

A NEW PLANT FROM THE LOWER OLD RED SANDSTONE OF SOUTH WALES

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ABSTRACT. A new plant is described from the Senni Beds of the Lower Devonian of South Wales. The naked axes were pseudomonopodially and dichotomously branched and contained protosteles in which the protoxylem was central. Terminal fructifications consisted of sporangia alternating with sterile bracts; the plant was homosporous. A comparison is made with other Devonian genera, which show similar organization in the fertile regions, and it is concluded that the plant should be placed in a new genus, *Krithodeophyton*, assigned to the Barinophytaceae (Incertae sedis).

THE fossils described in this paper were among those collected by Croft from the Brecon Beacons Quarry, also called the Storey Arms Quarry (Nat. Grid Ref. SO 972208) and are now in the Department of Palaeontology, British Museum (Natural History). The quarry is in the Senni Beds, which form the lower part of the Breconian Stage of the Lower Old Red Sandstone in South Wales (Croft 1953) and are probably equivalent to the Siegenian of Europe. Among the plants previously described from this locality are *Gosslingia breconensis*, *Zosterophyllum llanoveranum*, and *Drepanophycus spinaeformis* (Heard 1927 and 1939, Croft and Lang 1942, Edwards and Banks 1965, Edwards 1967). The majority of the plants were preserved as compressions in a fine-grained, blue-grey sandstone, but parts of the axes were sometimes petrified.

Small pieces of cuticle were recovered after bulk maceration of the rock in commercial strength (40%) hydrofluoric acid. These were then treated with Schulze's solution (concentrated nitric acid and potassium chlorate) for 1-8 hours and, when the carbon had oxidized and the outlines of cells were visible, the fragments were washed, immersed in Diaphane solvent and mounted in Diaphane (Distributors: Will Scientific Inc., New York 52, N.Y., U.S.A.). Pieces of carbon were also picked off both axes and sporangia with steel needles, macerated in Schulze's solution and mounted in the same way. Film pulls were made from those fossils, which were exposed on the surface of the rock. A solution of cellulose nitrate in amyl acetate was poured over the fossil and left to dry overnight. The resulting rough, transparent film was peeled off and mounted in Harleco Synthetic Resin (H.S.R.). (Distributors: Arthur H. Thomas Company, Philadelphia, Pa., U.S.A.).

The anatomy of the pyritised axes was investigated using a modification of the method described by Beck in 1955. A small piece of rock containing a petrified fossil was first embedded in the synthetic resin, Cemar, because the rock matrix tended to crumble when sawn (Leclercq and Noel 1953). The transparent block of plastic was trimmed to size and cut into sections about a millimetre thick. These were ground smooth on a glass plate with grade 600 carborundum powder, washed and then treated in chromic oxide powder until a good polish was obtained. After washing they were dried, soaked in xylol and mounted in H.S.R. The sections of the axes were then examined using a Leitz Ultropak microscope. All the preparations have been deposited in the Department of Palaeontology, British Museum (V26578, V26579, V52137-54).

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SYSTEMATIC DESCRIPTION

Family BARINOPHYTACEAE Kräusel and Weyland 1961

Genus KRITHODEOPHYTON gen. nov.

Type species. Krithodeophyton croftii sp. nov.

Diagnosis. Plant consisting of naked, pseudomonopodially branching axes with some dichotomous branching in distal parts. Simple protostele composed of mainly scalariform, but some reticulate tracheids; protoxylem central. Sporangia in terminal spikes. Dichotomous branching within the base of the fertile region or just below it. Oval sessile sporangia borne in two rows, one on either side of the axis. Narrow sterile appendages, attached at right angles to the axis, alternate with the sporangia. Bracts straight throughout their length or with distal parts curving downwards. Sporangium wall composed of isodiametric cells. Plant homosporous. Spores assignable to the dispersed spore genus *Apiculiretusispora* (*sensu* Streele 1964).

Krithodeophyton croftii sp. nov.

