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## The formation and significance of Carboniferous coal balls

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[Plate 1]

Coal balls (exceptionally preserved calcareous permineralized peat), widely described from tropical Carboniferous Euramerian coal seams, have yielded diverse data on the biology, ontogeny and ecology of swamp plants and ecosystems. Probably over 75% of the swamp taxa may have been preserved, in contrast to probably less than 10% in other contemporaneous environments, but the assemblages are species-poor and represent an evolutionarily conservative assemblage. The *in situ* nature of coal ball peats allows ecological changes to be identified from vertical profiles. Major changes in plant communities both within individual seams and between seams appear to reflect both local and widespread climatic changes, particularly in rainfall. The preservation of cell contents, plant apices, gametophytes, etc., demonstrates the contemporaneous or early diagenetic formation of coal balls. Their common association with marine sediments has supported arguments for a marine source for the carbonate. Stable oxygen and carbon isotope studies suggest a meteoric origin for some carbonate. No current model for the formation of coal balls completely explains their occurrence and rarity outside the Upper Carboniferous of Eurameria.

## 1. INTRODUCTION

Coal balls are limestone concretions encountered in coal seams which represent peat (*sensu* Cohen & Spackman 1977, 1980) that was permineralized by calcium and magnesium carbonates, before appreciable compaction or alteration took place, giving an exceptionally preserved fossil plant assemblage (Stopes & Watson 1908; Mamay & Yochelson 1962; Schopf 1975) (figures 2–5, plate 1). Coal balls not only preserve fine anatomical and histological details of the plants (figures 4, 5) but in some exceptional examples cell contents (Taylor 1977), including starch grains (Baxter 1964), nuclei (Millay & Eggert 1974), germinating spores (Scott 1904), gametophytes (Brack-Hanes 1978), pollen drops (Rothwell 1977), pollen tubes (Rothwell 1972) and plant apices (Good & Taylor 1972) have been described.

Coal balls may be regarded as permineralized peat but the remaining cell walls have usually reached the same rank as the surrounding coal (Hatcher *et al.* 1982). Peat may form under a wide range of conditions and in a variety of environments (McCabe 1984) and the permineralizing material may be carbonate, silica or pyrite (Schopf 1975). Many permineralized peats may be of small geographical or stratigraphical extent (for example, the Devonian Rhynie Chert, Scotland, the Devonian Hampshire Formation pyritized peats, West Virginia, the Tertiary Clarno Chert, Oregon) and in diverse geological settings, including volcanic terrains (for example, the Lower Carboniferous Pettycur Limestone, Scotland). In this paper we discuss

the preservation of coal balls which represent calcareous permineralized peat found in extensive coal seams.

Since their discovery in 1855 (Hooker & Binney 1855) coal balls have been found in more than 65 Upper Carboniferous coal seams at over 200 locations in nine countries (Phillips 1980), and more than 130 genera and 350 species have been described (Phillips 1980) in over 1000 publications. The first coal balls were described from the Lancashire and Yorkshire coal fields and were of Westphalian A age. In consequence much of the early work on the description of the plants they contained was undertaken by British researchers (especially Binney, Williamson, D. H. Scott). These works were beautifully summarized in the text books of Seward (1898–1919) and Scott (1920–23) and laid the foundations of research on coal ball floras. Coal balls were subsequently discovered in several European countries (for example, Belgium (Leclercq 1925), Holland (Koopmans 1934), and the U.S.S.R. (Snigirevskya 1972)) and even now many plants from these deposits remain to be described (Holmes & Fairon-Demaret 1984). The discovery of coal balls in North America (Noé 1923) led to numerous papers being published in several phases. Workers such as Schopf, Stewart, Andrews, Mamay and Baxter (Andrews & Mamay 1952) from the 1950s to 1960s demonstrated the wealth of data to be obtained from younger coal balls (mainly Westphalian D and Stephanian). More recently research has expanded rapidly and interest has centred on aspects of whole plant biology and ecology (see, for example, Pigg & Rothwell 1983; Rothwell & Warner 1984; Phillips & Peppers 1984).

There has been a significant concentration of research into coal ball floras but it may well be that these floras, which in fact contain a low diversity of taxa (Phillips & DiMichele 1981), represent a stunted flora adapted to the coal swamp environment (Rothwell & Warner 1984) and may therefore be giving a biased view on the evolution of past vegetations. Coal balls, though, offer a unique opportunity to study the biology and ecology of those plants that inhabited the coal swamp environment.

## 2. STRATIGRAPHICAL AND GEOGRAPHICAL DISTRIBUTION OF COAL BALLS

During the late Carboniferous, Europe and North America lay adjacent on the equator (Zeigler *et al.* 1981). This area belonged to the single biological province, Eurameria (Chaloner & Lacey 1973; Chaloner & Meyen 1973), where extensive tropical forest peats were deposited. It is in this region, mainly in the paralic basins (marine influenced) that coal balls are found (Phillips & Peppers 1984).

A comprehensive account of the stratigraphical and geographical distribution of coal balls has been provided by Phillips (1980) with additional data in Phillips & Peppers (1984). The oldest known coal balls come from the late Namurian of Czechoslovakia and Germany. Reported late Viséan coal balls from Northumberland (Absolam 1929) are of early Namurian age and may not be strictly coal balls. Most of the West European coal balls are of early Westphalian age but coal balls are known from throughout the Westphalian in the Donetz basin, U.S.S.R. (Snigirevskya 1972). In North America coal balls are more widespread, both geographically (from the Appalachian coal region, Illinois coal basin and interior coal province western region) and stratigraphically (mainly from the Desmoinesian and Missourian; late Westphalian to Stephanian).

From the distribution of coal balls it has not been possible as yet to identify for certain the

numerous controls on their origin. Recent discoveries of coal balls in the late Carboniferous of China promise an excellent comparison of swamp vegetation from another palaeobiological province (Cathaysian) (Tian 1979).

### 3. PRESERVATION, DIAGENESIS AND TECHNIQUES OF INVESTIGATION

Coal balls generally occur as isolated masses of carbonate usually spherical in shape of varying size, which may be distributed vertically or horizontally through a coal seam (figure 2).

While most coal balls were formed *in situ* within peats and remain in place, now occurring within coals, rarely they may be found reworked. At Stubenville, Ohio, coal balls occur in the Duquesne Coal (Rothwell 1976) in their original place of formation. In addition, channels cut the seam in which coal balls occur. These coal balls contain a similar flora to those *in situ* in the seam and have been reworked and rounded soon after their formation as the overlying sediments have been deposited on top of both the coal and channel (R. H. Mapes and G. Rothwell, personal communication).

Early work on coal balls relied on ground thin-sections. The development of the peel technique (Walton 1928) enabled many more sections to be prepared from each specimen. The introduction of the rapid peel technique in the mid 1950s (Joy *et al.* 1956) considerably speeded up palaeobotanical coal ball studies and has contributed to the increased output of research. These techniques are well described by Stewart & Taylor (1965) and by Phillips *et al.* (1976).

The vast majority of coal ball studies have been undertaken from coal balls collected from coal tips (Andrews & Mamay 1952). Recent interest in palaeoecological aspects has encouraged collection *in situ* within coals. This is especially useful when the coal balls dominate a coal seam and enable plant community changes to be identified. The technique of identifying and colour-coding coal ball zones has been developed by Phillips and his coworkers (Phillips *et al.* 1977; Phillips & DiMichele 1981). In the laboratory, percentage volume of taxa have been measured using a grid system on representative peels (Phillips *et al.* 1977).

For botanical investigations, slabbing and peeling of selected coal balls remains the standard technique. Deep etching in 5–10% (by volume) HCl and saturated EDTA has enabled the liberation of *in situ* spores (Taylor & Millay 1969; Courvoisier & Phillips 1975). Deep etched blocks can also be studied by s.e.m. (Chican *et al.* 1981). Ultrastructural studies of spores by using the t.e.m. have also been done (Taylor & Millay 1977). The serial sectioning and peeling through plant organs have revealed detailed anatomical structure and resulted in painstaking reconstruction of fossil plants (Holmes 1977, 1981). Generally information on the overall morphology of fossil plants comes from the study of fossils preserved as compressions. In some cases the same genus or even species has been studied in both preservation states (Galtier & Scott 1979). The development of microvibrotool techniques (Rothwell 1980) has allowed the morphology of some organs (for example, pteridosperm leaves) to be studied in addition to their anatomy (Mickle & Rothwell 1982; Beeler 1983). Other modern techniques such as bulk geochemistry and stable isotopes are opening new avenues of research into the problem of coal ball formation (Anderson *et al.* 1981).

#### (a) Previous preservation studies

Despite the vast literature on coal ball plants few papers have considered the nature and mechanics of coal ball preservation. The formation of coal balls has really remained an unsolved

problem in palaeobotany since their discovery by Hooker & Binney (1855). The earliest paper on the chemistry of coal balls was that of Stocks (1902). He also conducted the earliest experiments on carbonate permineralization and demonstrated that calcium carbonate was precipitated from sea water onto vegetable matter. This work was followed by the classic paper of Stopes & Watson (1908) on coal ball formation. They undertook detailed chemical analyses, conducted experiments and made detailed field observations. They conclude from this work that, first, coal balls formed *in situ* and, second, that sea water acted as an initial preservative and also as a source for calcium and magnesium carbonate ions. Stopes & Watson were firmly convinced that coal balls formed as a result of marine influence. Lomax (1902) was of the opposite opinion and proposed that the plant material and probably the coal balls had suffered transport and had not formed *in situ*.

One of the main problems in the discussion of coal ball formation is the source for the vast amount of carbonate permineralizing fluid that led to the formation of the coal balls. Several hypotheses have been made and the source has been attributed to a marine origin (Stopes & Watson 1908; Noé 1931; Mamay & Yochelson 1962; Perkins 1976) or to an indirect ground water origin (Feliciano 1924; Evans & Amos 1961; Phillips & DiMichele 1981) (figure 1*a-c*).

