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THE UNIVERSITY OF ALBERTA

A NEW SPECIES OF PSILOPHYTON FROM THE LOWER DEVONIAN OF NORTHERN NEW BRUNSWICK, CANADA

BY

JEFFREY B. DORAN

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

DEPARTMENT ..BOTANY..................

EDMONTON, ALBERTA

FALL, 1979

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled A new species of Psilophyton from the Lower Devonian of northern New Brunswick, Canada. submitted by JEFFREY B. DORAN in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Paleobotany.

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ABSTRACT

A new spiny species of Psilophyton is described from the lower Emsian (Lower Devonian) of Atholville, New Brunswick, Canada, where the specimens occur in a silicified tuff. Vegetative branches are 2 mm to 8.3 cm long, twice to seven times dichotomous and terminated by slender, rounded tips. Some vegetative divisions are two closely spaced dichotomies (double dichotomies) that appear as an apparent trifurcation; the central axis of the double dichotomy varies from about 1 mm to 2.5 cm in length. Fertile branch systems terminate a dichotomous axis or are spirally arranged, are consistently pendulous after the second or third dichotomy, 1-2 cm long, 5-7 times dichotomous in three dimensions, consistently covered with crenulations on the first few orders of branching and terminated by sporangia 3-5 mm long by 1-2 mm wide; sporangia are consistently twisted around each other.

In situ spores are 48-102 μm in diameter and are compared to the dispersed spore genus Apiculiretusispora. Stomata are reported but an epidermis is usually lacking. Spines are round in cross section, multicellular, up to 6 mm long, undivided, dichotomous or trifurcate. Crenulations are semicircular to oval and 100-200 um in diameter. Vascular strands are up to 1 mm in diameter and centrarch with metaxylem tracheids that have scalariform-bordered to circular-bordered pits.

Psilophyton crenulatus sp. nov. is placed in the Trimerophytina and represents morphologically the best known species in the subdivision. The large number of axes exhibiting

morphologic variability make it possible to define many whole-plant characters of the species and provide an opportunity for better understanding the morphology of primitive land plants. The information may, in turn, 1) provide a better understanding of the presumed relationships between trimerophytes and certain Carboniferous ferns (e.g. Botryopteris (Phillips 1974) and Psalixochlaena (Holmes 1977) and 2) show that Psilophyton exhibited wide variability in its lateral branches.

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INTRODUCTION

The genus Psilophyton, established by Dawson in 1859, has had a long and confusing nomenclatural and systematic history that has been clarified by several authors (Kasper et al. 1974, Banks et al. 1975). Hueber (1968) and Banks et al. (1975) have emended the generic diagnosis and Doran et al. (1978) have listed the distinguishing features among the known species of Psilophyton and other members of the Trimerophytina.

Several studies describe the characteristics that unify members of the Trimerophytina (Hopping 1956, Banks 1968, Hueber 1968, Andrews et al. 1968, Kasper and Andrews 1972, Kasper et al. 1974, Banks et al. 1975, Granoff et al. 1976, Doran et al. 1978, Gensel 1979). The characteristics are dichotomous and pseudomonopodial axes, terminally borne sporangia that dehisce longitudinally, and centrarch protosteles. Psilophyton is the only known trimerophyte that is well enough preserved to provide anatomical data for comparison with more highly evolved plants. The oldest progymnosperms, the aneurophytes, are perhaps related to the trimerophytes through their possession of lobed protosteles (e.g. Scheckler and Banks 1971a, b) and tracheids with scalariform- or circular-bordered pits. Similarly, some Carboniferous ferns may be related to trimerophytes. Most of these Carboniferous ferns (filicalean ferns in part) are protostelic, some have tracheids with scalariform-, multiseriate scalariform- or circular-bordered pits (Phillips 1974), add some have a variable branching pattern (Holmes 1977). Because P. dawsonii (Banks et al. 1975) exhibits a distinction between main axes and possible precursors of leaves and putative roots, its vegetative appendages, in part, are thought to foreshadow the axillary branches found in *Botryopteris* and *Psalixochlaena* (Holmes 1977). Holmes (1977) describes the variable branching patterns of the Lower Pennsylvanian fern *Psalixochlaena cylindrica*. He considers *Psilophyton*, because of its stelar anatomy and stelar changes during dichotomy and the departure of some lateral traces, to be the type of trimerophyte that "could have given rise to ancestral forms of the coenopterid stock." In addition, the Carboniferous ferns and progymnosperms are stratigraphically younger than most known trimerophytes, hence strengthening their presumed evolutionary relationship (Banks 1968).