PLATE 130, figs. 1–12; Plate 132, figs. 1–10

Diagnosis. Plant, at least 10.0 cm. high, consisting of naked, pseudomonopodially branching axes, 1.5–4.3 mm. wide, with some dichotomous branching in the distal parts; wide angles ($< 80^\circ$) at branching points. Small bud-like lateral branches about 4.0 mm. long. Simple, circular protostele, average diameter 0.5 mm., composed of mainly scalariform, with some reticulate, tracheids; smallest elements at the centre of the xylem. Outer cortex composed of elongate, thick-walled cells, 36–60 μ in diameter. Epidermis composed of short, fusiform cells. Sporangia aggregated into terminal spikes, 2.5–3.0 mm. wide and up to 1.3 cm. long. Dichotomous branching within the base of the fertile region or just below it. Oval sessile sporangia, 1.25–1.5 mm. long and 0.8–1.0 mm. wide borne in two rows, one on either side of the axis. Narrow sterile appendages up to 2.5 mm. long, given off at right angles to the axis, alternate with the sporangia. Bracts straight throughout their length or with distal parts curving downwards. Sporangium wall composed of isodiametric cells, of average diameter 27 μ . Homosporous. Spores approximately circular in outline, average diameter is 60 μ ; simple trilete $\frac{2}{3}$ – $\frac{3}{4}$ of the spore radius long; variable wall elements up to 3 μ high (the majority being under 1 μ); ornament reduced or absent in contact area. Assignable to the dispersed spore genus *Apiculiretusispora*.

EXPLANATION OF PLATE 130

Figs. 1–12. *Krithodeophyton croftii* sp. nov. 1, 4, Rock bearing fertile spikes, $\times 1.1$ (V26578 and V26579 respectively). 2, 5, Sterile axes, $\times 0.9$ (V52154 and V52152 respectively). 3, Film pull showing epidermal cells, $\times 80$ (V52151, BMP 25). 6, Film pull from axis showing small lateral branch. (Inset = specimen before treatment), $\times 6$ (V52154, BMP 12). 7, Film pull from axis showing cortical cells, $\times 50$ (V52144, BMP 1). 8, Central strand after treatment with Schulze's solution, $\times 200$ (V52137, BMM 22). 9, Central strand on film pull, $\times 100$ (V52145, BMP 2). 10, T.S. axis showing xylem strand before a division, $\times 108$ (V52150, RS1/8). 11, T.S. pyritised xylem strand with centre not preserved, $\times 108$ (V52138, RS1/4). 12, T.S. part of outer cortex, $\times 108$ (V52150, RS1/5).

Locality. Brecon Beacons Quarry, abandoned roadside quarry on the A470 between Brecon and Merthyr, approximately 7½ miles south of Brecon.

Horizon. Senni Beds, Breconian, Lower Old Red Sandstone of South Wales (= Siegenian).

Holotype. Specimen V26579, Department of Palaeontology, British Museum (Natural History), London.

Description of vegetative parts. The over-all height, branching frequency, and basal parts of the plant are unknown. The most complete fertile specimen found was 10 cm. long, with axes 2 mm. in diameter. There were two branching points (3.4 cm. apart) in the vegetative region, and a further dichotomy occurred within the base of the spike of sporangia. The diameter of the sterile axes ranged between 1.5 and 4.0 mm. and axes of similar size were always found together. Hence it is probable that larger ones formed the basal, and small axes the more terminal, parts of the plant. Branching was pseudo-monopodial in these wider axes, and the narrower 'lateral' branch formed a wide angle with the 'main' axis (Pl. 130, fig. 2). These axes tended to be slightly flexuous and, in addition to a central line, 0.5 mm. in diameter, faint longitudinal striations were sometimes visible. Small, lateral bud-like structures up to 4.0 mm. long, which tapered in width from base to apex were also present (Pl. 130, fig. 6). Each was supplied with a central strand of xylem. The axes associated with the fertile regions were much narrower (< 20 mm. wide) and branched dichotomously.

Film pull and maceration preparations revealed some cellular detail of the outer layers of the axes. The outer cortex was the tissue most frequently recovered and consisted of very long cells with thick walls, 36–44 μ apart. Occasionally the tapering, overlapping ends of these cells were seen (Pl. 130, fig. 7). Scattered among the thick parallel walls were thinner, irregular lines probably representing the remains of underlying tissue. The outer cortical cells were represented in the transverse sections of petrified axes by 1 or 2 layers of angular cells (35–60 μ in diameter) surrounding a structureless mass of pyrites, containing a circular protosteles. The outer walls of the cortical cells were often broken down giving the surface of the axis a hairy appearance (Pl. 130, fig. 12). In one instance only, a piece of cuticle was found where the cells had thinner walls, were fusiform in shape and relatively short (Pl. 130, fig. 3). It is probable that this was the epidermis.