Mamay & Yochelson (1962) first reported on marine animal remains within coal balls from North America. They demonstrated that coal balls were not as uniform in composition as had been previously assumed and recognized three types of coal ball: (i) normal, containing only plant remains; (ii) mixed, containing animal and plant remains and (iii) faunal, containing only animals. They proposed that the mixed coal balls had been formed by marine mud rollers containing animal remains flung by wave action into the swamp. Assuming this mud was calcareous it may have provided a source of carbonate for normal coal balls and that local pH changes may have dictated the precipitation of carbonate. It is interesting to note that in the coal balls of the Westphalian of Britain and Europe marine animals are exceedingly rare and in fact only one coal ball containing animal remains has been described (Holmes & Scott 1981).

The variation in preservation of coal ball plants prompted Perkins (1976) to suggest that the transport of plant fragments was important. What is perhaps more influential on the preservation is the timing of their formation. Permineralization may have taken place at any time during or after peat formation as late as during the peatification stage or early enough for the process to have resulted in the death of the swamp plants. It is particularly in the latter example that exceptionally fine preservation may be found.

The most recent investigation of coal ball formation was by Anderson *et al.* (1981) who undertook stable oxygen and carbon isotope analyses of coal balls. Their results indicated that the permineralizing fluids were probably derived from a meteoric source but some marine influence was also possible. They could add nothing to the earlier proposals regarding sources of the carbonate.

#### (b) *The present study*

In the present work detailed petrological studies have been made on normal and stained thin sections (by using the technique of Dickson (1966)) on coal balls from a range of localities from the Westphalian A of Britain (Deerplay, Clough Foot, Hough Hill, Hapton Valley, Hill Top, Rowley, Shore, Townley, Old Meadows) and Europe (Bouxharmont (Belgium) and Finefrau-Nebenbank (Netherlands)). Also a number of sections from the Pennsylvanian of North America (Middle Pennsylvanian of Lewis Creek, East Kentucky; Mapel Grove, Indiana;



Lynneville, Indiana; Herrin no. 6 Coal Illinois and the Upper Pennsylvanian Duquesne Coal, Stubenville, Ohio).

By using these sections under normal and polarized light the petrology, mineralogy and generations of carbonate cement within the coal balls could be determined. The stained sections (with Alzarin Red–Potassium Ferricyanide) indicated the chemistry, and its variation, of the carbonates within the coal balls. Recent collections from the tip-heaps at Deerplay, north of Bacup, Lancashire, enabled sections to be made from a number of coal balls from the same locality and hence enable the variation in the mineralogy and chemistry to be observed. Sections were also prepared through single coal balls to examine the variation in the chemistry and mineralogy.

One of the most surprising features resulting from this study was the uniformity in the crystal structure of the carbonate between the coal balls from all the localities examined. In all the sections examined the dominant carbonate was in the form of fine fibrous crystals (figure 7, plate 1). This fibrous carbonate was best developed where there had been initial voids in the peat, such as pith cavities within axes, cortical cavities within stigmarian or *Psaronius* rootlets, sporangial cavities in *Lepidocarpon*, or voids where the peat was initially uncompacted (figures 1 *d*, 6). The mineralization had frequently nucleated on the organic walls of plant organs and then radiated out into the cavities within the peat (figure 7). This radiating fibrous crystal growth commonly showed zoning structures indicating that crystal growth occurred in a series of pulses as a result of fluctuations in the presence of the permineralizing fluid, that is, crystallization was not continuous from a single carbonate solution. The fibrous calcite was developed into 'zones' which were not intergrown but separated by distinct margins (figure 8). At the cellular level the cells were not filled with a single crystal but contained numerous fine, fibrous crystals which were optically continuous between cells. This fibrous carbonate dominated all the coal ball sections examined. Less common are subanhedral crystals of sparite. Sparite is always present within late veins that cross-cut the coal balls but was occasionally present filling fractures within the plant organs (figure 9). These may represent late fracturing of the tissues possibly resulting from compaction or shrinkage of the peat. Sparite is also present at the centre of some void fills, the bulk of the fill being composed of the fibrous carbonate, indicating that the sparite crystallized after the fibrous carbonate.

Recrystallization of the fibrous carbonate within the coal balls was rarely observed. Only in a few cases was there evidence of recrystallization. In these cases sparite had recrystallized at the expense of the fibrous carbonate. This had mainly occurred at the margins of the fibrous carbonate 'zones' (figure 1 *d*). The only coal balls examined in this study that showed extensive recrystallization were those from Finefrau–Nebenbank (Holland). In these coal balls the primary carbonate was in the form of the fibrous crystals but this had suffered extensive recrystallization to numerous small rhombs of dolomite that were abundant in the sections. This development of secondary dolomite resulted in the destruction of fine cellular detail and is indicated by the overall poor preservation of these Dutch coal balls described by Koopmans (1934). This extensive secondary dolomitization was well developed in all the Dutch coal balls examined but was not observed in the British or American coal balls studied.

The chemistry of the carbonates forming the coal balls varied from dolomite through to ferroan calcite but calcite was the most common carbonate mineral. Much of the fibrous carbonate was calcite. Fibrous ferroan calcite often filled the centres of voids that were composed entirely of fibrous calcite. Where sparite was developed at the centres of void fill,

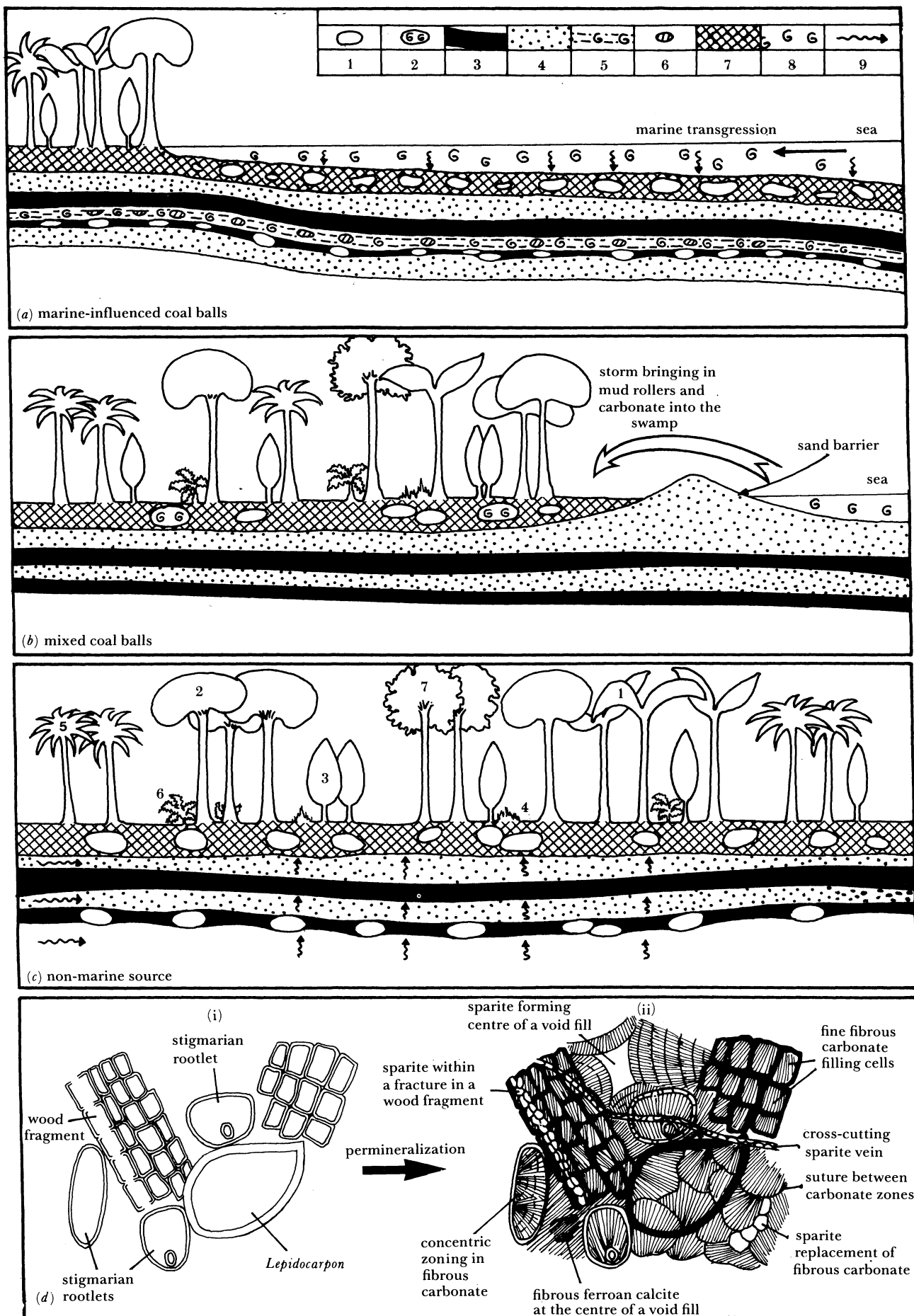


FIGURE 1. For description see opposite.

it was composed of ferroan calcite. Therefore the late permineralizing fluids seem to have been enriched in iron. It is not possible though to give any indication of the timing between these two generations of calcite but it appears likely that they were not separated by any extensive time interval. In other sections examined this relationship between the 'earlier' formed calcite and the 'later' ferroan calcite is not so well defined and it seems that in some cases both minerals were crystallizing out of solution at the same time. Therefore, there seems to have been small scale local fluctuations in the chemistry of the permineralizing solutions within the peat.