The plant to be described in this report is placed in the genus *Psilophyton* and will be described as a new species, *P. crenulatus*. This species has vegetative axes that divide dichotomously and pseudomonopodially with a variability in branching that is unparalleled among known trimerophytes. Fertile material exhibits a uniformity in branching patterns as well as characteristic sporangial morphology and ontogeny and spore morphology. Vascular strands are protostelic and tracheids have scalariform and circular-bordered pits. The descriptive features of *P. crenulatus* bear a threefold significance: 1) *P. crenulatus*, in comparison with other known trimerophytes, exhibits various attributes that further our understanding of the genus *Psilophyton* and suggest some relationship with the genus *Pertica*, 2) the large number of axes exhibiting morphologic variability make it possible to provide a more complete circumscription of the whole-plant characters of the species and makes *P. crenulatus* the best morphologically known species in the Trimerophytina and 3) the variable branching, stelar anatomy and quality and quantity of preserved axes of P. crenulatus provide an opportunity for better understanding the morphology and presumed developmental stages of primitive land plants which, in turn, may provide a better understanding of relationships among early land tracheophytes and their evolution toward more advanced plant forms.

MATERIALS AND METHODS

The specimens are embedded in a greyish to rust colored secondarily silicified tuff (Plate 1, Fig. 1). Petrographic thin sections reveal detrital clasts such as clays and fine organic matter (major detrital components) and some minor feldspars. Volcanic ash is, under certain conditions, easily changed into secondary silica. A transformation of this sort might be accomplished by a flooding of the ash, thus causing the silica to go into solution momentarily with a later recrystallization. Volcanic ash might have been the primary matrix; if this is so, the apparent singed nature of plant axes and paucity of preserved epidermal structures are better explained. The tuffaceous beds below and a thin sedimentary sequence above these fossiliferous beds further confirm this suggestion. The detrital clasts, especially the clays and fine organic matter, suggest a quiet water site of deposition which might have been lacustrine or a back levee flood plain of a meandering river. The mat of plant axes in Plate 1, Fig. 2 suggests that the plants were buried in situ.

Several techniques were employed throughout this project. Degaging (Leclercq 1960) was of limited value in studying axes due to irregular fracturing of the matrix causing a considerable loss of specimen detail along coaly plant axes. Bulk maceration using 48-52% (technical grade) hydrofluoric acid was the most useful technique for liberating plant axes from the matrix with minimal damage to the plant material. The apparatus in Text-fig. 1 was used to facilitate the removal of plant axes from the acid bath with minimal damage.

Specimens, submerged in water, were studied initially using a Wild M-5 dissecting microscope. Some specimens were air dried, placed on a stub, sputter coated with gold and then studied using a Cambridge S-150 scanning electron microscope (SEM). Others were placed on a slide, before or after treatment with Schulze's clearing solution (HNO_3 and $KClO_3$), covered with Turtox CMC-9 water soluble mounting medium and a coverslip and observed using a Zeiss photomicroscope.

To avoid shadows when photographing with the Leitz Aristophot the apparatus in Text-fig. 2 was used. Specimens were photographed on both sides when detail was obscured by overlying axes or when only both photographs provided a better record of the specimen. The axes were then air dried, restudied under a dissecting microscope and finally placed in Ward's Bio-Plastic (36 W 1020 Ward's Bio-Plastic Curriculum Aid Kit).

LOCALITY AND STRATIGRAPHY

The specimens in this study are from a road cut located on Beauvista Street, about 300 yards south from the corner of Route 134, in Atholville, New Brunswick (47° 59' 35" North, 66° 42' 36" West). The major portion of the road cut is a whitish grey tuff, but about midway through the tuff is a thin, recessive sedimentary sequence. The grey to rust colored fossiliferous beds are about 2 to 8 cm thick and are interbedded with about one meter of the lighter colored tuff at the base of the sedimentary sequence.

