process may only have reached the state of lignite ('brown-coal'). We believe despite the limited choice of our material, we are seeing phenomena resulting from universal physical processes which will apply with minor modifications to plant fossils from a wide age range.

The size scale effect

The degree of deformation affecting a plant organ is to some extent a function of the scale of the whole plant structure concerned. Plant stems which have suffered burial and have been compressed typically show a change in the shape of their cross-section from circular to elliptical. Close examination of the topography of the stem surface after deformation shows that, on a microscopic scale, distortion was much less pronounced. For example, Chaloner and Collinson (1975) demonstrated that in compression fossils of *Sigillaria* the ribs had been reduced to a flat ribbon-like form whereas the stomatal pits showed no comparable distortion. It would appear that compression is acting in this case on the macrostructure of the plant, but smaller scale topography is somehow sheltered from the deformation.

Spicer (1977) showed a possible mechanism that may explain this size scale phenomenon. He demonstrated that an iron-rich encrusting layer can build up on leaf surfaces only a few weeks after entry into the depositional environment. Spicer postulates that such an encrustation may be the basis of impression fossils replicating epidermal features in much finer detail than the sediment grain size would seem to allow. Comparing Recent leaves with fossil leaves from the Dakota sandstone, he showed by X-ray analysis that the fossil leaves had a very high iron-peak compared to silicon, indicating that the leaf impression surface was characterized by a concentration mainly of iron-rich material. This 'iron-coating' may limit biological degradation and may also serve as a structural protection for the microtopography of the plant surface during subsequent compression. This has the effect of preserving, apparently more or less undistorted, small features of the plant surface, e.g. stomatal pits, while the cross-sectional shape of the whole stem is drastically modified by collapse and compression.

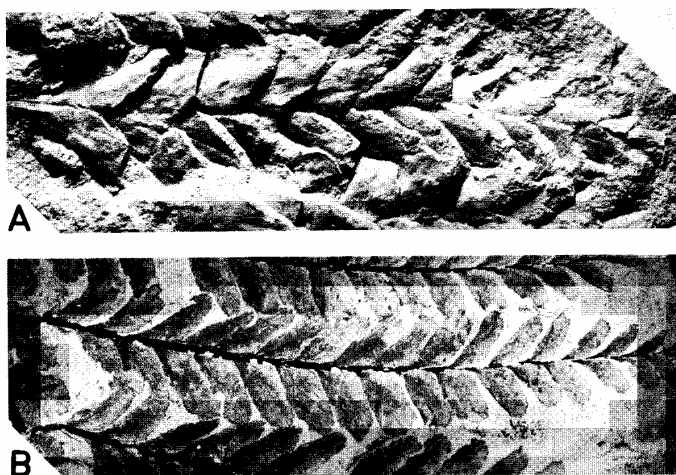
Sediment grain size

During the deposition of sediments compaction occurs as a result of water movement and the pore-volume is consequently reduced. Coarse-grained sediments, e.g. sands, will hold very little water and maximum compaction will occur early in diagenesis. Porous sediments which are very fine-grained or composed of colloidal constituents retain large amounts of water. The initial water content of most argillaceous muds is 50-80%; compaction of this type of mud will be accompanied by extensive dewatering. Animal or plant organs incorporated within sands or muds will suffer diagenetic deformation (compression) as a result of compaction of their own tissue and of the sediment. The

degree to which the plant or animal is deformed is a function of the amount and type of sediment that surrounds and infiltrates the structure of the dead organism. For example, sandy pith cavity infills of *Calamites* will be much less distorted than an argillaceous infill. This is because the sand grains tend to support each other, halting compaction of the infill (but not of the plant tissue) at an early stage. The clay minerals of an argillite on the other hand align themselves and move together producing a platyness, losing a large amount of water which was trapped between the clay particles in the process. It is therefore the compressibility of the matrix in which the organism is incorporated that dictates the final form of the compression fossil. The thickness of the coaly matter produced will, in contrast, show very little variation in either case, since it is the original amount of organic matter contained by the organism or plant that dictates the thickness of the residual coal layer.

These general statements require qualifying where early cementation of the matrix gives it a rigidity unrelated to its particle size. This is the process described by Schopf (1975) as authigenic preservation, typically involving 'early precipitation of authigenic minerals in sediment pore space'. It is represented by the plants preserved in the Mazon Creek nodules, and the comparable clay-ironstone nodules from other parts of the world. As Schopf remarks 'the distinction between . . . (such preservation) . . . and coalified compression is not absolute probably because of variation in degree and time of cementation'.

The effect of compressibility of the matrix on the final form of the fossil is illustrated in a direct way by the leafy shoot of *Archaeopteris* from the Devonian of Ireland shown in text-fig. 1B. The shoot ('frond' of earlier workers) has been compressed in an argillaceous matrix resulting in the formation of a very flat compression fossil. In text-fig. 1A a shoot of the same species was buried in a less compressible, sandy matrix (within the same rock unit of the 'Kiltorcan Beds'). Here, the fossil formed shows a closer approximation to the original form of the leafy shoot, in which the leaves ('pinnules' of earlier workers) are seen to be borne all around the stem ('rachis'). It was the very flat, two-dimensional state of the leafy shoots, compressed in fine-grained matrices, which encouraged earlier authors to interpret the *Archaeopteris* leafy shoot as a pinnate, fern-like frond. Only



TEXT-FIG. 1. A. *Archaeopteris hibernica* (Forbes) Dawson, preserved in a coarse-grained matrix giving the compression fossil greater relief, showing the true arrangement of leaves around the axis. $\times 0.7$. B. *A. hibernica* preserved in a fine-grained matrix giving a 'flat compression', suggestive of a pinnate leaf. $\times 0.7$. Both specimens are from Kiltorcan Old Quarry, Kilkenny, Republic of Ireland, Upper Devonian.

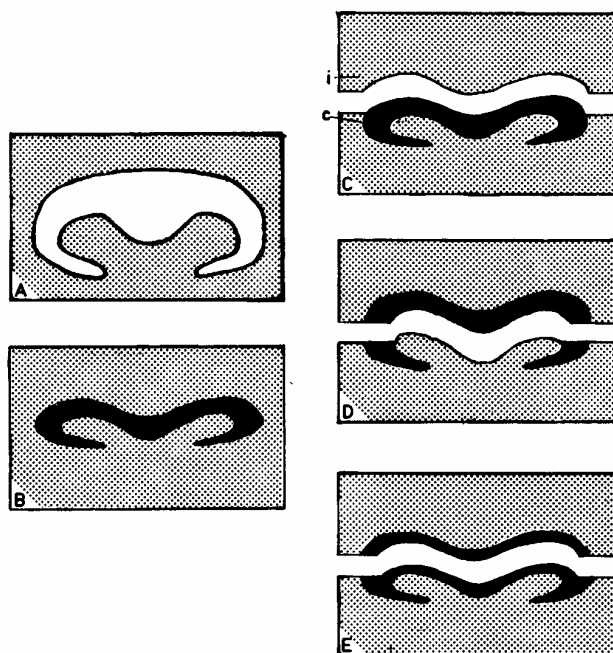
subsequent work on permineralized material, and the degaging of compressions demonstrated the original three-dimensional character of this fossil (Beck 1971).

A considerable amount of work has been undertaken by invertebrate palaeontologists to examine and recognize the effects of early diagenesis on invertebrate shells (Moore 1979) and on arthropods (Conway Morris 1979). The way in which ammonite shells react to compression is evidently very different to that of higher plant tissue, since the shell has a rigidity and toughness not diminished by biological degradation. Arthropods behave rather more similarly to plants than do ammonoid shells, for here the tough chitinous exoskeleton in the former has something of the physical properties of a thick plant cuticle enclosing readily degradable soft tissue. The role of such chitin layers in governing fracture planes is dealt with below.

THE PATHWAY OF FRACTURE PLANES

An important factor affecting the form of a plant compression fossil is the fracturing of the matrix which resulted in its exposure. The pathway of the fracture is governed by the characteristics of the matrix, the fossil-matrix interface, and the shape and orientation of the actual plant fossil.