Examination of 15 sections from 15 coal balls from Deerplay showed that the mineralogy and chemistry was identical between the coal balls. Again fibrous carbonate was the dominant mineral but this had the composition of slightly ferroan dolomite. Since dolomite crystallizes as rhombs then it appears that these coal balls have undergone secondary dolomitization probably from calcite. Hence these coal balls have suffered a secondary chemical change but this was not accompanied by a physical recrystallization. Examination of sections through a single coal ball indicated that the mineralogy and chemistry was constant throughout the entire coal ball, for example, a coal ball from Townley (Lancashire, U.K.) was composed entirely of fibrous calcite with 'later' ferroan calcite filling the centre of each void. Iron pyrites is a common mineral within coal balls and is often seen filling late fractures within the peat. The presence of pyrites has been considered to represent reducing conditions within the peat (Perkins 1976).

In conclusion, the structure of the carbonate is very similar throughout all the coal balls examined. The dominant carbonate is always fibrous in form and frequently is calcitic in composition. A maximum of two generations of carbonate have been observed. This usually consists of an 'earlier' calcite phase and a 'later', usually minor ferroan calcite phase which may be fibrous or in the form of sparite. Dolomitization occurred after the fibrous carbonate crystallized and most dolomitic coal balls appear to have formed from the chemical alteration of fibrous calcite without any recrystallization. Only in the Dutch coal balls was secondary dolomitization accompanied by rhomb growth and this resulted in the destruction of cellular

#### DESCRIPTION OF FIGURE 1

FIGURE 1. Postulated models for the formation of coal balls. Explanation of key: 1, coal ball; 2, mixed coal ball; 3, coal seam; 4, sediment between coal seams; 5, marine shale; 6, roof nodule; 7, uncompacted peat; 8, goniatites; 9, pathway of the carbonate-rich permineralizing fluids.

(a) Marine influenced coal balls (after Stopes & Watson 1908). In this model coal ball formation is directly related to a marine transgression that drowns the coal swamp. Carbonate is precipitated directly from the sea water into the uncompacted peat. Each coal-ball-bearing seam must therefore be overlain by a marine shale.

(b) Mixed coal ball formation (after Mamay & Yochelson 1962). The sea and coal swamp are separated by a barrier which is breached during a storm. This brings carbonate-rich mud and animal remains into the swamp. Carbonate is precipitated into the peat from the mud and result in the formation of plant-bearing and animal-bearing coal balls; coal ball with marine cores being common.

(c) Non-marine formation of coal balls. In this model the carbonate-rich permineralizing fluids are derived from a non-marine source such as an aquifer or ground water supply. These fluids permeate the peat and precipitate carbonate. The typical coal swamp vegetation is represented diagrammatically (1, *Sigillaria*; 2, *Lepidodendron*; 3, *Calamites*; 4, *Sphenophyllum*; 5, tree ferns; 6, pteridosperms; 7, *Cordaites*) and no implications of palaeoecology are implied.

(di) Diagram of unpermineralized peat showing various plant organs and voids within the peat.

(dii) Diagram showing the common mineralogical textures within coal balls. The fibrous carbonate dominates, it is frequently concentrically zoned and is developed into distinct zones separated by sutures. Sparite may be contemporaneous with the fibrous carbonate, or represent the late filling of fractures, or be replacing the fibrous carbonate.



detail. Therefore there seems to have been late Mg-rich fluid permeating the peat. The mineralization was often well developed associated with stigmarian rootlets and it appears that these may provide channels or pathways through the compacted peat for the permineralizing fluids. It would appear from this study that mineralization occurred at different times during peatification, in some cases early, exquisitely preserving the fine detail of the plant organs, but at other times after the peat had begun to decay and compact; this resulted in poorly preserved plant tissues within the coal balls. The fact that the vast majority of coal balls are solid suggests that carbonate migrated from a central place but may have had several nucleation points, the calcite coalescing to give a solid structure.

Klappa (1980) has described 'root petrifications' (rhizoliths) from Quaternary calcretes in which the cell voids are filled with needle fibres of calcite (p. 625). He also considers that the middle lamella of the cell walls, which originally contained calcium pectate, is a preferential site for calcification. Growth of calcium carbonate would, therefore, be expected to be initiated from such calcium rich 'templates' (Klappa 1980, p. 627). The process of calcite precipitation may take place during the life of the root or during its decay (Klappa 1980). The observation in coal balls that the nucleation of calcite needle crystals is often seen on plant cell walls (figure 7) may be significant. There are many problems concerning coal ball formation that are not easily answered.

(i) Coal balls, in the restricted sense used here, are unique in their preservation and have not been discovered outside the Carboniferous. They differ significantly from limestones from other sedimentary provinces.

(ii) In Britain and Europe most coal balls occur in the Westphalian A (in Europe they also occur at the B-C boundary) whereas in North America they are found throughout the Pennsylvanian. This may imply some tectonic or climatic control on coal ball formation. Also the lack of marine organisms within European coal balls contrasts strongly with American coal balls where marine organisms are common. This indicates that conditions were not uniform

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#### DESCRIPTION OF PLATE 1

FIGURES 2-9. Illustrations of Upper Carboniferous coal balls.

FIGURE 2. *In situ* coal balls in the Uppeleaf of the Springfield no. 5 Coal, Eby Pit, Lynville, Indiana.

FIGURE 3. Cut coal balls in coal matrix from an unnamed coal in the Tradewater Formation, Middle Pennsylvanian, Mapel Grove, Indiana. (Magn.  $\times 0.5$ .)

FIGURE 4. Typical British coal ball with abundant lycopod remains including *Lepidostrobus*, Westphalian A, Lancashire. (Magn.  $\times 2$ .) BMNH, D. H. Scott Collection, 2835.

FIGURE 5. Thin section of a coal ball showing pteridosperm and fern axes with stigmarian rootlets, Westphalian A, Lancashire. (Magn.  $\times 2$ .) BMNH, D. H. Scott Collection, 935.

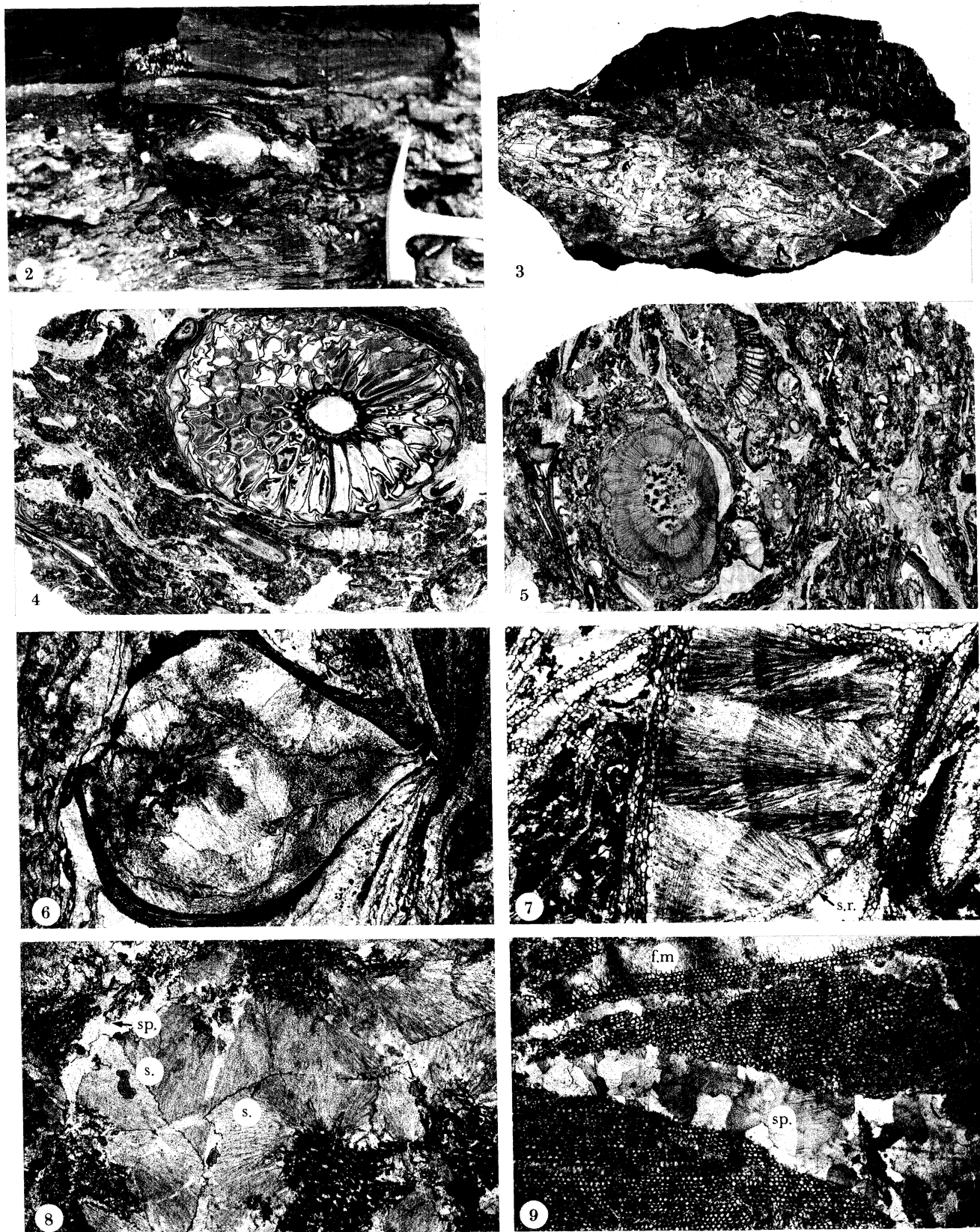
FIGURE 6. Thin section of an American coal ball from Kentucky in cross-polarized light showing the typical development of fibrous carbonate within an original cavity in the peat, in this case a *Lepidocarpon*. (Magn.  $\times 12$ .)

FIGURE 7. Thin section of a British coal ball from Deerplay, Lancashire, in cross-polarized light showing fibrous carbonate present within the pith cavity of a stigmarian rootlet (s.r.). The fine, radiating carbonate is concentrically zoned. (Magn.  $\times 15$ .)