The central strand of xylem was composed mainly of scalariform tracheids in which pits on adjacent walls were opposite (Pl. 130, figs. 8 and 9). A few elements showed reticulate pitting. Sections through petrified xylem revealed similar anatomy. The central part was usually not preserved (Pl. 130, fig. 11), but a decrease in tracheid diameter from the outside of the xylem inwards was always apparent. In a few cases, very small elements could be seen at the centre. The protoxylem is therefore considered to be central. The largest tracheids measured 35 μ in diameter and the distance between the horizontal bars of the scalariform tracheids was sometimes as great as 10 μ .

In one axis only could stages in the division of the xylem be seen. A few millimetres below the branching point, the xylem became oval in cross section (Pl. 130, fig. 10) and divided to give two circular strands of approximately the same diameter. The axis itself then divided into two.

I have found well-preserved pyritised axes with similar anatomy to those described above at the same locality. I include a detailed account of them here to emphasize this

close anatomical and morphological similarity, but in the absence of any reproductive parts in the new specimens, I feel it would be unwise to conclude that the two sets of remains belong to the same plant.

The axes were at least 10.0 cm. long and 2.0–3.0 mm. wide. They branched dichotomously and were slightly flexuous. One axis bore a small protuberance 2.0 mm. long and 1.5 mm. wide (Pl. 131, fig. 1) comparable to the small lateral branch in *Krithodeophyton*. The surfaces of the axes were striated. Film pulls showed thick longitudinal walls similar to those described above and sometimes smaller fusiform cells were seen (Pl. 131, fig. 4).

Transverse and longitudinal sections through petrified axes showed a circular proto-stele composed predominantly of scalariform tracheids (Pl. 131, figs. 2 and 5). Some reticulate pitting was seen. The widest tracheids were found to the outside of the xylem. The cells at the centre were either not preserved or very small and crushed (Pl. 131, fig. 5). Immediately outside the xylem was a narrow band of squashed thin-walled cells. One or two layers of thick-walled cells, circular to angular in cross-section, with an average diameter of 49 μ , formed the outermost layer of the axis. The outer walls of these cells were eroded away so that the radial walls project into the matrix, giving the axis a hairy outline (Pl. 131, fig. 6) which is also seen in *Krithodeophyton*. In longitudinal sections, the cortical cells had tapering ends (Pl. 131, fig. 3). They were, on average, 350 μ long.

Stages in the division of the xylem below a branching point are illustrated in Plate 131, figs. 5–10.

Description of fructifications. The sporangia were aggregated into terminal spikes. A few millimetres below the fertile region an axis dichotomised and this was followed by a further dichotomy immediately below or within the base of the fructification (Pl. 130, fig. 4). Isolated fructifications were common in the matrix (Pl. 130, fig. 1). The spikes were at least 1.3 cm. long and, on average, were 2.75 mm. wide. The majority were incomplete at the apex and 6.0–8.0 mm. long. At the base they were parallel-sided, but there was a gradual decrease in width in the distal parts and the apices were rounded (Pl. 132, fig. 4). No organization was apparent in the distal parts. The sporangia were oval in outline, 1.25–1.5 mm. long and 0.8–1.0 mm. wide (Pl. 132, fig. 2). They were sessile on a central axis (0.3 mm. diameter) which was often obscured by the sporangia themselves. The sporangia appeared to be arranged in two rows one on either side of the axis, each row containing at least eleven sporangia. It is unlikely that this arrangement was produced by compression of an originally spiral or whorled organisation as the sporangia are quite distinct. At the base of the spike the long axes of the sporangia were orientated at right-angles to the central axis, in the distal part they were directed toward the apex. Alternating with the sporangia and extending beyond them out into the matrix were thin, possibly spine-like appendages up to 2.5 mm. long (Pl. 132, figs. 3 and 5).

EXPLANATION OF PLATE 131

Figs. 1–10. *Krithodeophyton croftii* sp. nov. 1, Branching sterile axes from Brecon Beacons Quarry (small lateral projection indicated by arrow), $\times 1$ (DE 32/1). 2, Section through petrified axis, L.S. xylem strand composed of scalariform tracheids, $\times 108$ (32–4–33). 3, As last, L.S. outer cortical cells, $\times 108$ (32–4–35). 4, Film pull of surface of axis showing epidermal cells, $\times 80$ (DE32, P77). 5–10, Series of sections of petrified axis showing division of xylem at a branching point, $\times 51$ (Series 32–4).