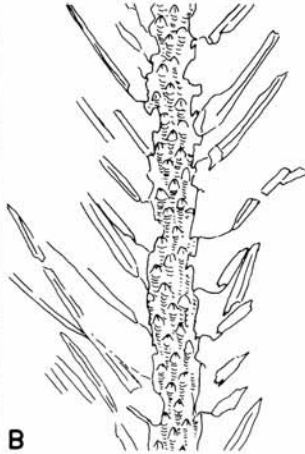
Coaly matter is usually retained on one or other face of the matrix exposed by fracture (text-fig. 2). The surface bearing the coaly matter is in this case commonly called a 'compression', while the fracture surface showing no organic matter is referred to as an 'impression' fossil (showing a mould of the fossil's surface topography, text-fig. 2c). Sometimes a fracture plane passes unevenly through the minute 'coal seam' constituting the plant material giving two 'incomplete compressions'



TEXT-FIG. 2. A. Vertical section of a leaf buried in matrix. B. Leaf after compression; the plant tissues have collapsed and been altered to coaly matter. C. Fracturing of the matrix produces an impression fossil (i) and a compression fossil (c). D, E. Different pathways of fracture produce two different versions of an 'incomplete compression'.



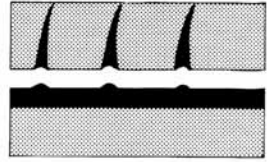
A



B



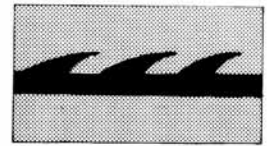
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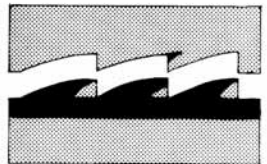
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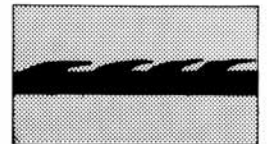
F



G



H



I



(text-fig. 2, D and E). The pathway of the fracture surface dictates the extent to which the fossil is exposed.

The manner in which a fracture plane exposes a fossil has been discussed by Conway Morris (1979) with reference to arthropods from the Burgess Shale. He has found that these invertebrates do not occupy a single bedding plane but cross two or more levels of microbedding. The appendages of the arthropods are separated by thin layers of sediment. Whittington (1975) showed that slight variations in the plane of splitting determined which part of the arthropod was exposed. This plane of splitting, according to Whittington, is governed by competition as a pathway for fracture between various parts of the arthropod body and is dictated by: (a) the surface area of the structure; (b) its thickness; and (c) its angle to the bedding. Conway Morris (1979) demonstrates this pathway of the fracture plane with reference to *Canadia spinosa* in determining which parts of the animal are exposed and which remain buried in the matrix. This role of fracture planes can be similarly demonstrated in plant compression fossils, for example in the leafy shoots of lepidodendrids. The angle between the leaf and the stem, as seen at the side of the fossil stem helps to explain the pathway of fracture seen over the central part of such a fossil. For example, *Lepidodendron wortheni* bears leaves which make an angle of about 60° with the stem. When this species is exposed by fracturing, the fossil seen on the fracture surface is of a stem, bearing leaf cushions, with leaves seen at both sides lying 'in profile' in the matrix. This has understandably led some workers (e.g. Crookall 1964) to identify 'leaf scars' on the cushions of *L. wortheni* even when leaves have been described attached at the sides of the stem. Close examination of these 'scars' shows them to be irregular and structureless, and these fracture features have been designated 'false scars' (Chaloner and Boureau 1967), in contradistinction to true abscission scars formed in life.

It appears that such a break across the coalified leaf, lying in the matrix, occurs when the angle between the bedding plane and the coalified plant organ gets too steep for the fracture plane to run on along the leaf surface (text-fig. 3, A-C), and the leaves are removed in the counterpart. Where the angle between leaf and stem is more acute (e.g. as in *L. acutum* or *L. simile*) the fracture above the stem surface runs some or all the way along the leaf, revealing partial or complete leaf surfaces (e.g. *Bothrodendron minutifolium*) overlying the stem (text-fig. 3, G-I). An intermediate condition occurs in *L. simile* where leaves of sigmoidal profile leave the stem surface at a moderate angle. Here the fracture plane runs a short distance along the leaf surface, so showing short, truncated leaf segments above the stem on the compression fossil (text-fig. 3, D-F).

METHODS OF INVESTIGATING COMPRESSION FOSSILS

Since the early years of the last century many palaeobotanists have regarded plant compression fossils as essentially two-dimensional objects, rather comparable to 'pressed plants' (herbarium specimens). Where angiosperm leaves or large multipinnate fronds are concerned, this is a reasonable approximation. The earlier view that such fossils were in effect entirely two-dimensional objects is well exemplified by Johnson's (1913) quoted remark that splitting open the Kiltorcan shales to reveal plant fossils was 'like turning over the leaves of a picture-book'.

This 'herbarium view' of compression fossils tended to discourage serious consideration of the vertical dimension in such fossils and the complexity of factors governing their form. Walton (1936) was probably the first palaeobotanist to give serious consideration to the vertical dimension in compression fossils. Significantly it was he who developed one of the most fruitful ways of studying such fossils beyond direct observations of the exposed fracture surface (Walton 1923).

Five principal methods have been developed by palaeobotanists for looking at the 'third dimension' of compression fossils. We enumerate these here briefly to emphasize that while they involve different procedures, they have in common that they contribute to our knowledge of the vertical dimension of the compressed plant material.

The transfer technique

This procedure, developed by Walton (1923), consists of sticking the exposed (fracture) surface of plant material to a transparent surface (plastic film or balsam on glass) and dissolving the rock matrix with appropriate acid

(e.g. hydrofluoric acid). The coaly film is then available, free of matrix, to be examined on either surface, and the topography of the surface previously hidden in the matrix, revealed.

Vertical sectioning

This is a standard procedure used for examining permineralized plant material, but has been used very little in the study of compression fossils. A few authors have sectioned such specimens; Selling (1944), for example, studied a Calamitean cone compression in this way and Boulter (1968) sectioned lycopod sporophylls, both using information from the sections to interpret the three-dimensional form of the collapsed plant organ.

Degagement

Leclercq (1960) pioneered the development of this technique, which involves removing the matrix 'grain by grain' to expose the plant fossil in depth, below the initial fracture plane. It has been highly successful in revealing the three-dimensional character of branch systems lacking large laminar appendages, particularly those preserved in non-indurated coarse matrices, e.g. *Rhacophyton*—Leclercq (1951), *Calamophyton*—Leclercq and Andrews (1960), *Archaeopteris*—Beck (1971).

Solution of matrix

If the plant tissue is sufficiently coherent (undegraded), dissolution of the matrix with HF may release entire branch systems in a three-dimensional state. This technique has been used with notable success by Doran (1980) in his preparations of Canadian *Psilophyton*.

Direct observation of the fractured surfaces (part and counterpart)

Many workers have used information gathered from the examination of the plant compression fossil as it has been exposed, by fracturing of the matrix, to reveal the two faces (part and counterpart) of the fossil. The data obtained has been used to make reconstructions of how the extinct plant fossil may have looked in life. For example, Plumstead (1952) used this method in postulating the structure of *Glossopteris* fructifications and Rigby (1978) has recently used this method in producing a rather different interpretation of comparable structures. The divergence of opinion arising with such reconstructions (see, for example, discussion in Plumstead 1952; Rigby 1978) emphasizes the incompleteness of our knowledge of the configuration of plant organs resulting from the compression process.

EXPERIMENTS IN THE PROCESS OF FOSSILIZATION

PREVIOUS WORK

Transport processes

The process by which plant material becomes incorporated in sediment is obviously very relevant to the study of compression fossils. Ferguson (1971) was one of the first people to investigate this, and conducted a series of experiments to determine how thick and thin leaves reacted to water transport. He constructed an apparatus consisting of water and sand filled cylinders, in which leaf fragments suffered the equivalent of 80 km transport along a river system. At the end of that period neither the thick nor thin leaves showed any signs of degradation.