FIGURE 8. Thin section of a British coal ball from Shore, Lancashire, in cross-polarized light showing the sutures (s.) that form between the carbonate zones. Some of the fibrous carbonate has been recrystallized to sparite (sp.). (Magn.  $\times 17$ .)

FIGURE 9. Thin section of a British coal ball from Deerplay, Lancashire, in cross-polarized light. The carbonate is in the form of large sparite (sp.) crystals. Fibrous carbonate (f.m.) is also present within the section. (Magn.  $\times 20$ .)





FIGURES 2-9. For description see opposite.

(Facing p. 130)



across the Euramerian coal province. The uniform nature of the mineralization within the coal balls, does, though, seem to indicate that the source of the permineralizing fluid was similar across the entire coal province.

(iii) Coal balls are not constant in their occurrence but occur within some seams and not in others. Their distribution also varies within a single seam. Carbonate must therefore have been precipitated at very precise conditions within the peat probably as a result of a sophisticated mixing process of fluids derived from marine and non-marine sources resulting in the precipitation of carbonate within the coal basin.

#### 4. PLANT BIOLOGY

Most early workers concentrated on the anatomical description of coal ball plants (see, for example, Scott 1906) and emphasis lay on taxonomy and affinity. More recently emphasis has been placed on whole plant reconstructions and an attempt to understand the biology of the plants (see, for example, Rothwell 1981; Rothwell & Warner 1984, which had begun with the pioneering work of Oliver & Scott (1904)). Despite many monographic studies relatively few plants have been reconstructed (but see Ramanujam *et al.* 1974; Stewart & Delevoryas 1956; Rothwell & Warner 1984). While we know the broad affinities of many plant organs we can put together only a handful of whole plant species. This relates to a general problem with plants where organs (leaves, stems, roots, fertile organs) easily become separated before or during the fossilization process. Techniques in the reconstruction of individual whole plants involve foremost the discovery of the connection of plant organs, often using a large number of specimens (see, for example, Rothwell 1981; Holmes 1977, 1981; Rothwell & Warner 1984). Another approach that attempts to make generalized reconstructions of broad plant types uses a technique of common association and anatomical similarity of plant parts (DiMichele 1981). As a result we still have relatively few whole plants reconstructed from coal balls despite the vast output of research over a considerable period of time. It is perhaps worth emphasizing that whole plant species are rare, but most coal ball organs can be related generically with other parts of the 'whole plant genus' to which they belong.

The reproductive biology of these coal ball plants is of current interest (Taylor 1983). There has been considerable discussion on the relation of lycopod reproductive biology and ecology. Phillips (1979) in an elegant paper argued strongly for a close relationship between lycopod sporophyll morphology and anatomy to their adaptation to standing water. He concluded that the sporophylls borne by *Lepidophloios* were adapted to wetter conditions than those of *Lepidodendron* and *Paralycopodites*. This interpretation has led Phillips to a number of important palaeocological conclusions (Phillips & DiMichele 1981; Phillips & Peppers 1984) concerning the plants growing in the swamp, that is, *Lepidophloios* was adapted to living on the wetter areas of the swamp whereas *Lepidodendron* was adapted to life in drier habitats. Thomas (1981) challenged Phillips's (1979) interpretations preferring a wind dispersal adaptation for the sporophylls. Clearly the implications of each biological model has significant implications for ecological interpretation.

The exquisite preservation of plant apices, gametophytes and various growth stages of coal ball plants throw new light on the process of ontogeny in these plants. In particular the discovery of a determinant growth pattern in the arborescent lycopods was of major biological significance (Andrews & Murdy 1958; Eggert 1961). For ontogenetic studies coal balls offer a treasure house

of data (Delevoryas 1964). In a review of palaeobotany in the 1970s Knoll & Rothwell (1980) list 21 taxa which had been investigated with regard to ontogeny. Seventeen of these were of coal ball plants. The continued application of new techniques and discovery of new material will lead to further work on the biology of these plants.

### 5. ECOLOGY

A major development over the past 15 years has been the increase of palaeocological studies. In the marine roof shales of the British early Westphalian coal seams that yield coal balls (and indeed some that do not) nodules occur (called roof nodules or bullions) which are cemented by carbonate and which contain a marine fauna including goniatites together with permineralized plants. D. H. Scott noted in several papers (for example Scott 1906) that plants found in the roof nodules of the Upper Foot seam in Lancashire differed from those in coal balls from the coal at the same locality. This was strikingly seen at Shore, Littleborough where Stopes & Watson (1908) recorded eight species found in the roof nodules and not in the coal balls. The taxa included the genera *Sutcliffia*, *Tubicaulis* and *Mesoxylon*. They made the first palaeocological interpretation of the coal-forming environment and concluded that 'coal balls in the coal are the relics of a forest which grew quietly in a swamp in places where they are now found, while the plants in the shales and in the roof nodules above had drifted out to sea from other districts and bear in the character of their structures the impress of the different types of land on which they lived'. Coal ball floras from the Westphalian A of Lancashire are dominated by arborescent lycopods. 'Roof nodule' floras are, however, dominated by pteridosperms and ferns. This ecological distinction between swamp and non-swamp floras is now widely recognized (Scott 1978; Phillips 1981).

Most of our recent knowledge of the ecology of the vegetation preserved in coal balls comes from the work of T. L. Phillips and his coworkers (Phillips *et al.* 1977; Phillips 1981; Phillips & DiMichele 1981; Phillips & Peppers 1984). Phillips had used both old museum collections as well as extensive quantitative field sampling. This approach has been combined with palynology of the associated coals to give an overview of late Carboniferous swamp vegetation (Phillips & Peppers 1984).

On a local scale detailed vertical sampling has allowed changes in the swamp vegetation through the seam to be analysed. Phillips *et al.* (1977) demonstrated the changing percentage of different plant organs. Phillips & DiMichele (1981) were, however, unable to identify any successional relationships in the vegetation. No overall pattern of peat development could be deduced. The distribution and ecology of the cordaites has aroused considerable interest. There are arguments for both coastal and upland species (see Scott 1977, 1979) but there is substantial evidence to suggest that some species lived in brackish mangrove-like habitats (Raymond & Phillips 1983; Rothwell & Warne 1984). Changes in vegetation at such sites indicated by the vertical profiles might also be caused by salinity variation, in addition to the other common effects of droughts and fires.

Phillips & Peppers (1984) have also considered the longer scale vegetational changes in coal swamp ecology based upon both coal ball and palynological studies. Phillips and others (Phillips *et al.* 1974; Phillips & Peppers 1984) have concluded that there is a major drying episode at about the Westphalian–Stephanian boundary. This is illustrated by the extinction of wet-adapted lycopods such as *Lepidophloios* and *Lepidodendron* and the rise to dominance of the



tree ferns (*Psaronius*) in swamp vegetation. These observations appear to reinforce Phillips's (1979) interpretations regarding the reproductive biology of these arborescent lycopods. It is also interesting to note that those taxa that were recorded from the Westphalian A roof nodules representing plants living outside the swamps were progressively introduced into the swamps through the later Carboniferous. Significantly the tree fern *Psaronius* belongs to this group.

Most forest communities show an ecological stratification. In forests, plants may be ground-dwelling, climbers, lianas, etc. It is clear that the representation of some of these elements may be small in coal balls. The roots of various ground-dwelling taxa together with trunks will tend to dominate assemblages. More delicate leaves and reproductive organs that lived above ground may be abundantly represented in some coal balls and some groups such as lianas may also be identified (for example, some species of *Medulosa*, Baxter (1949)). Equally the wettest (?*Lepidophloios*) communities will be species-poor with few floor-dwelling taxa while drier habitats may support more diverse communities. Such biased representation of the swamp assemblages must be considered when trying to assess ecosystem dynamics.

While many types of plants have been described from coal balls it is surprising that almost no terrestrial animals have been found. Only a few arthropod cuticles have been reported and Scott & Taylor (1983) point out that it is probably a lack of using the right technique rather than their real absence. There is abundant evidence of plant–animal (arthropod) interaction in coal ball biotas (Taylor & Scott 1983; Scott & Taylor 1983). This consists of damage to plant tissue, coprolites and certain aspects of plant anatomy and morphology. Coprolites of various sizes containing plant material are very abundant (Scott & Taylor 1983) and have many similarities to those produced by mites, collembola and millepedes in modern soil ecosystems. Similar occurrences are known from the Devonian (Rolfe 1980).

## 6. DISCUSSION AND CONCLUSIONS

Coal balls represent peat permineralized by carbonate found in the humic coals of late Carboniferous age predominantly in Europe and North America and are an excellent example of fossil Lagerstätten. The carbonate was deposited before appreciable compaction occurred possibly even while the peat was still forming. This is demonstrated by the exceptional preservation of some plant tissues. The mineralization within coal balls is surprisingly uniform across the Euramerian province. The predominant carbonate (usually calcite) is always developed as fine, fibrous crystals (figure 7). Ferroan calcite is a minor component in most coal balls and crystallized slightly later than the calcite forming in the centre of voids. Dolomitic coal balls formed as a result of a secondary chemical alteration of the fibrous calcite and this occurred in most cases without any recrystallization of the fibrous calcite. Secondary dolomitization, though, within Dutch coal balls from Finefrau–Nebenbank was accompanied by recrystallization of the fibrous carbonate resulting in the destruction of fine cellular detail. Therefore, there seems to have been late permeation of the peat by Mg-rich solutions resulting in secondary dolomitization.

A basic problem in our understanding coal ball formation is the path that the carbonate-rich waters may have taken through the peat. From this study it is most clearly developed associated with original voids in the peat and early crystallization was apparently nucleated on plant tissues. The most well preserved plant tissues showing exceptional details appear to have been

permineralized very early before any decay processes had begun. There is a range in the degree of good preservation within coal balls and it appears that the permineralizing fluids permeated the very compacted peat along channels provided by hollow stigmarian and *Psaronius* rootlets.