These arose at right angles to the fructification axis and sometimes curved downwards at their tips. The exact relationship between sporangium and lateral appendage or bract could not be determined with certainty as the structures were very heavily carbonised. In some cases, the base of a sterile bract extended down the central axis partially covering the sporangium below, giving the impression that the sporangium and the bract above it formed a single unit (Pl. 132, fig. 1). Plate 132, fig. 2 shows a fructification, where sporangia only are visible, while in Plate 132, fig. 6 only bracts are present. Where sporangia and bracts were slightly superimposed the sporangia appear beaked. At the moment it seems very likely that the appendages were not attached to the sporangia, but that both were borne separately on a central axis.

Description of spores. Maceration and film pull preparations showed spores adhering to the sporangium wall. The cellular structure of the walls was not preserved, but some very fragmentary remains indicated that part of the wall was composed of isodiametric cells, around $27\ \mu$ in diameter. Imprints left by the spores could frequently be seen in the sporangium wall (Pl. 132, fig. 7). A small number of spores were recovered by dissolving the film pull bearing a sporangium (Pl. 132, figs. 8–10). They were all approximately the same size, with an average diameter of $58\ \mu$ (range: 55 – $68\ \mu$). The spores were almost circular in outline. The position of the trilete was usually difficult to establish because of heavy folding, but in one case a simple Y-mark was observed. The length of the trilete was almost equal to the spore radius. The wall ornament was made up of rather variable elements ranging from conical to spinous, which were $1\ \mu$ or less high. Narrower parallel-sided elements with truncated tips occasionally reached a height of $3\ \mu$. There was a well-developed contact area, where the ornament was much reduced or absent. These spores are assignable to the dispersed spore genus *Apiculatiretusispora* (*sensu* Streel 1964) and are comparable to the species *A. brandtii* (Streel 1964).

In conclusion it must be emphasized that no anatomy has been detected in the axes attached to the fertile regions. The sterile and fertile parts are thought to belong to the same plant because they are always found in close association, no other plant being present, and where fructifications terminate relatively long axes, the latter have the same dimensions, surface features, and branching angles as do the sterile axes.

Discussion. Plants with a similar arrangement of sporangia in terminal spikes and, in some cases, with sterile and fertile appendages intermixed, are known from other Devonian deposits. These include *Barinophyton*, *Protobarinophyton*, *Pectinophyton*, and the possible reproductive parts of *Enigmophyton*. Høeg (1942) described some fertile axes, which he considered were probably attached to *Enigmophyton superbum*. These plants came from the upper Middle Devonian of Spitzbergen. As in the Welsh plant, the sporangia, which alternated with sporophylls, were arranged in two rows, with dichotomous branching occurring both below and within the base of the fructification. Høeg, however, thought that the two rows were produced by compression of an originally verticillate or spiral arrangement of appendages. He considered the sporangia to be borne proximally on the upper surfaces of the sterile bracts. Unlike *Krithodeophyton*, this plant was heterosporous, and Vigran (1964), described the spores in detail. She identified the microspores as *Phyllothecotriletes microgranulatus* (average diameter $72\ \mu$) and called the megaspores *Enigmospora simplex* (200 – $70\ \mu$ diameter). Although the microspores are comparable in size to those spores isolated from *Krithodeophyton*, the

ornament is quite different. Nothing resembling the fan-shaped leaves of *Enigmophyton superbum* has been found at the Brecon Beacons Quarry.

Earlier, Høeg (1935) had described a Middle Devonian plant from Norway, in which naked axes, with mainly pseudomonopodial branching had fructifications terminating the 'lateral' branches. The sporangia, or perhaps the organs bearing the sporangia, were arranged in two rows, both borne on the lower surface of the fructification axis. Høeg called this plant *Pectinophyton norvegicum* and Ananiev (1957), described another species *P. bipectinatum*, where the axis of the fructification bore two rows of long, lateral appendages, twisted towards the axis. On the inside of the resulting coils were attached the sporangia. The axis had a central strand of annular tracheids. Whereas Petrosyan, in Lepekhina, Petrosyan, and Radchenko (1962) considered the above two species to be identical, Høeg (1967) maintained that they were two distinct species on the basis of differences in sporangial shape and arrangement. Not enough is known of Høeg's plant to make a satisfactory comparison with *Krithodeophyton*, but *P. bipectinatum* with its apparently complex organisation in the sporangial region, is quite unlike the Welsh plant.