Spicer (1980, 1981) has also considered the manner by which plant organs become incorporated in sediment. He has examined modern sedimentary environments, e.g. fluviolacustrine delta in an artificial lake, and shown

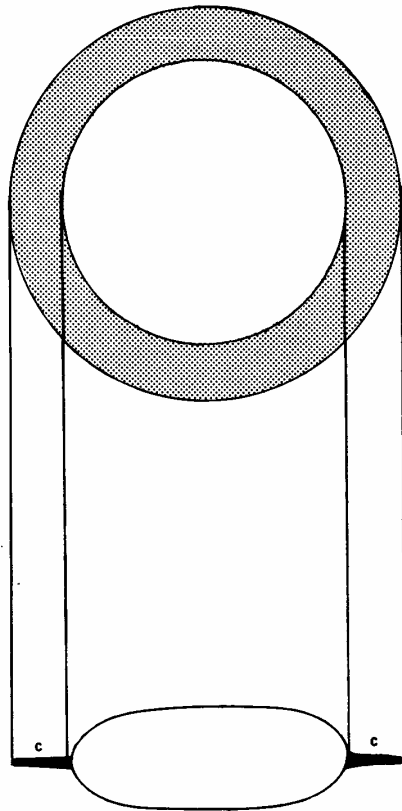
TEXT-FIG. 3. (*opposite*) A. Leafy shoot of *Lepidodendron wortheni* Lesquereux. $\times 0.6$. B. Tracing of the specimen showing detail of the leaf orientation. C. Diagrammatic vertical section through *L. wortheni*. The fracture plane that exposes the fossil passes along the stem surface, leaving the steeply rising leaves in the counterpart. D. *Lepidodendron simile* Kidston. $\times 3$. E. Tracing of the specimen showing detail of the leaf orientation. F. Diagrammatic vertical section through *L. simile*. The fracture plane runs a short distance along the leaves, then reverts to the bedding planes. G. *Bothrodendron minutifolium* (Boulay). $\times 3.5$. H. Tracing of the specimen showing detail of the leaf orientation. I. Diagrammatic vertical section through *B. minutifolium*. The fracture plane runs along the almost horizontal leaf surfaces above the stem, so that the entire leaf outline is exposed. (A: Institute of Geological Sciences, Kidston Collection, No. 1013, D: No. 4890, G: No. 1472. All are from the Coal Measures of Yorkshire.)

where plant organs, mainly leaves, are deposited along the sedimentary system. The leaves form distinct leaf beds, one on the lake bottom and one on the foreset slope of the delta. The major mechanisms by which plant material is deposited appear to be selective transport of plant organs and biological and mechanical degradation.

Processes in the sediment

The manner in which plant material behaves once it is buried in sediment has been investigated experimentally by very few workers. Walton (1936) was the first palaeobotanist to consider the mechanisms by which plant material was compressed in sediment. He did not describe any experimental investigation of the mechanism, although it is believed that he did carry out experiments (T. M. Harris pers. comm. 1981). Instead he published a theoretical account of the processes involved. Walton postulated that after a plant fragment had undergone burial in mud the horizontal components acting on the plant were zero, the only remaining force being vertical. As a result of this, water was displaced upwards and the plant fragment suffered considerable reduction in the vertical dimension with no horizontal deformation occurring. As an example Walton considered a hollow cylinder of fairly compressible tissue embedded in a less compressible matrix which also infilled the cylinder; this is the type of fossil represented by a *Calamites* pith cast. Walton postulated that after compression the horizontal diameter of the fossil would be the same as that of the original axis. The collapsed plant tissue formed a 'compression border' at the sides (text-fig. 4), its width being a measure of the thickness of the woody cylinder.

The first account of actual experimental work is given by Harris (1974) who considers compression mechanisms as they apply to spherical pollen grains. This work arose in the course of an investigation of the colpus-like folds of distorted *Williamsoniella* pollen grains. Harris constructed hollow balls of various artificial materials which were then compressed between flat surfaces. The results showed that such spheres do expand horizontally.



TEXT-FIG. 4. The result of compression of a cylinder of highly compressible material infilled with sediment. The compressible material forms compression borders (c) bounding the infill. (After Walton 1936.)

Harris also carried out a preliminary investigation of spores buried in matrix, again using artificial materials, e.g. wax and plastic balls in sand. In this case no measureable horizontal extension occurred, largely as Walton had predicted. After examining many dispersed spores within sediments, Harris concluded that the spores showed no evidence of spreading laterally into the enclosing matrix.

This was the first experimental work attempted since Walton set out his hypothesis in 1936. It is clear that spore exines retain a resilience and elasticity after their contents have been degraded which may not be matched in larger plant structures. In this respect, the behaviour of his spore models may differ from the collapse of plant tissue undergoing biodegradation; but Harris's work has shown that experiments with simple, physical models of the plant-matrix system can help to elucidate the structure of the fossil as it is observed in the rock.

Whether distortion during compression is only in the vertical plane and that the diameter of the fossil is the same as that of the original plant, was investigated by Niklas (1978), in an attempt to test Walton's assumptions. Niklas calculated that total flattening of a cylinder would produce a maximum diameter increase of 57%. A series of experiments designed to monitor the deformation of a cylinder during compression, using artificial materials, were conducted; he also conducted further experiments using natural materials such as sand, clay, and mud with fresh plant axes embedded in them. Unfortunately, Niklas does not describe the actual procedure adopted for any of these experiments, but several conclusions are given. These include:

1. That horizontal deformation (expansion) of a cylindrical body may occur during compression.
2. That the theoretical maximum diameter increase is never reached.
3. That solid cylinders of tissue show a maximum 10% diameter increase.

This work was the first really to consider compression of stems experimentally, but the detailed mechanisms of collapse and compression of the plant organs does not emerge from the results published so far.

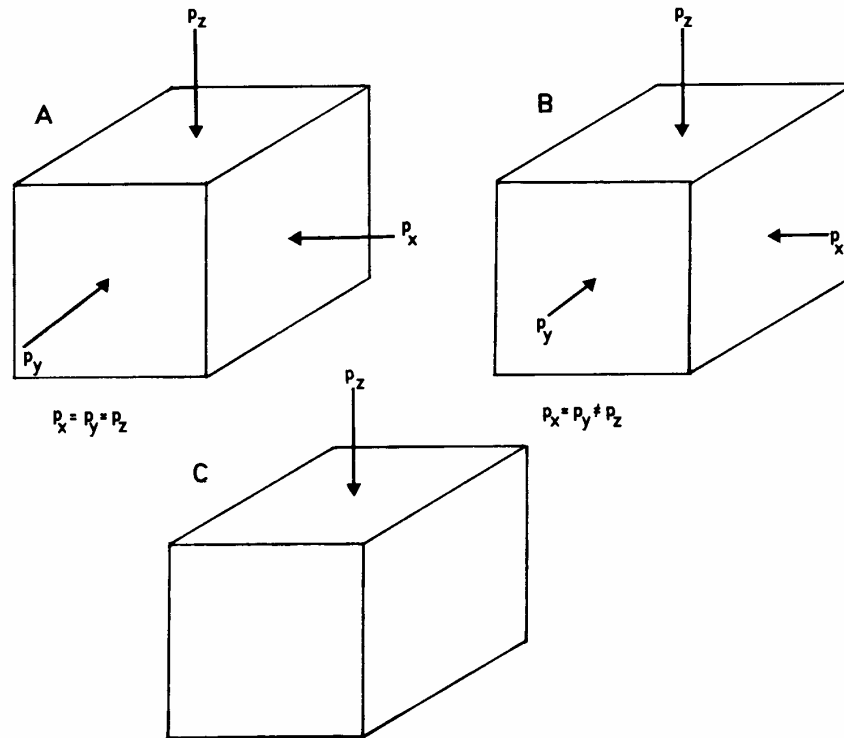
THE PRESENT WORK

General considerations

In order to investigate compression processes experimentally, we have constructed an apparatus in which the vertical dimension can be observed during the experiment. Rieke and Chilingarian (1974) considered the type of mechanism required to experiment with compaction processes, i.e. the best means of reproducing conditions existing in naturally compacting sediment. They consider that during the initial stages of sedimentation the pressure was hydrostatic (three principal stresses are equal) (text-fig. 5); as sedimentation proceeds, the pressure becomes biaxial (two out of the three principal stresses are equal, namely those in the horizontal plane). As the overburden increases and the matrix becomes more rigid, the pressure, in effect, becomes uniaxial; that is, the compression force is parallel to the vertical axis. Using this principle, an apparatus was constructed in which the pressure was uniaxial, thereby creating conditions comparable to those which occur after burial of plant material with an overburden.

The apparatus consisted of a piston system which acted on the contents of a loading box $19.0 \times 19.0 \times 1.5$ cm in which the individual 'fossils' were placed and sealed in by a vertical perspex cover. The piston system was operated by a large screw mechanism (Pl. 30).