A major problem remains; all coal balls are solid and permineralized throughout and yet only rarely form 'beds' and generally occur in zones within the coal seams. The larger coal balls are sometimes composed of aggregates of smaller coal balls and sometimes plant structures may be followed from one coal ball to another. Therefore, there seems to have been a considerable fluctuation in the chemistry of the water within the swamp and that only at very precise conditions within the peat was carbonate precipitated.

Numerous authors have suggested a marine origin for the permineralizing carbonate by using the occurrence of marine roof sediments to the coals and marine animals in some coal balls as evidence. Stable isotopic evidence has also been used to suggest that while some carbonate is certainly of marine origin other carbonate is probably of meteoric origin. There is no modern analogue for coal ball formation. The original source and hence control of carbonate distribution remains problematical (figure 1*a-c*).

The abundant interbedded limestones between coal seams in both the U.S.A. and U.S.S.R. might help explain the abundance of coal balls there, and their relative scarcity elsewhere, but the conclusion that at least some carbonate has a non-marine origin causes some difficulty in establishing a single source and mechanism. The close relationship between coals and marine sediments in the Namurian (Limestone Coal Group) of Scotland might have favoured the formation of coal balls. None has, however, been recorded and the rarity of limestones in the sequence (Francis 1983) might explain this. Much more work on petrology, geochemistry and isotopic composition is needed to help answer these questions. We have as yet no idea what controls the size and distribution of coal balls. The role of dolomite and pyrite in coal ball formation is equally unclear but recent work by Perkins (1976) and Love *et al.* (1983) suggests that at least some of the pyrite may have been an original permineralizing agent rather than being a calcite replacement. Equally problematic is the stratigraphical distribution of coal balls in Europe and North America. Why do they occur in some coals and not others? Their distribution seems to indicate a distinct fluctuation of conditions of water (whether marine or meteoric) within the swamp, the details of which remain obscure.

The flora preserved in coal balls is that of a tropical or subtropical swamp vegetation which may be regarded as a specialist habitat with a restricted flora compared with other lowlands (Phillips 1979). The exceptional preservation of the plants tends to overemphasize the importance of the flora when considering the overall vegetation. The consideration of plant diversity based on coal ball and compression records must be treated with caution. It has been asserted by Niklas *et al.* (1980) that diversity curves from coal ball data would tend to give an overestimate for the Carboniferous. The problem remains that the vegetation preserved in coal balls represents the most complete data set for any plant habitat.

While we have some comparisons with coal balls with regard to the preservation of an ecosystem, for example, the early Devonian Rhynie Chert or the Tertiary Princeton Chert or Clarno Chert, none of these is widespread geographically or extends over a comparable age range.

Coal balls offer a unique opportunity to examine detailed biological and ecological changes in one environment over a 20 Ma time span. This, in turn, has tended to overemphasize the importance of coal ball plants within an evolutionary context. We emphasized that the swamp

habitat was probably an evolutionary conservative one (see also Knoll, this symposium) and that major evolutionary innovations probably took place within other environments (for example, extra basinal lowlands). The abundance of material, exceptional preservation and ease of study have all contributed to the expansion of coal ball research. In spite of these comments it is clear that much work needs to be done on the coal ball plants, their ecology and preservation. Coal balls will certainly remain one of the most important sources for Carboniferous plants of the palaeotropics and also continue to provide important detailed data on extinct plant groups.