The genus *Barinophyton* was erected by White (1905), when he re-investigated some plants from the Upper Devonian of Perry, Maine. He distinguished three species, *Barinophyton richardsonii* (*Lepidostrobus richardsonii* Dawson 1861, *Lycopodites richardsonii* Dawson 1863), *B. obscurum* (*Pecopteris* (?) *obscurum* Dun 1898), and *B. perryanum*. The most completely described species in the literature are *B. citrulliforme* from the Upper Devonian of New York (Arnold 1939) and *B. richardsonii*, re-described by Pettitt (1965). Arnold showed that branching in the sterile region was pseudomonopodial but that the fructifications, much larger than in *Krithodeophyton*, terminated lateral branches. In both *Barinophyton* species the fructification axis bore on its dorsal surface two rows of appendages between which were found the sporangia. They were unlike *Krithodeophyton* in that the appendages did not extend beyond the sporangia and were discoidal in shape. In addition, in Pettitt's re-construction two sporangia occurred between successive bracts in each row. Where the sporangia were borne in two rows, one on either side of the fertile axis, i.e. the normal *Krithodeophyton* arrangement, Arnold thought the arrangement was produced during fossilization. Both species were heterosporous. A Middle Devonian species, *B. sibiricum* (Lepekhina *et al.* 1962) differed from the Welsh plant in having long, lax, pendant spikes of sporangia.

In 1954, Ananiev described *B. obrutschewii* from the Lower Devonian of the U.S.S.R. This differed from previously described species of *Barinophyton* in that branching was dichotomous not pseudomonopodial. On the basis of this difference alone, he transferred the plant to a new genus *Protobarinophyton obrutschewii* (Ananiev 1957). Although in 1954, Ananiev had briefly mentioned sporophylls associated with the sporangia, in later papers by him and other authors no mention is made of them. Certainly *Protobarinophyton obrutschewii* f. *mucronata* (originally *Distichophytum mucronatum* Ananiev) transferred

EXPLANATION OF PLATE 132

Figs. 1-6. Fructifications of *Krithodeophyton croftii* sp. nov.: *s*, sporangium; *b*, bract; *d*, branching within the base of the fertile region. 1, $\times 5$ (V26579). 2 and 6, $\times 2.3$ (V26578). 3-5, $\times 5$ (V26578). 7, Sporangium wall with spores attached, $\times 500$ (V52146, BMM 12). 8-10, Spores isolated from sporangia. 8, $\times 500$ (V52146, BMS 1). 9 and 10, $\times 1000$ (V52146, BMS 1).

to the genus by Lepekhina *et al.* (1962) had no bracts in the fertile region. Ananiev (1963) stated that the sporangia of *P. obrutschewii* contained spores of one size only (70 μ diameter).

Krithodeophyton and *Protobarinophyton* resemble each other in many ways. Indeed, considering such characters as their similar age, the aggregation of oval, sessile sporangia into terminal spikes, homosporous and dichotomous branching in the fertile regions, they might be included in the same genus. However, until more is known of the detailed organization of the spikes (e.g. whether or not bracts are present), about the spores and the anatomy of the axes of *Protobarinophyton*, I feel justified in erecting a new genus for the Welsh plant. Differences include the absence from *Krithodeophyton* of U- and H-branching, the absence of dehiscence lines on the sporangia and the presence of scalariform not annular tracheids in the protosteles. In addition, the spikes in *Krithodeophyton* were much smaller, more compact and had distinctly protruding bracts. The specimen illustrated in Plate 132, fig. 2, in which no bracts are visible, most closely resembles the Russian plant. It is possible that this specimen represents a late stage in the maturation of a spike, where the sporangia were large and completely obliterated the bracts. This explanation could be applied to the apparently bractless condition seen in *Protobarinophyton*. Variation within the species has been indicated by Lepekhina *et al.*, who distinguished a *P. obrutschewii* f. *minuta* from *P. obrutschewii* f. *typica*, but little is known of the variation in fructification morphology within a single population.