In this first investigation into the behaviour of plant and matrix on compression we wished to use the simplest system possible. One of the difficulties in studying the compaction of natural sediments is to reproduce the effect of upward movement of water through the sediment. In order to do this a water-tight apparatus is required in which there is a strict control over the movement of water out of the system. Another problem to consider in this type of study is the impossibility of reproducing the load of hundreds of metres of sediment exactly as it occurs in sedimentary basins. We therefore decided to use an apparatus in which simple artificial models could be compressed using a totally dry system, thereby removing the problems described above. We considered it was important to begin an investigation of this type to see if such experimental modelling could help us to interpret what we observe in plant compression fossils. Foam rubber was chosen to represent plant tissue since it is easily prepared and is very compressible (by 85% of its original volume under our maximum load). Finely sieved sawdust was used as matrix since it was particulate, could be packed freely around the fossil like settling sediment, but was less compressible than foam rubber (compresses by 47% of its original volume under our maximum load). It also becomes tightly compacted, i.e. increases in rigidity with compression, like natural fine-grained sediments. Air in the matrix interstices in effect



TEXT-FIG. 5. Different loading stresses on sediments in laboratory experiments. A. Hydrostatic loading, the three principal stresses are equal $p_x = p_y = p_z$. B. Triaxial loading in which only the two horizontal principal stresses are equal, $p_x = p_y \neq p_z$. This situation develops as the matrix consolidates. C. Uniaxial loading, only one principal stress acting in the vertical axis; this is the condition in a consolidated matrix under heavy load. (After Reike and Chilingarian 1974.)

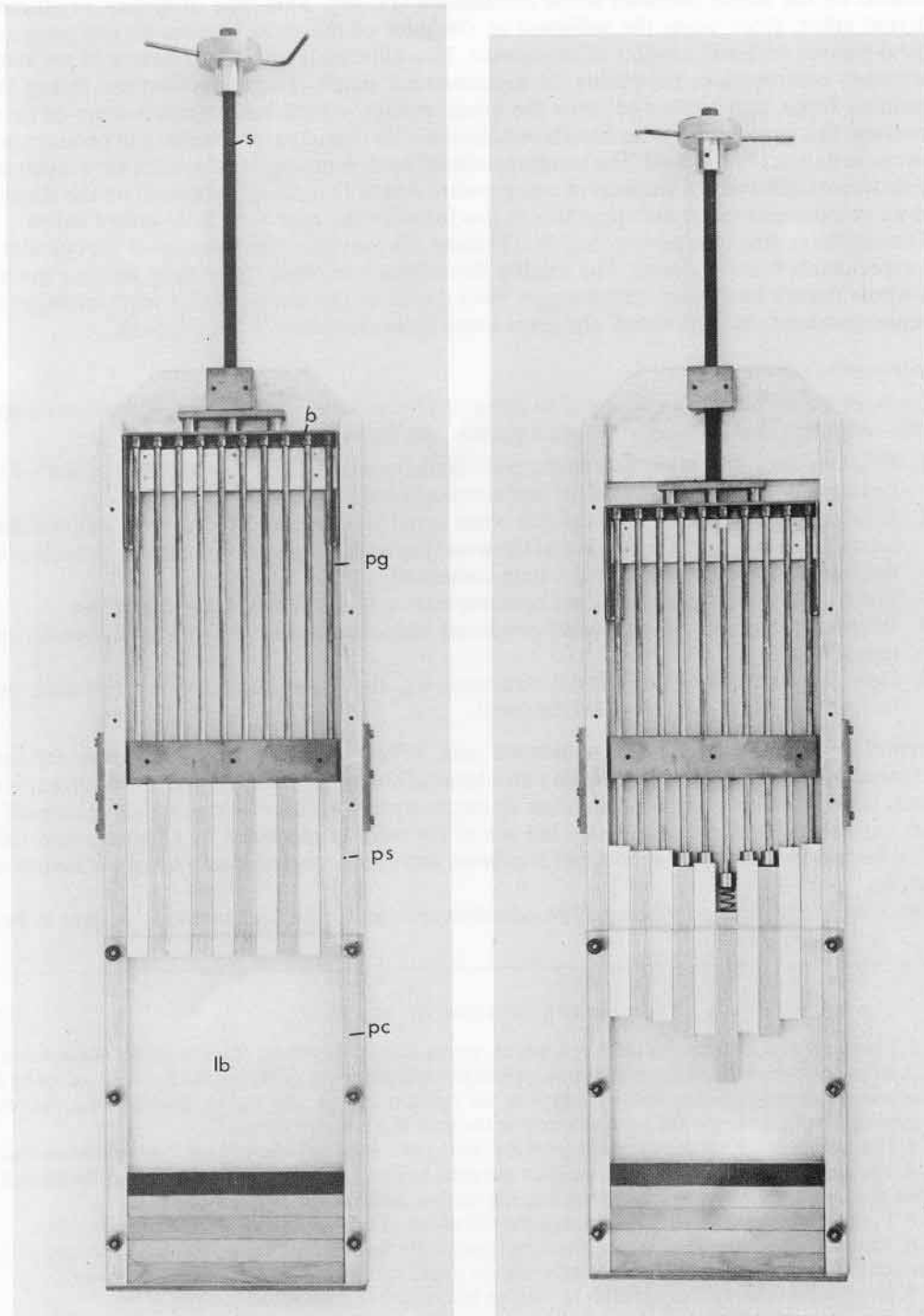
took the place of the water in a natural sedimentary system, and was, of course, displaced freely during compression.

The design of the piston system was changed during the course of experimentation. Originally we used a single piston but this did not produce the results seen in compression fossils. Using this type of system resulted in sediment at the margins of the cylinder becoming totally compacted and so holding up the descending piston, preventing further deformation of the 'plant' material (Pl. 31, 1-2).

In order to get a form closer to known compression fossils the piston system was changed to a parallel series of ten independent pistons each 1.9 cm wide. Each piston was spring-loaded, still being

EXPLANATION OF PLATE 30

The compression apparatus used in the experimental work. $\times 0.3$. This consists of a large screw mechanism (s) which acts on a bar (b) to which ten plungers (pg) are attached. On compression the plungers push into ten independent spring-loaded pistons (ps). Each piston will move independently when acting on the matrix in the loading box (lb) in which the plant and matrix are placed, and sealed by a perspex cover (pc). In the right-hand photograph the central piston has been dropped to reveal the expanded end of the plunger and the spring, which is recessed into the upper part of all the pistons.



REX and CHALONER, compression apparatus

operated by the single common screw mechanism (Pl. 30). This type of system produced a very different effect, since when the sediment at the sides of the stem became totally compacted the central pistons were still capable of movement. This allowed further deformation of the stem and it underwent compression, producing an asymmetrical shape. The upper surface, facing the compressional force, had 'collapsed' into the lower surface, which had retained some of its original curvature; this gave the compression an orientation with regard to the direction of pressure, as is seen to occur in nature (Pl. 31, 3-4). The results produced by this 'multipiston' system were much nearer to the structures observed in sections of compression fossils than those produced by the single piston, and we subsequently used the apparatus in this form for the experiments described below.

During the course of experimentation it became obvious that the diameter of the cylinder used in the experiments was important. The smaller the compressed plant structure in relation to the size of the whole matrix body (our compression box) the more the matrix at the margins supported the compression load and 'protected' the plant tissue from distortion (Plate 31, 5-8).