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## REFERENCES

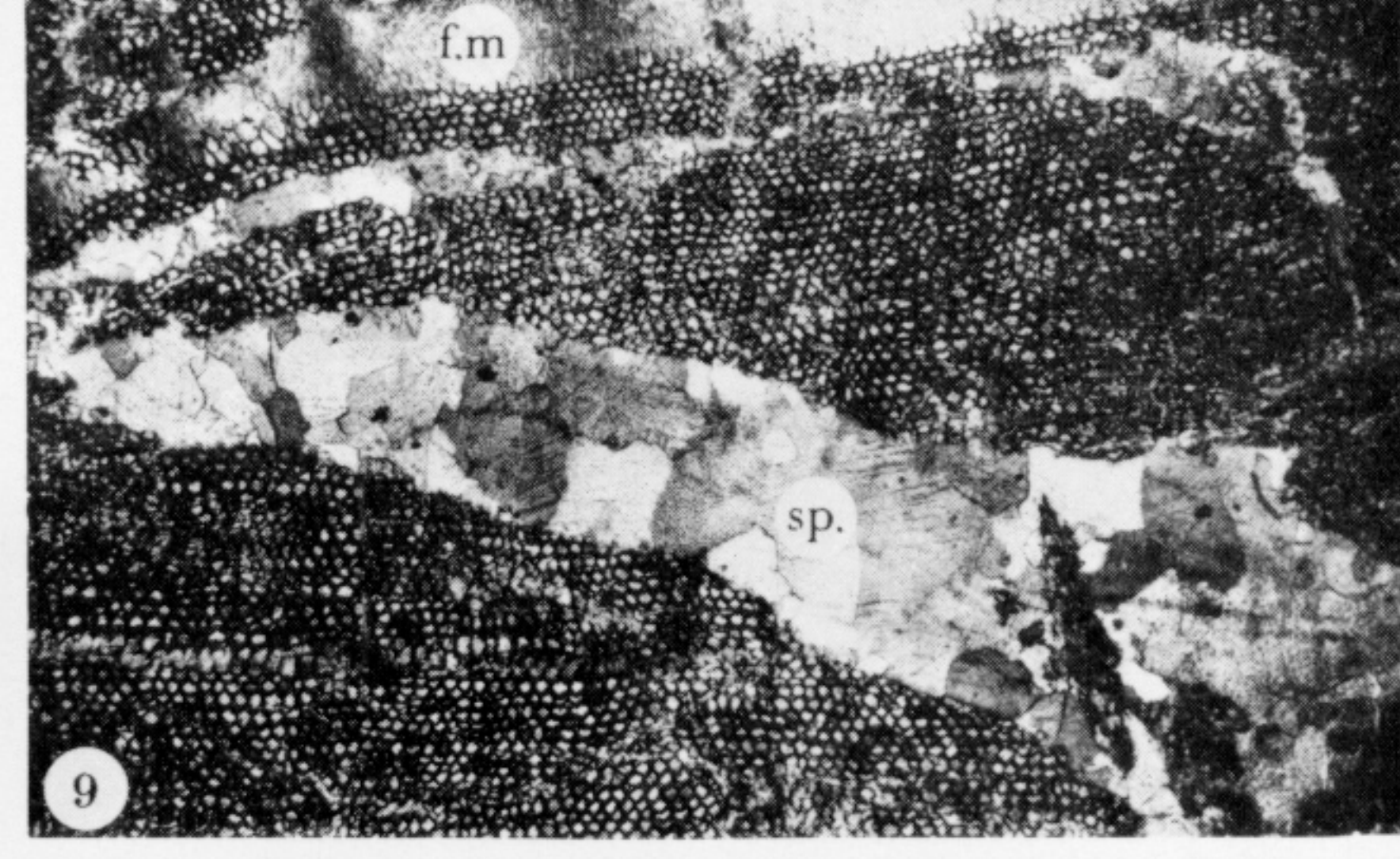
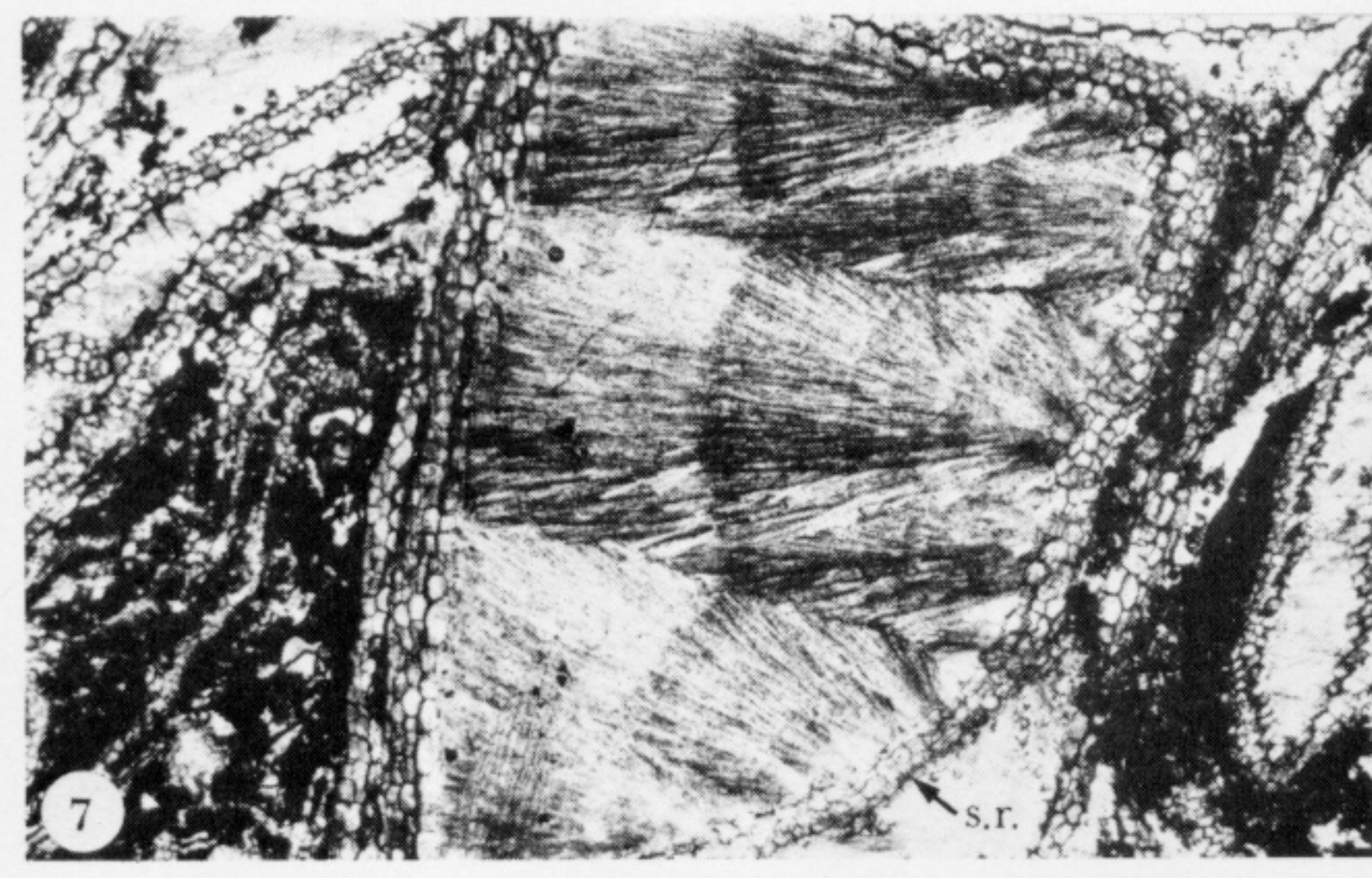
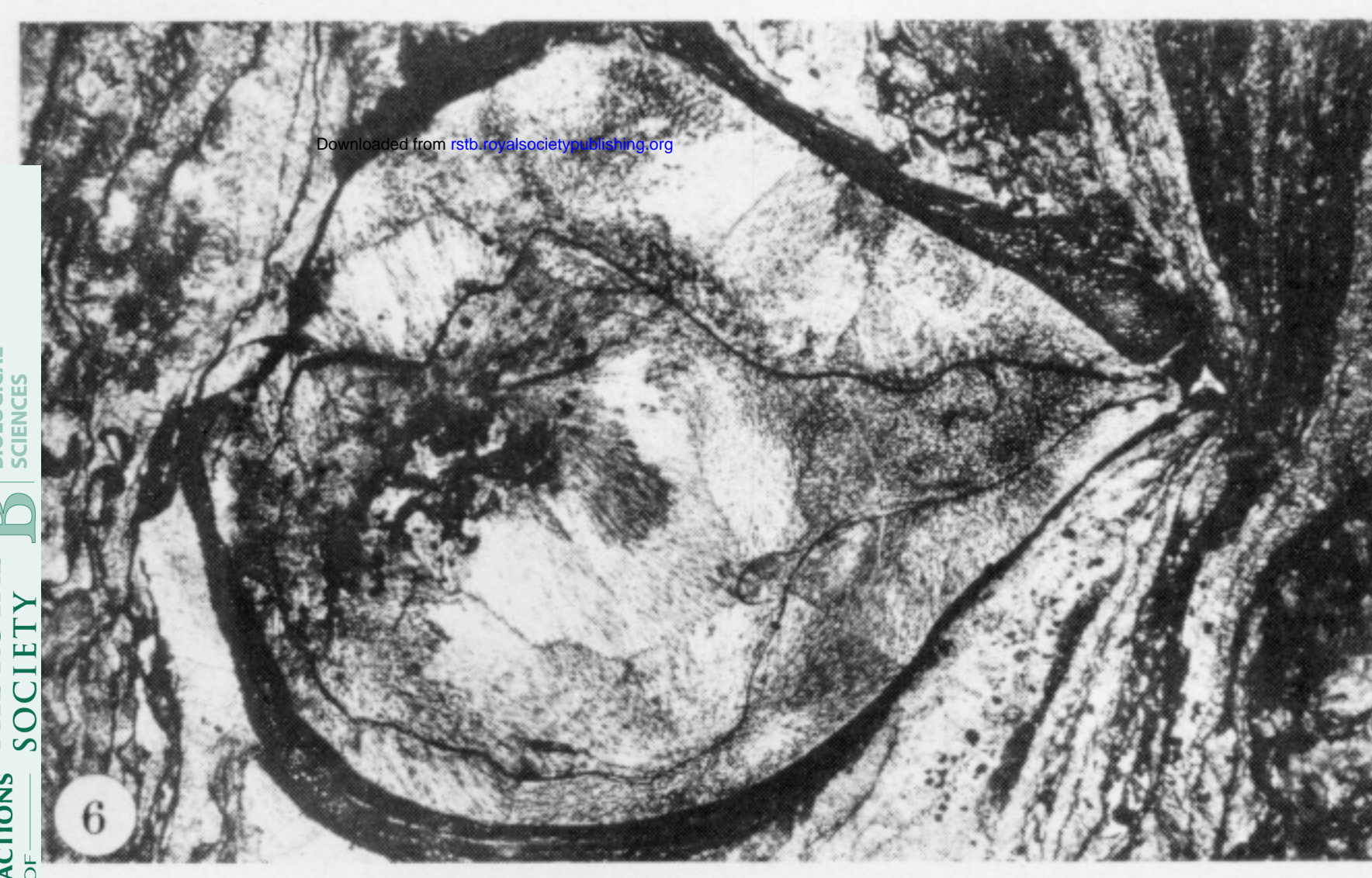
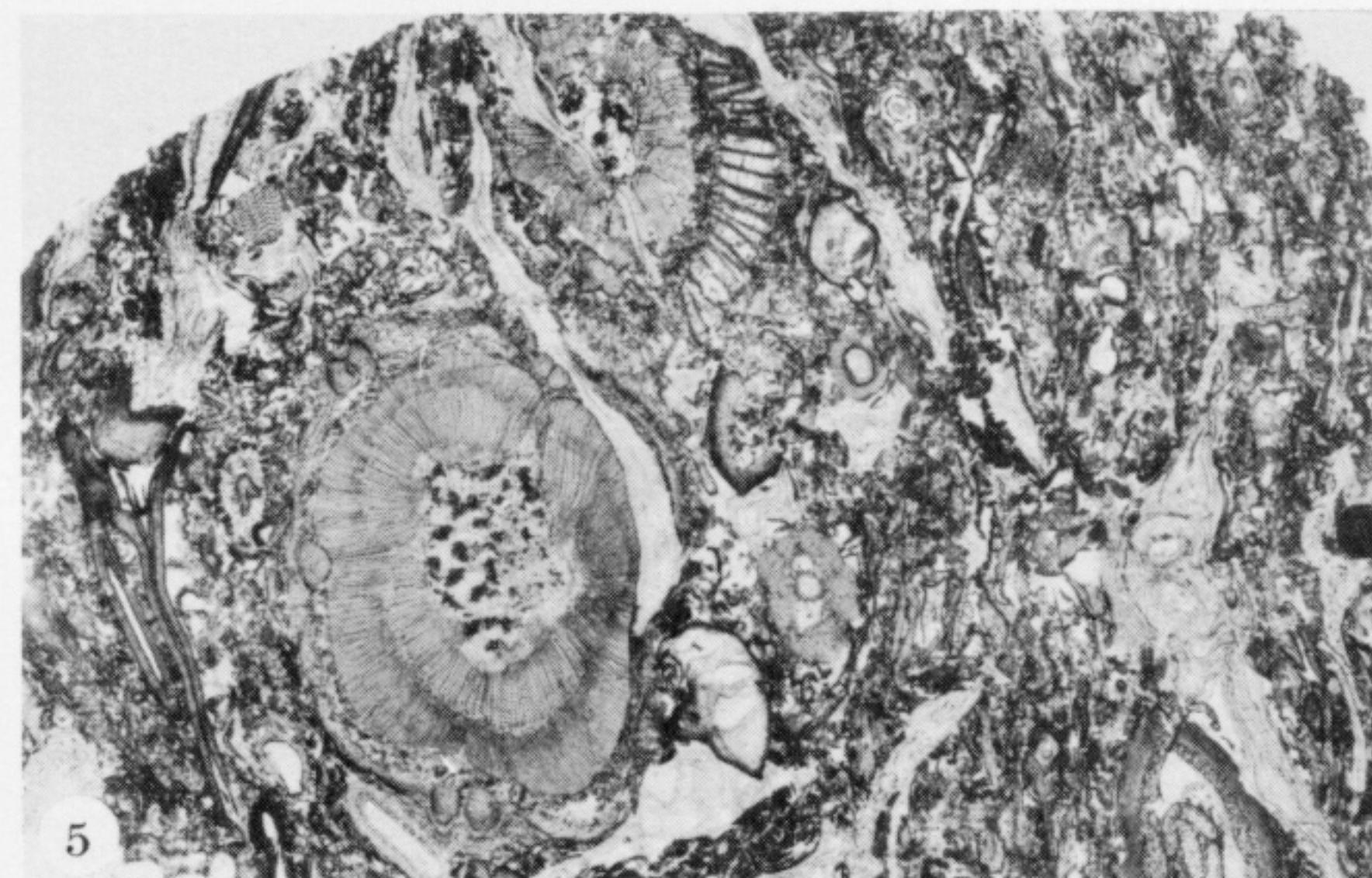
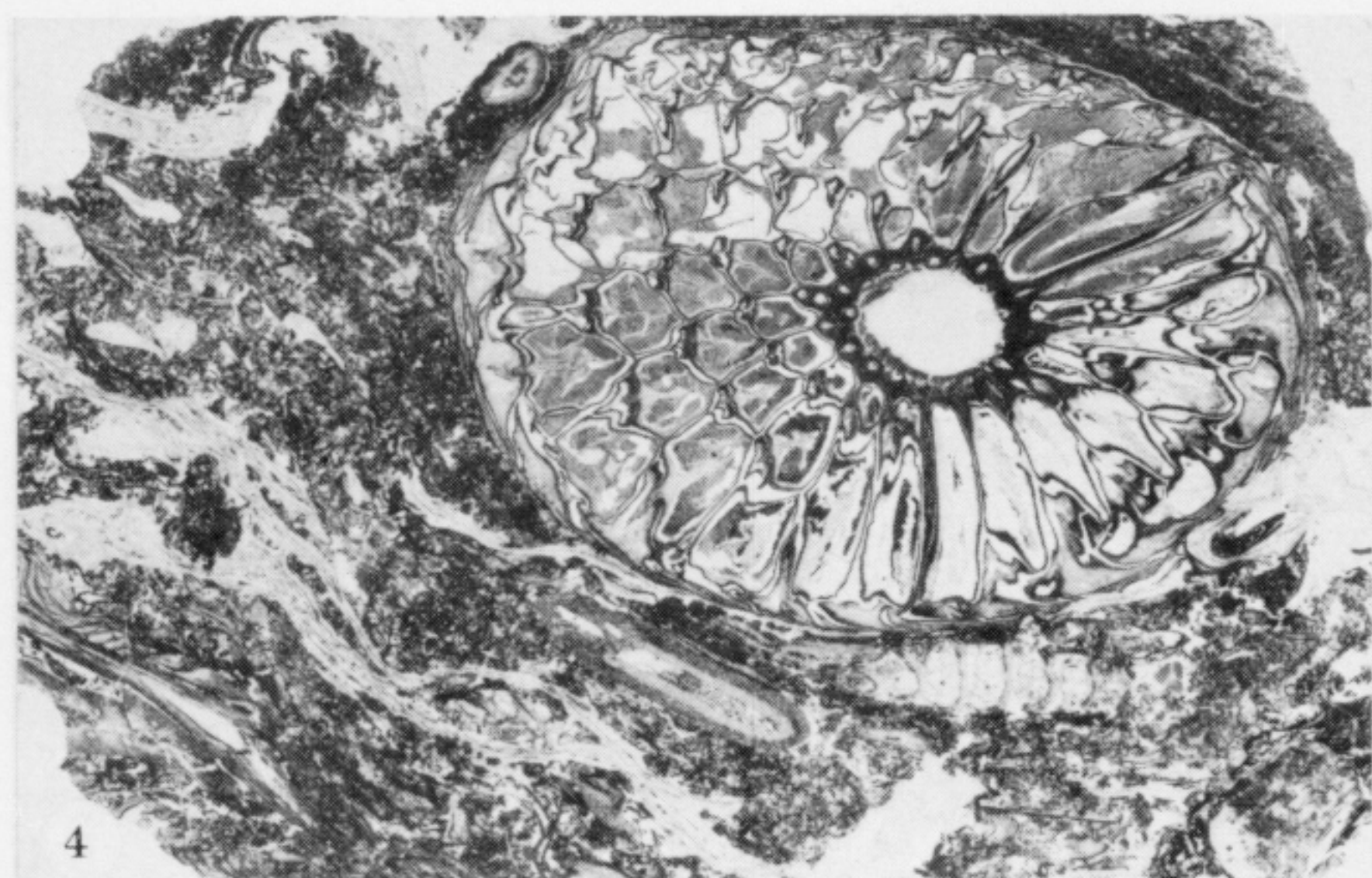
- Absolam, R. G. 1929 Lower Carboniferous coal-ball flora of Haltwhistle, Northumberland. *Proc. Univ. Durham Phil. Soc.* **8**, 73–87.
- Anderson, T. F., Brownlee, M. E. & Phillips, T. L. 1981 A stable isotope study on the origin of permineralized peat zones in the Herrin coal. *J. Geol.* **88**, 713–722.
- Andrews, H. N. & Mamay, S. H. 1952 A brief conspectus of American coal ball studies. *Palaeobotanist* **1**, 66–72.
- Andrews, H. N. & Murdy, W. H. 1958 *Lepidophloios* and ontogeny in arborescent lycopods. *Am. J. Bot.* **45**, 552–560.
- Baxter, R. W. 1949 Some pteridosperm stems and fructifications with particular reference to the Medullosae. *Ann. Miss. Bot. Gdn* **36**, 287–353.
- Baxter, R. W. 1964 Paleozoic starch in fossil seeds from Kansas coal balls. *Kansas Acad. Sci. Trans.* **67**, 418–422.
- Beeler, H. E. 1983 Anatomy and frond architecture of *Neuropteris ovata* and *N. scheuchzeri* from the Upper Pennsylvanian of the Appalachian Basin. *Can. J. Bot.* **61**, 2352–2368.
- Brack-Hanes, S. D. 1978 On the megagametophytes of two lepidodendracean cones. *Bot. Gaz.* **139**, 140–146.
- Chaloner, W. G. & Lacey, W. S. 1973 The distribution of late Palaeozoic floras. In *Organisms and continents through time* (ed. N. F. Hughes). *Spec. Pap. Palaeont.* **12**, 271–289.
- Chaloner, W. G. & Meyen, S. V. 1973 Carboniferous and Permian floras of the northern continents. In *Atlas of palaeobiogeography* (ed. A. Hallam), pp. 169–186. Amsterdam: Elsevier.
- Chican, M. A., Taylor, T. N. & Smoot, E. L. 1981 The application of Scanning Electron Microscopy in characterization of Carboniferous lycopod wood. *Scanning Elect. Microsc.* **111**, 197–201.
- Cohen, A. D. & Spackman W. 1977 Phytogenic organic sediments and sedimentary environments in the Everglades–Mangrove complex. Part II. The origin, description and classification of the peats of southern Florida. *Palaeontographica B* **162**, 71–114.
- Cohen, A. D. & Spackman, W. 1980 Phytogenic organic sediments and sedimentary environments in the Everglades–Mangrove complex. Part III. The alteration of plant material in peat and origin of coal macerals. *Palaeontographica B* **172**, 125–149.
- Courvoisier, J. M. & Phillips, T. L. 1975 Correlation of spores from Pennsylvanian coal-ball fructifications with dispersed spores. *Micropaleontology* **21**, 45–59.
- Delevoryas, T. 1964 Ontogenetic studies of fossil plants. *Phytomorphology* **14**, 299–314.
- Dickson, J. A. D. 1966 Carbonate identification and genesis as revealed by staining. *J. sed. Petrol.* **36**, 491–505.
- DiMichele, W. A. 1981 Arborescent lycopods of Pennsylvanian age coals. *Lepidodendron*, with description of a new species. *Palaeontographica B* **175**, 85–125.
- Eggert, D. A. 1961 The ontogeny of Carboniferous arborescent Lycopsidea. *Palaeontographica B* **108**, 43–92.
- Evans, W. D. & Amos, D. H. 1961 An example of the origin of coal balls. *Proc. Geol. Ass.* **72**, 445–454.
- Feliciano, J. M. 1924 The relation of concretions to coal seams. *J. Geol.* **32**, 230–239.
- Francis, E. H. 1983 Carboniferous. In *Geology of Scotland* (ed. G. Y. Craig), pp. 253–296. Edinburgh: Scottish Academic Press.
- Galtier, J. & Scott, A. C. 1979 Studies of Paleozoic ferns: on the genus *Corynepteris*. A redescription of the type and some other European species. *Palaeontographica B* **170**, 81–125.