In conclusion it is stressed that not enough is known of the details of anatomy and morphology of any of the plants discussed above. It may be that ultimately they will all be placed in the same genus. Indeed Arnold believed that this was true for *Pectinophyton* and *Barinophyton*. On the information available at the moment, I propose to place this relatively completely described Lower Devonian plant in the new genus *Krithodeophyton* (Derivation: *Krithodes*—like barley).

Classification. Ananiev (1963) included *Protobarinophyton*, with *Zosterophyllum* and *Bucheria* in the Zosterophyllaceae. My own observations on the anatomy of *Z. llanoveranum* show that *Krithodeophyton* is not related to this species, because the latter had an elliptical exarch protostele, and therefore should not be placed in the same family. In his contribution to the second volume of the *Traité de Paléobotanique* (ed. Boureau 1967), Høeg included the Barinophytaleae as an order, Incertae Sedis, containing two families, Barinophytaceae and Barrandeiaceae. The former included, in addition to *Barinostrobus*, all the genera mentioned above with the exception of *Enigmophyton*. It is suggested that *Krithodeophyton* should also be placed in this family.

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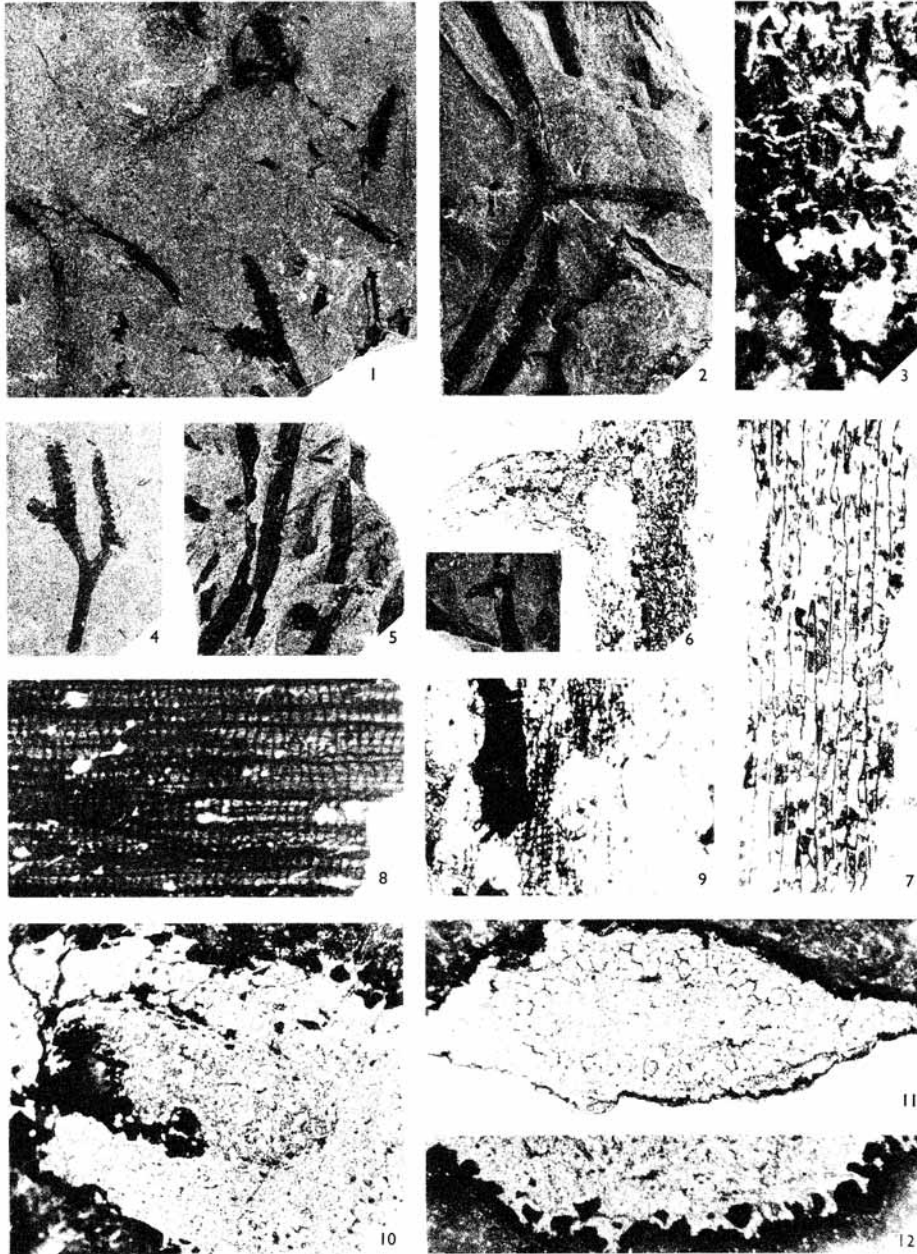
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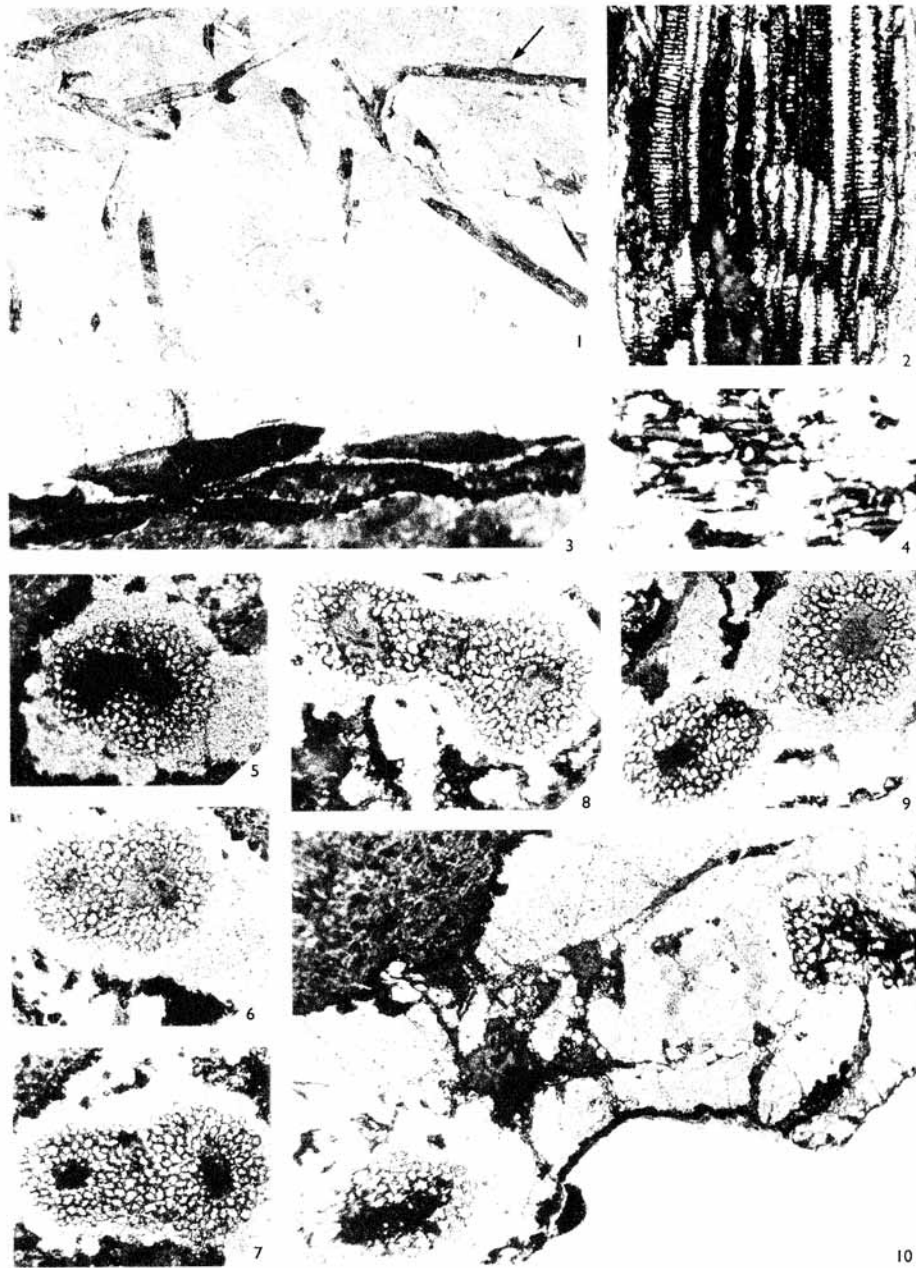
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