Experimental results

A series of experiments was designed to attempt to reproduce experimentally known compression fossils using artificial materials. We were particularly interested to see:

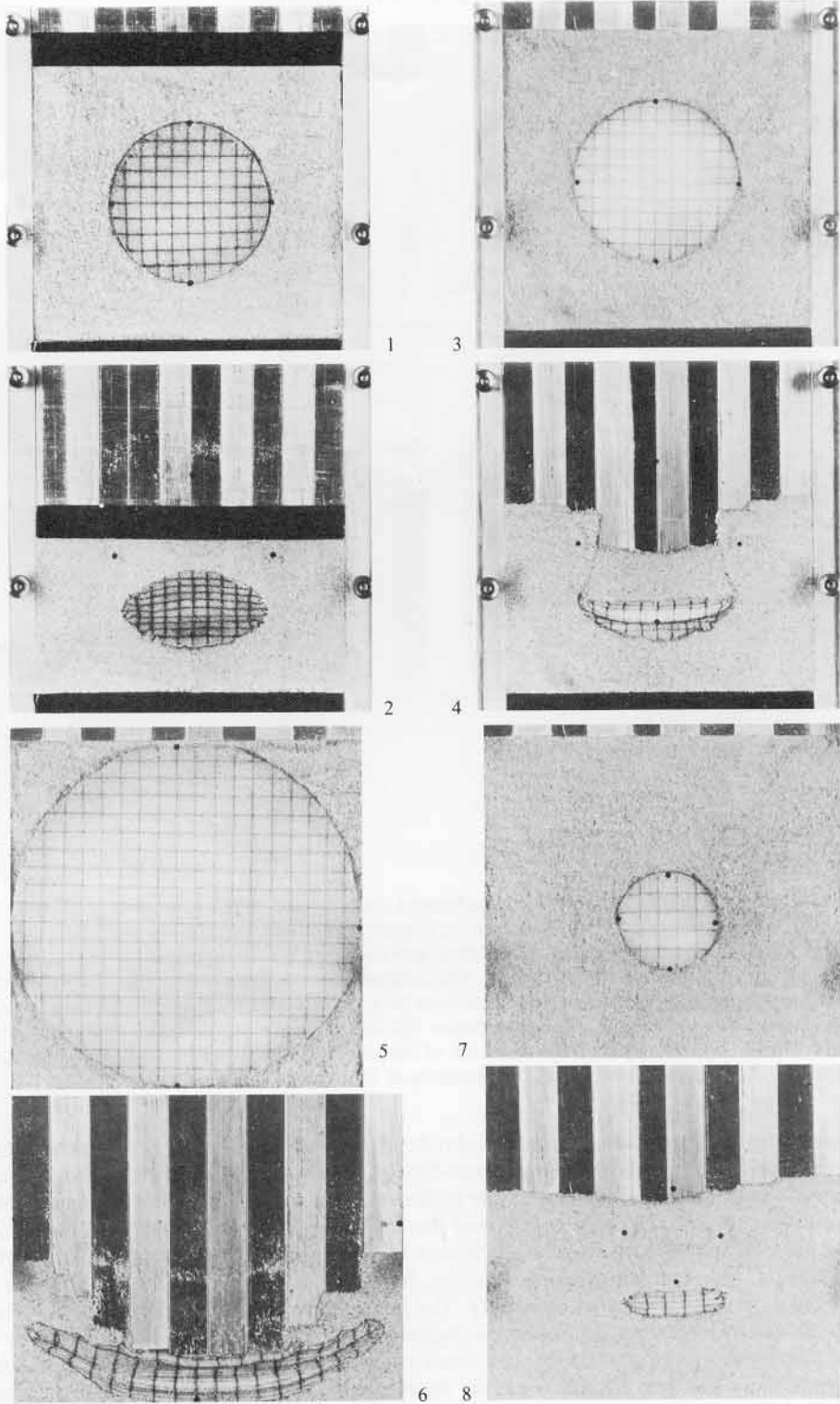
1. Whether the external features of the plant could appear on an internal cast, e.g. leaf cushions in *Lepidodendrids* appearing on an 'endocortical cast'.
2. Whether the internal features of the plant could be translated on to the outer surface of the fossil, e.g. 'ribs' on the inner face of the woody cylinder in *Calamites*, appearing as topographic features on the outer surface of a stem compression.
3. The way in which spines behaved on compression of a spiny axis, e.g. *Sawdonia*.
4. Whether the compression border predicted and observed by Walton in *Calamites* could be reproduced.
5. How the collapse of an internal structure, e.g. the woody cylinder in *Stigmaria*, produces features on the outer surface of the fossil.

External features appearing on an internal cast. When species of *Lepidodendron* are found as compression fossils, only a piece of the outer layer of the stem (broadly, the outer cortex) is usually found, bearing leaf cushions, rather than an entire stem. This may be due to 'sloughing off' of the outer (primary) stem surfaces during the life of the tree, as suggested by Chaloner and Collinson (1975) for the '*Syringodendron*' state of *Sigillaria*, or to post-mortem break up of the hollow cortical cylinder.

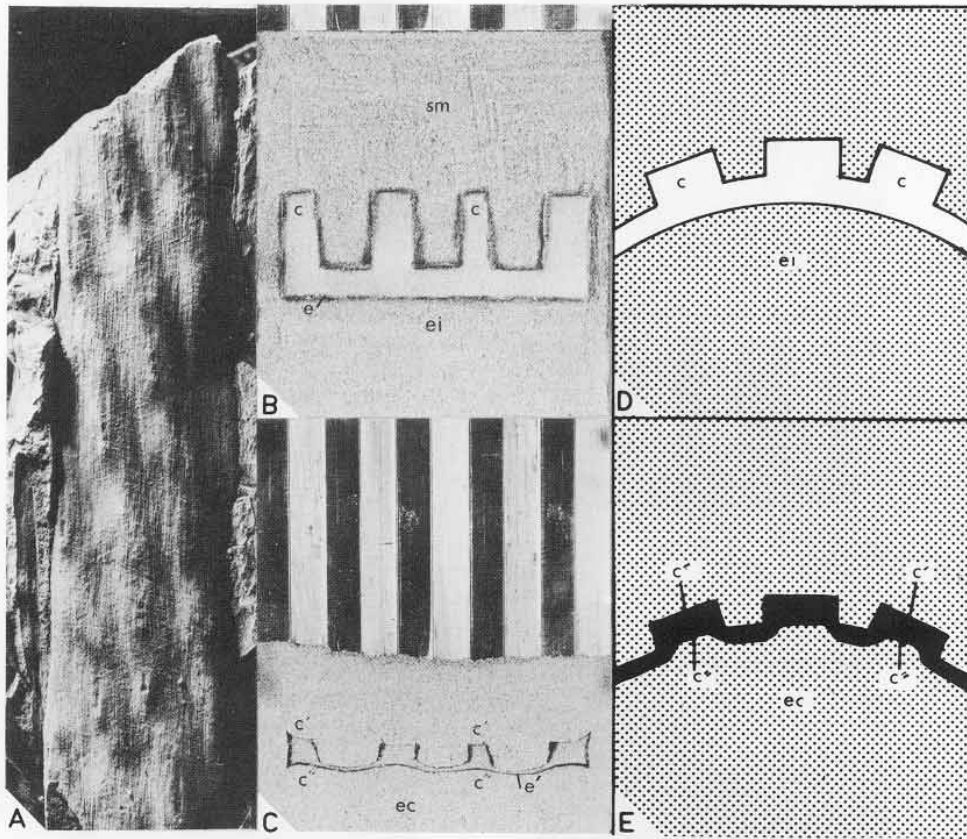
On careful examination of some *Lepidodendron* specimens, the 'leaf cushions' appear to be poorly

EXPLANATION OF PLATE 31

- Fig. 1. The single piston system before compression, acting on a solid cylinder of foam rubber in a sawdust matrix.
 Fig. 2. After compression, the cylinder shows only slight collapse effect; compression has been halted by the total compaction of the sediment at the margins of the cylinder. (Note here and in the following, the four spots outlining the plant axis on the perspex cover at the start of each experiment.)
 Fig. 3. The multipiston system, before compression, acting on a solid cylinder of foam rubber in a sawdust matrix.
 Fig. 4. The same after compression; the matrix marginal to the cylinder has compacted, but the central pistons have continued independent movement, causing further deformation of the cylinder.
 Fig. 5. Foam rubber cylinder reaching across the full width of the loading box, before compression.
 Fig. 6. The same after compression; the resulting form of the foam rubber shows that the curvature of the lower surface has been retained to some extent while the upper surface has collapsed into the lower.
 Fig. 7. Small solid foam rubber cylinder in loading box before compression.
 Fig. 8. The same after compression; distortion of the cylinder is much less than in 6, as the completely compressed matrix at either side of the cylinder protects it from further deformation.
- (All, $\times 0.5$.)