- Good, C. W. & Taylor, T. N. 1972 The ontogeny of Carboniferous articulates: the apex of *Sphenophyllum*. *Am. J. Bot.* **59**, 617–626.
- Hatcher, P. G., Lyons, P. C., Thomson, C. L., Brown, F. W. & Maciel, G. E. 1982 Organic matter in a coal ball: peat or coal? *Science, Wash.* **217**, 831–833.
- Holmes, J. 1977 The Carboniferous fern *Psalixochlaena cylindrica* as found in Westphalian A coal balls from England. Part 1. Structures and development of the cauline system. *Palaeontographica B* **164**, 33–75.
- Holmes, J. 1981 The Carboniferous fern *Psalixochlaena cylindrica* as found in Westphalian A coal balls from England. Part II. The frond and fertile parts. *Palaeontographica B* **176**, 147–173.
- Holmes, J. & Fairon-Demaret, M. 1984 A new look at the flora of the Buxharmont coal balls from Belgium. *Ann. Soc. Geol. Belg.* **107**, 73–87.
- Holmes, J. & Scott, A. C. 1981 A note on the occurrence of marine animal remains in a Lancashire coal ball (Westphalian A). *Geol. Mag.* **118**, 307–308.
- Hooker, J. D. & Binney, W. W. 1855 On the structure of certain limestone nodules enclosed in seams of bituminous coal, with a description of some trigonocarbons contained in them. *Phil. Trans. R. Soc. Lond.* **B 145**, 149–156.
- Joy, K. W., Willis, A. J. & Lacey, W. S. 1956 A rapid cellulose peel technique in palaeobotany. *Ann. Bot.* **20**, 635–637.
- Klappa, C. F. 1980 Rhizoliths in terrestrial carbonates: classification, recognition, genesis and significance. *Sedimentology* **27**, 613–629.
- Knoll, A. H. & Rothwell, G. W. 1981 Palaeobotany: perspectives in 1980. *Paleobiology* **7**, 7–35.
- Koopmans, R. G. 1934 Researches on the flora of the coal-balls from the 'Aegir' horizon in the Province of Limburg (The Netherlands). *Geol. Bur. Heerlen* 1933, 45–46.
- Leclercq, S. 1925 Introduction a l'étude anatomique des végétaux houillers de Belgique: les coal balls de la couche Buxharmont des Charbonnages des Wéristers. *Mém. Soc. Géol. Belg.*, pp. 1–79.
- Lomax, J. 1902 On the occurrence of the nodular concretions (coal balls) in the Lower Coal Measures. *Abstr. Brt. Ass. Sec. K. Belfast.*
- Love, L. C., Coleman, M. L. & Curtis, C. D. 1983 Diagenetic pyrite formation and sulphur isotope fractionation associated with a Westphalian marine incursion, northern England. *Trans. R. Soc. Edinburgh., Earth Sci.* **74**, 165–182.
- McCabe, P. J. 1984 Depositional environments of coal and coal-bearing strata. *Spec. Publ. int. Ass. Sediment.* **7**, 2–30.
- Mamay, S. H. & Yochelson, E. L. 1962 Occurrence and significance of marine animal remains in American coal balls. *U.S. Geol. Soc. Prof. Pap.* **354 I**, 193–224.
- Mickle, J. E. & Rothwell, G. W. 1982 Permineralized *Alethopteris* from the Upper Pennsylvanian of Ohio and Illinois. *J. Paleont.* **56**, 392–402.
- Millay, M. A. & Eggert, D. A. 1974 Microgametophyte development in the Paleozoic seed fern family Callistrophytaceae. *Am. J. Bot.* **61**, 1067–1075.
- Niklas, K. J., Tiffney, B. H. & Knoll, A. H. 1980 Apparent changes in the diversity of fossil plants. *Evol. Biol.* **12**, 1–89.
- Noé, A. C. 1923 Coal balls. *Science, Wash.* **57**, 385.
- Noé, A. C. 1931 Review of American coal-ball studies. *Ill. Acad. Sci. Trans.* **24**, 317–320.
- Oliver, F. R. & Scott, D. H. 1904 On the structure of the Palaeozoic seed *Lagenostoma lomaxi*, with a statement of the evidence upon which it is referred to *Lyginodendron*. *Phil. Trans. R. Soc. Lond.* **B 197**, 193–247.
- Perkins, T. W. 1976 Textures and conditions of formation of Middle Pennsylvanian coal balls, central United States. *Univ. Kansas. Kansas Palaeont. Contrib. Pap.* **82**, 1–13.
- Phillips, T. L. 1979 Reproduction of heterosporous arborescent lycopods in the Mississippian–Pennsylvanian of Euramerica. *Rev. Palaeobot. Palynol.* **27**, 239–289.
- Phillips, T. L. 1980 Stratigraphic and geographic occurrences of permineralized coal-swamp plants – Upper Carboniferous of North America and Europe. In *Biostratigraphy of fossil plants* (ed. D. L. Dilcher & T. H. Taylor), pp. 25–92. Stroudsburg, Pennsylvania: Dowden, Hutchison and Ross.
- Phillips, T. L. 1981 Stratigraphic occurrences and vegetational patterns of Pennsylvanian pteridosperms in Euramerican coal swamps. *Rev. Palaeobot. Palynol.* **32**, 5–26.
- Phillips, T. L., Avcin, M. J. & Berggren, D. 1976 Fossil peat from the Illinois basin. A guide to the study of coal balls of Pennsylvanian age. *Ill. State Geol. Geol. Serv., Ed. Ser.* **11**, 1–39.
- Phillips, T. L. & DiMichele, W. A. 1981 Paleocology of Middle Pennsylvanian age coal swamps in southern Illinois–Herrin Coal member at Sahara mine no. 6. In *Paleobotany, paleoecology and evolution* (ed. K. J. Niklas), pp. 231–284. New York: Praeger.
- Phillips, T. L., Kunz, A. B. & Mickish, D. J. 1977 Paleobotany of permineralized peat (coal balls) from the Herrin (no. 6) Coal Member of the Illinois Basin. In *Interdisciplinary studies of peat and coal origins* (ed. P. N. Given & A. D. Cohen), pp. 18–49. Washington, D.C.: Geological Society of America.
- Phillips, T. L., Peppers, R. A., Avcin, M. J. & Laughnan, P. F. 1974 Fossil plants and coal: patterns of change of Pennsylvanian swamps of the Illinois Basin. *Science, Wash.* **184**, 1367–1369.
- Phillips, T. L. & Peppers, R. A. 1984 Changing patterns of Pennsylvanian coal-swamp vegetation and implications of climatic control on coal occurrence. *Int. J. Coal Geol.* **3**, 205–255.