REX and CHALONER, the deformation of cylinders of varying dimensions



TEXT-FIG. 6. A. Endocortical cast of a lepidodendrid showing the spiral arrangement of leaf cushions indistinctly. $\times 1.7$. From Radstock, Somerset. B. Experiment constructed to explain this specimen. This consists of a strip of foam rubber sculptured into 'leaf cushions' (c). Endocortical infill (ei), surrounding matrix (sm), inner surface of 'cortex' (e). C. On compression the inner surface (e') of the 'cortex' has collapsed into the cushions (c') taking up their form (c'). D. Explanatory diagram showing leaf cushions and infill before compression. E. On compression the cortical tissue is altered to coaly matter and the endocortical cast (ec) takes up a subdued version of the form of the outer cushions (c'). The surface of the endocortical cast (e') is the same as that shown in the fossil in A.

defined structures, lacking leaf scars and cellular detail but showing the spiral arrangement of the leaf cushions common to the Lepidodendrids (text-fig. 6A). It is suggested that this effect is produced by the pattern of the cushions appearing on the endocortical cast, when this has collapsed into the leaf cushions on compression. In order to produce this effect experimentally, a strip of foam rubber was sculptured into leaf cushions as they might be seen in section and then compressed in a matrix of fine sawdust (text-fig. 6B). On compression (text-fig. 6C) the topography of the cushions on the outer surface of the strip was lowered considerably. The much more interesting effect was that the grooves (infilled with matrix) between the cushions impressed their topography as ridges on to the inner surface of the strip. Correspondingly, the inner surface of the leaf cushions formed depressions. Hence, where there had been no relief on the inner surface of the strip (bounding the endocortical cast) before deformation, on compression the pattern of the cushions was translated on to the

endocortical cast. The surface labelled e' on our experiment corresponds to the exposed surface of the fossil shown in text-fig. 6A. The fact that such cushions on the endocortical cast are positive features may misleadingly encourage the observer into believing he is seeing a poorly preserved original surface topography.

The extent to which external topography is communicated to a cortical infill (endocortical cast) is evidently a function of cortical thickness, and compressibility of matrix. Generally it seems that a lycopod with rather thin development of cortex preserved in a coarse matrix will show positive 'external' topography (cushions) on the endocortical cast more readily than one of thicker cortical development and finer grained matrix.

Internal features appearing on an external surface. The reverse situation of the above is where the internal features of the plant are translated on to the outer surface during the compression. For example, the internal topography of the pith cavity wall appearing on the outer surface. This is seen in some *Calamites* specimens where internal ribs appear on the outer surface of a stem compression, where in effect the coaly residue of the stem tissue is 'draped' over the pith cast. Such a specimen is not technically a pith cast, but rather a pith cast lying within a stem compression, but this term has been used loosely for material of this kind.

An experiment was devised to reproduce this effect; foam rubber was sculptured into ribs and embedded in a sawdust matrix. On compression, the ribs were transmitted from the internal surface of the layer on to the external surface (Pl. 32, 1-3), a process obviously closely analogous to that described above for a lycopod leaf cushion.

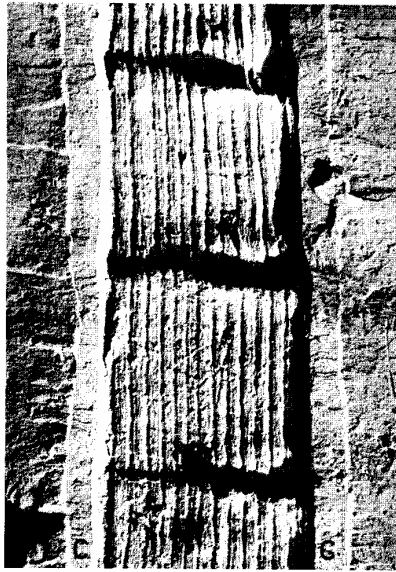
The behaviour of spines during compression. When examining compression fossils one of the most interesting aspects is the behaviour of appendages such as spines on plant axes. Chaloner *et al.* (1978) examining *Sawdonia* specimens from borehole cores in Oxfordshire suggest the processes that may have affected the axis during compression, but did not investigate this experimentally.

If we consider what happens to a spiny axis when it touches and lodges on a river or lake bottom, we may picture the spines facing the sediment acting as supports, holding the stem slightly above the sediment surface. In this situation it is unlikely that sediment will get into the gaps between the spines and the sediment surface below the stem until burial has occurred, while sediment will continue to settle gradually on the upper (exposed) surface of the axis as it is buried.

We designed an experiment to copy this process as closely as possible. As compression proceeded the lower spines gradually 'sank' into the sediment and the hollow axis (left hollow in our model since *Sawdonia* had a relatively small stele, and its fossils show no sedimentary infill) gradually closed up. During closure, the upper surface gradually 'collapsed' into the lower producing an asymmetric, C-shaped section. The spines borne laterally on the stem were reduced considerably in thickness but retained their original length. Those spines facing the compression on the upper surface shortened considerably and showed some distortion (Pl. 32, 4-6). The lower spines shortened but not to the same extent. It appears that most of the deformation is taken up by 'collapse' of the stem and the subsequent deformation of the spines on the upper surface. The spines on the lower surface seem to have been more 'protected' from the compression than was suggested to be the case by Chaloner *et al.* (1978).

Formation of compression borders. Walton (1936) suggested that on either side of a matrix infill ('pith cast') a flattened coaly margin would form; he also suggested a similar process occurred with a leaf having an incurled margin (text-fig. 2). In both cases the greater compressibility of plant tissue adjoining the less compressible matrix infill produced a 'compression border', the width of which represents the thickness of the original plant structure (woody cylinder, leaf thickness). Modelling of this in our apparatus produced a result similar to Walton's predictions (Pl. 32, 7-9) and is shown in some *Calamites* specimens (text-fig. 7). This compression border, as indicated earlier, is produced only when multiple pistons are used rather than the 'single piston' earlier version of the apparatus.

The effect of collapse of an internal structure on the outer surface of the fossil. Examination of compression fossils of *Stigmara* show interesting features beyond those considered above. In fossils



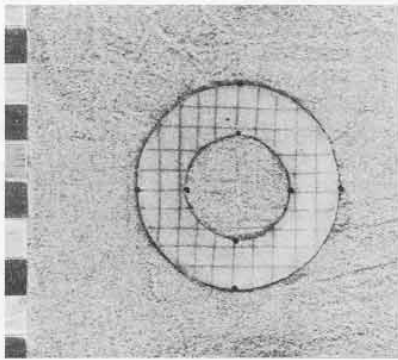
TEXT-FIG. 7. *Archaeocalamites radiatus* (Brongn.) Stur. This shows an impression of internal ribs and the formation of compression borders (c) produced by the collapse and compression of secondary xylem bounding the infill. The fossil is therefore a pith cast, within an impression. The high compressibility of the oil shale matrix produced a fossil of very low relief. Oil shale, Calciferous sandstone series, Lower Carboniferous, Scotland. $\times 2$.

of this type, a very thin coaly layer, bearing impressions of points of attachment of rootlets (commonly called 'rootlet scars') bounds a matrix-filled cylinder (an endocortical cast). Examination of a vertical section of the infill often shows the presence of the highly compressed woody cylinder bounded at its margins, as would be expected, by small compression borders (Pl. 33, fig. 3).

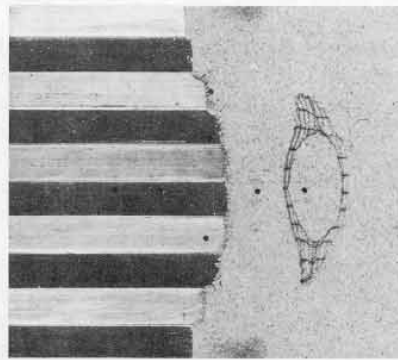
The stele (woody cylinder) is often seen to be displaced in such *Stigmaria* compressions, commonly lying either against the upper or lower inner surface of the cortical cylinder. The stele evidently became separated from the cortex during growth by a 'middle cortex cavity'. The stele was free to either float or sink within the cortex, or to lodge in the mid point of the infill. *Stigmaria* often shows the presence of a groove running along one of the outer surfaces. This was thought by Pant (1956) to be related to the late collapse of the xylem cylinder, after infill of the cavity. The groove was considered by Walton (quoted in Pant, loc. cit.) to occur only on the upper surface of the stigmarian axis, since orientated specimens (e.g. Williamson's specimen of *Stigmaria ficoides* from Clayton, Lancs., held at the Manchester Museum) sometimes show the groove to be on this surface. This is

EXPLANATION OF PLATE 32

- Fig. 1. Experiment to investigate the behaviour of internal ribs (r) on a woody cylinder during compression. Initial state.
- Fig. 2. On compression the outer surface collapses onto the ribs (r) and the surrounding outer matrix (sm) takes up the form of the internal ribs (r'). This is very similar to, but the reverse of, what is described in text-fig. 6.
- Fig. 3. Close up of the above to show detail.
- Fig. 4. Experiment to investigate the behaviour of spines during compression. Initial state.
- Fig. 5. On compression the marginal spines are flattened. The spines directed upwards are shortened to a greater extent than those on the lower surface.
- Fig. 6. Close up of the above to show detail.
- Fig. 7. Experiment to investigate formation of a *Calamites*-type fossil. Initial state.
- Fig. 8. Under load, compression borders (c) form at the margins of the infill. These have the horizontal dimension (diameter) of the original cylinder.
- Fig. 9. Close up of the above to show detail.



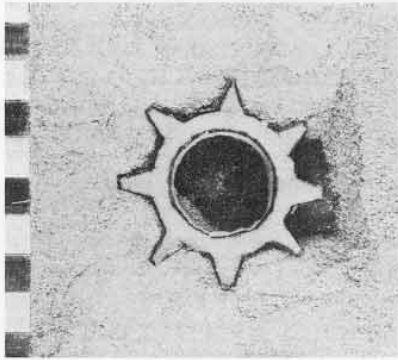
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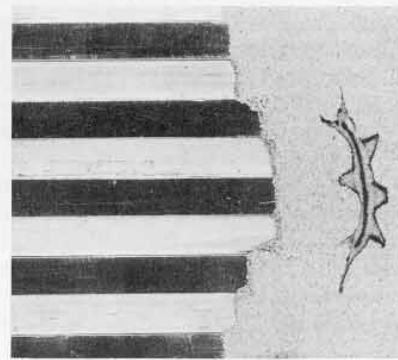
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9



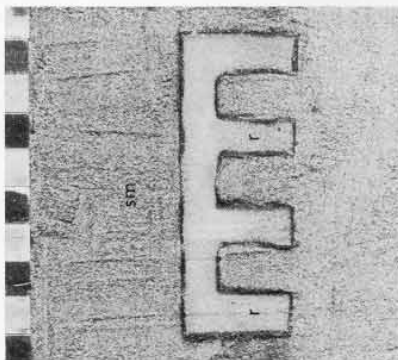
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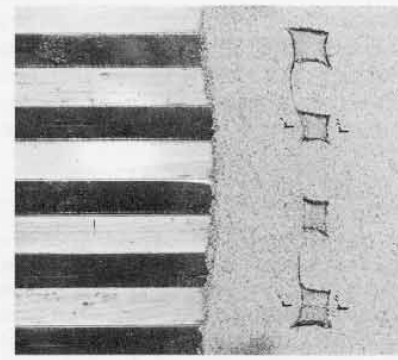
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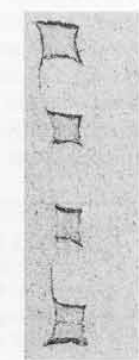
6



1



2



3

REX and CHALONER, experiments showing the compression of different plant structures

evidently not always the case since material we have collected *in situ* from Swillington Quarry (Yorkshire) (Scott 1978) shows that a groove may be present on the lower surface in some circumstances.

In fossil stigmarians of this type there are evidently three fracture planes along which plant material may be exposed (text-fig. 8). One is the (compressed) outer surface (A) the other, the outer surface of the woody cylinder (B). A specimen exposed by fractures may accordingly show outer surface with rootlet attachment at the margin and internally the exposed woody cylinder (C). Pant (1956) showed that specimens known as *Gymnostrobus* were in fact the isolated woody cylinders of *Stigmaria*, exposed by a fracture plane running along the inner surface of the stele infill (pith cast) and through the woody cylinder at either side, and not cones, as they had originally been thought to be by Lesquereux (1879–80) and Bureau (1914).

Small spirally arranged lenticular structures are seen on the surface of the exposed stele. Frankenburg and Eggert (1969) have identified in petrifications of *Stigmaria* what they call 'lateral appendage gaps' on the inner surface of the stele. These are the points from which the traces to the rootlets arose and in any transverse section are seen as small gaps which cause division of the woody cylinder into blocks. During infill of the axis these gaps filled with sediment producing the lenticular structures observed on the compression of the woody cylinder.

Experiments were constructed to see if we could reproduce this stigmarian-type fossil with its stelar groove. The model used consisted of a very thin outer cylinder of foam rubber with a thicker inner cylinder, all infilled with matrix. First, the stele was placed in a central position and compressed, the stele formed compression borders and a 'stelar groove' appeared in the upper surface of the cylinder (Pl. 33, 1–3). In a separate experiment the stele was placed at the outset towards the top of the cylinder. On compression the stele formed compression borders and became slightly asymmetric, while a furrow of the same width as the stele diameter (Pl. 33, 4–6) began to appear on the upper surface.

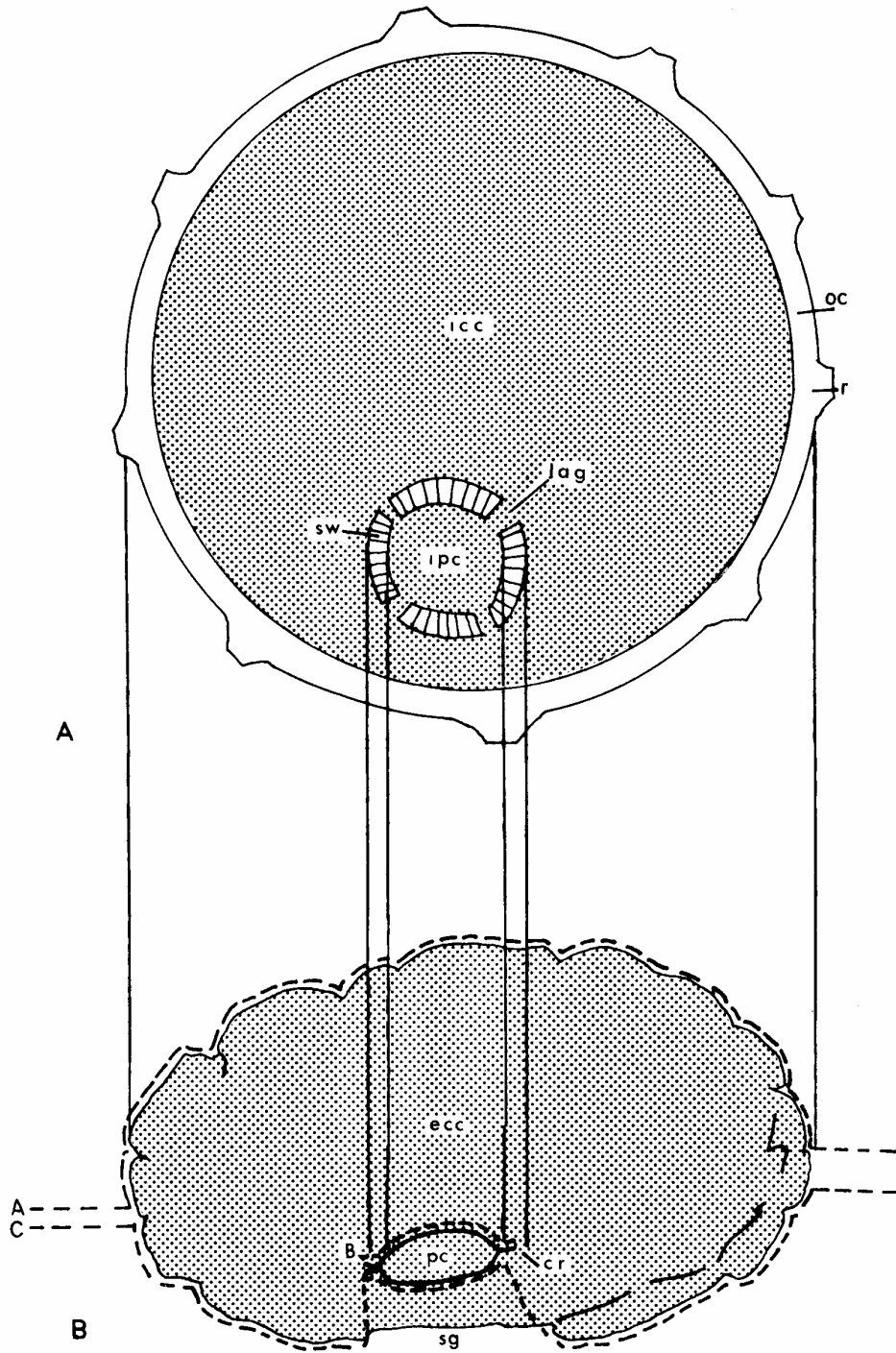
When in a further experiment the stele was placed at the bottom of the cylinder, a slight unevenness formed on the lower surface, but not a distinct groove (Pl. 33, 7–9).