- Pigg, K. B. & Rothwell, G. W. 1983 *Chaloneria* gen.nov.; heterosporous lycophytes from the Pennsylvanian of North America. *Bot. Gaz.* **144**, 132–147.
- Ramanujam, C. G. K., Rothwell, G. W. & Stewart, W. N. 1974 Probable attachment of the *Dolerotheca* campanulum to a *Myeloxylon–Alethopteris* type frond. *Am. J. Bot.* **61**, 1057–1066.
- Raymond, A. & Phillips, T. L. 1983 Evidence for an Upper Carboniferous mangrove community. In *Tasks for vegetation science* (ed. H. J. Teas), vol. 8, pp. 19–33. The Hague: Junk.
- Rolfe, W. D. I. 1980 Early invertebrate terrestrial faunas. In *The terrestrial environment and origin of land vertebrates* (ed. A. Panchen), pp. 117–157. London: Academic Press.
- Rothwell, G. W. 1972 Evidence of pollen tubes in Paleozoic pteridosperms. *Science, Wash.* **175**, 772–774.
- Rothwell, G. W. 1976 Petrified Pennsylvanian age plants of eastern Ohio. *Ohio J. Sci.* **76**, 128–132.
- Rothwell, G. W. 1977 Evidence for a pollination-drop mechanism in Paleozoic pteridosperms. *Science, Wash.* **198**, 1251–1252.
- Rothwell, G. W. 1980 A technique for revealing the surface features of permineralized ‘coal-ball’ plants. *J. Paleont.* **54**, 1131–1133.
- Rothwell, G. W. 1981 The Callistophytales (Pteridospermopsida) reproductively sophisticated Paleozoic gymnosperms. *Rev. Palaeobot. Palynol.* **32**, 103–121.
- Rothwell, G. W. & Warner, S. 1984 *Cordaixylon dumusum* n.sp. (Cordaitales). 1. Vegetative structures. *Bot. Gaz.* **145**, 275–291.
- Schopf, J. M. 1975 Modes of fossil preservation. *Rev. Palaeobot. Palynol.* **20**, 27–53.
- Scott, A. C. 1977 A review of the ecology of Upper Carboniferous plant assemblages with new data from Strathclyde. *Palaeontology* **20**, 447–473.
- Scott, A. C. 1978 Sedimentological and ecological control of Westphalian B plant assemblages from West Yorkshire. *Proc. Yorks. Geol. Soc.* **41**, 461–508.
- Scott, A. C. 1979 The ecology of Coal Measure floras from northern Britain. *Proc. Geol. Ass.* **90**, 97–116.
- Scott, A. C. & Taylor, T. N. 1983 Plant/animal interactions during the Upper Carboniferous. *Bot. Rev.* **49**, 259–307.
- Scott, D. H. 1904 Germinating spores in a fossil fern sporangium. *New Phytol.* **3**, 18–23.
- Scott, D. H. 1906 On *Suicliffia insignis*, a new type of Medulloseae from the Lower Coal-Measures. *Trans. Linn. Soc. Lond. 2nd Ser. Bot.* **7**, 45–68.
- Scott, D. H. 1920 *Studies in fossil botany*, vol. 1, *Pteridophyta*. London: A. & C. Black. 434 pages.
- Scott, D. H. 1923 *Studies in fossil botany*, vol. 2, *Spermophyta*. London: A. & C. Black. 446 pages.
- Seward, A. C. 1898–1919. *Fossil plants*, vol. 1. (1898) 452 pages. Vol. 2 (1910) 624 pages. Vol. 3 (1917) 656 pages. Vol. 4 (1919) 543 pages. Cambridge: Cambridge University Press.
- Snigirevskaya, N. S. 1972 Studies of coal balls of the Donets Basin. *Rev. Palaeobot. Palynol.* **14**, 197–204.
- Stewart, W. N. & Delevoryas, T. 1956 The medullosan pteridosperms. *Bot. Rev.* **22**, 45–80.
- Stewart, W. N. & Taylor, T. N. 1965 The peel technique. In *Handbook of paleontological techniques* (ed. B. Kummel & D. Raup), pp. 224–232. San Francisco: W. H. Freeman.
- Stocks, M. B. 1902 On the origin of certain concretions in the Lower Coal Measures. *Q. Jl Geol. Soc.* **58**, 46–58.
- Stopes, M. C. & Watson, D. M. S. 1908 On the present distribution and origin of the calcareous concretions in coal seams, known as ‘coal balls’. *Phil. Trans. R. Soc. Lond.* **B200**, 167–218.
- Taylor, T. N. 1977 Toward an understanding of the reproductive biology of fossil plants. In *Geobotany* (ed. R. C. Romans), pp. 77–93. New York: Plenum.
- Taylor, T. N. 1983 Reproductive biology in early seed plants. *Bioscience* **32**, 23–28.
- Taylor, T. N. & Millay, M. A. 1969 Application of the scanning electron microscope in paleobotany. *Scanning Elect. Microsc.* 1969, 107–115.
- Taylor, T. N. & Millay, M. A. 1977 The ultrastructure and reproductive significance of *Lasiostrobus* microspores. *Rev. Palaeobot. Palynol.* **23**, 129–137.
- Taylor, T. N. & Scott, A. C. 1983 Interactions of plants and animals during the Carboniferous. *Bioscience* **33**, 488–493.
- Thomas, B. A. 1981 Structural adaptations shown by the Lepidocarpaceae. *Rev. Palaeobot. Palynol.* **32**, 377–388.
- Tian, Bao-Lin 1979 Coal balls in the coal seams in China. *Abst. IX. int. Cong. Carb. Strat. Geol. Urbana, 1979*, p. 214. University of Illinois.
- Walton, J. 1928 A method of preparing sections of fossil plants contained in coal balls or in other types of petrification. *Nature, Lond.* **122**, 571.
- Zeigler, A. M., Banbach, R. K., Parrish, J. T., Barrett, S. F., Gierlowski, E. H., Parker, W. C., Raymond, A. L. & Sepkoski, J. J. 1981 Paleozoic biogeography and climatology. In *Paleobotany, paleoecology and evolution* (ed. K. Niklas), vol. 2, pp. 231–266. New York: Praeger.





FIGURES 2-9. For description see opposite.