It would appear that the furrow is in fact related to the presence of the stele near the upper or lower surface of the cylinder; it provides a local area of further compressibility after the sedimentary infill has compacted causing this feature of a stelar groove to be produced. It would appear that the closer the stele is to either surface of the axis, the greater the effect on the external topography of the outer surface.

CONCLUSIONS

The outcome of this preliminary excursion into the formation of compression fossils has been to show that the deformation observed in such specimens can be reproduced in a simple mechanical model. As we learn more of this interaction of collapsing plant tissue and the enclosing matrix, it should become possible to extrapolate back to the original three-dimensional form from the many compression fossils where we have no information from permineralized specimens. This is important for our understanding of the many genera of plants based only on compression or impression states of preservation.

TEXT-FIG. 8 (*opposite*). A. Diagrammatic section through an infilled Stigmarian axis. *oc*: outer cortex; *r*: rootlets; *icc*: infill of cortical cavity; *lag*: lateral appendage gap; *sw*: secondary xylem; *ipc*: infill of pith cavity. B. Compression fossil of a *Stigmaria*, showing a vertical section, drawn from a specimen found at Swillington Quarry, Yorkshire. Westphalian B. The three possible fracture planes that may expose the fossil are: (A) the fracture plane passing over the outer surface of the axis; (C) the fracture plane which exposes the outer surface of the axis and then 'jumps' into the infill to expose the outer surface of the stele compression (*sc*); (B) the fracture plane which exposes the compression of the stele only, occurring as isolated cylinders, and is the '*Gymnostrobus* state' of *Stigmaria* (see this page). *sg*: stelar groove; *cr*: compression rim; *ecc*: endocortical cast; *pc*: pith cast. $\times 1$.



One particularly important aspect of the behaviour of compressed plant material is that topography on one surface of the plant organ may be 'printed through it' during compression to appear on the opposite face. This means that a positive topography of, for example, leaf cushions on a matrix surface must not be construed as proof that outer surface is being seen; on the contrary, it is likely to be matrix which has collapsed into the site of cushions from the endocortical cavity (e.g. *Lepidodendron*). Equally, stelar features may show, in various ways, as the outer surface of a compression (e.g. *Stigmaria*).

A further complicating factor in our interpretation of compression fossils is that the configuration of the plant material itself influences the fracture surface which reveals the fossil. The way in which leafy shoots of lycopods are exposed by fracture demonstrates that the rock cleavage may be diverted from the bedding planes by the extent and angle of inclination of the coaly layers constituting the substance of the fossil. Plant compression fossils are in these various aspects very different from a 'pressed plant' lying on a fracture surface. Further experimentation using plant tissue in actual water-lain sedimentary environments is most desirable in order to substantiate (and no doubt modify) the conclusions offered here.

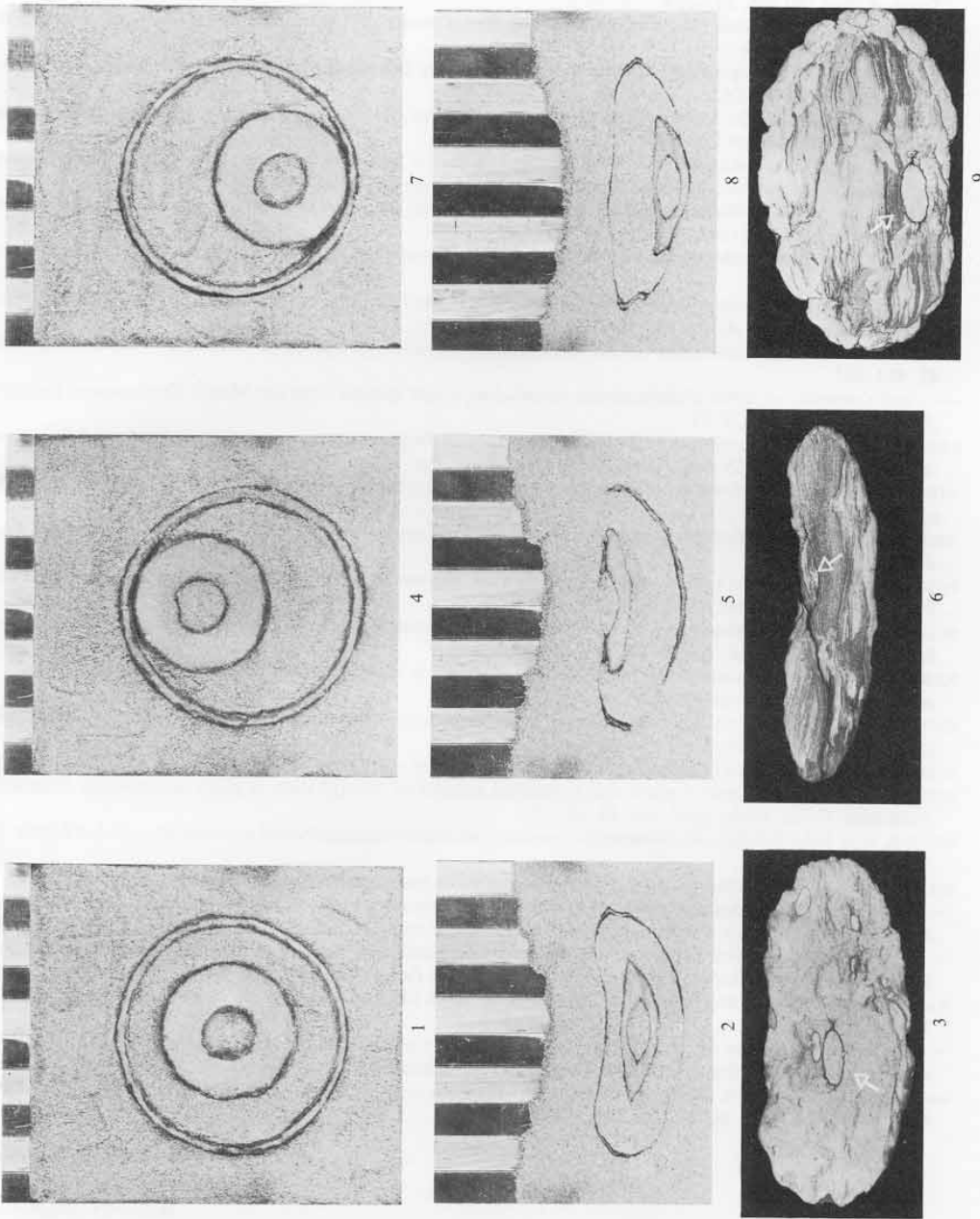
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EXPLANATION OF PLATE 33

- Fig. 1. Experiment to reproduce the Stigmarian type fossil in which the stele is central, bounded by a thin outer cortex. $\times 0.5$.
- Fig. 2. Result on compression of above; a 'stelar groove' is formed in the outer surface of the compression above the stele. The stele shows compression rims. $\times 0.5$.
- Fig. 3. Vertical section through a fossil *Stigmaria* showing central position of stele (arrow). $\times 0.75$. This and the other *Stigmaria* specimens on this plate were collected *in situ* at Swillington Quarry, near Leeds, Yorkshire (Westphalian B), so that their orientation in the matrix is known.
- Fig. 4. Experiment to reproduce the Stigmarian type of fossil in which the stele is displaced towards the upper surface. $\times 0.5$.
- Fig. 5. On compression the stele becomes asymmetric and compression rims form. A stelar groove forms in the upper surface of the compression. $\times 0.5$.
- Fig. 6. Vertical section through a fossil *Stigmaria* showing initial upward displacement of the stele (arrow), and the stelar groove lying above it. $\times 0.5$.
- Fig. 7. Experiment to reproduce the Stigmarian type of fossil in which the stele is displaced towards the lower surface. $\times 0.5$.
- Fig. 8. On compression the stele forms compression rims and a slight concavity on the lower surface of the outer cylinder is produced.
- Fig. 9. Vertical section through a *Stigmaria* in which the stele (arrow) is displaced towards the bottom of the cylinder and a stelar groove has been formed in the outer surface of the cylinder. $\times 0.75$.



REX and CHALONER, compression experiments reproducing known vertical sections of *Stigmaria*

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G. M. REX and W. G. CHALONER
 Department of Botany
 Bedford College
 University of London
 Regent's Park
 London NW1 4NS

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