Alcock (1935) mapped these volcanics and sediments as Lower Devonian deposits and Greiner (preliminary map 74-114) has mapped them as part of the Lower Devonian Dalhousie Group. These beds are not specifically illustrated by Dinely and Williams (1968), but would, no doubt, be included in their "Lower Devonian Volcanics" which unconformably underlie the brecciated basal strata of the Atholville Beds (basal La Garde Formation). Correlation of the "Lower Devonian Volcanics" has been made (Dinely and Williams 1968) with the York River Formation (McGerrigle 1950) in eastern Gaspé. McGregor's (1966, 1973, 1977) studies of the Lower and Middle Devonian spores of eastern Gaspé have led to the conclusion that the lowest beds of the York River Formation are late Siegenian or lower Emsian age and the higher strata of the York River Formation are probably lower Emsian (McGregor 1977). It seems likely that the volcanics and sediments in Atholville, and in particular the fossiliferous beds of the present study, are lower Emsian (= Lower Devonian) in age (Text-fig. 3).

TERMINOLOGY

Before a description of Psilophyton crenulatus is given, it seems appropriate at this point to define the terms used to describe the various branching patterns exhibited by P. crenulatus.

In this paper dichotomous or isotomous branching refers to the division of an axis into two axes of equal size and, presumably, vigor. Pseudomonopodial or anisotomous branching refers to the unequal division of the shoot apex into two parts, one of which is more vigorous in growth and subsequently appears as the main axis. The other, overtopped axis, usually follows one of two paths of development: 1) growth is initially epidogenetic and later menetogenetic in which case the axis increases in size and vigor until it is equal or nearly equal to that of its parent axis or 2) growth is apparently apoxogenetic (determinate) in which case the axis develops as a lateral appendage. The terms apoxo-, epido- and menetogenetic refer, in a strict sense (Eggert 1961), to properties of the primary vasculature (decrease, increase and no change in diameter, respectively). For this study, however, I have also applied these terms to the diameter of the axes involved because changes in the diameter of the primary xylem are virtually unknown. But where primary xylem data are known, for example, in the Carboniferous fern Psalixochlaena (Holmes 1977), such changes in axial diameter do occur.

MORPHOLOGY AND HISTOLOGY

Most axes of the Psilophyton crenulatus specimens are flattened so that only their general morphology is apparent. Occasionally, however, cells are three dimensionally preserved so that a better understanding of the arrangement of tissue systems within the plant axes is possible. In general, it appears as though there was an outer cortex made up of thick-walled cells, an inner cortex (parenchyma?) - the cells of which have deteriorated, and the vascular strand. The epidermis is usually not preserved. Spines and crenulations are present on the surface of many axes. This arrangement of tissues, except for the spines and crenulations, is similar to that described for Psilophyton dawsonii (Banks et al. 1975).

Plate 1, fig. 3 illustrates a flattened axis where the outer cortex has been preserved. It is several cells wide with each cell having thick walls, a diameter of 12 to 34 µm, and slightly oblique to perpendicular end walls. The epidermis is generally absent. The outer cortex of the plant probably provided some support. This function is inferred by the thick-walled cells of the outer cortex and the relatively small size of the vascular strand.

CRENULATIONS

A characteristic that distinguishes this species from other species of Psilophyton is the presence of wart-like crenulations (Plate 1, figs. 6-9; Plate 2, figs. 14-17 and Plate 10, fig. 77) on most and sometimes all orders of fertile branching (a consistent characteristic), some main axes, some vegetative axes, and some spine bases. The crenulations appear scale-like when observed along the margins of axes and are semi-circular in shape (Plate 1, fig. 6; Plate 2, figs. 14 & 16 where "C" delimits area with marginal crenulations). A more accurate representation of the morphology of these structures can be seen where they are observed in face view. Here, away from the margins, they resemble small, apparently unicellular, circular to oval glandular hairs (Plate 1, figs. 6-9). The crenulations have a diameter of 100-200 µm. There is no evidence to suggest that crenulations are epidermal outgrowths. On the contrary, the absence of a covering epidermis on the crenulations, suggests that they are part of the outer cortex. Their function is uncertain.

SPINES

The spines that occur on main axes and many branches are round in cross section (Plate 1, fig. 5) and vary in size (from less than 1 mm to 6 mm), appearance (most are stout but some are hair-like) and distribution. Main axes and vegetative branches bear the majority of spines with occasional spines on the first two or three orders of some fertile branches. Spines are densely packed around assumed apical regions (Plate 5, figs. 42, 46, arrows) and obscure the distal portions of vegetative axes on which they are borne. An apparent fundamental difference between main axes and lateral appendages is the presence and relative abundance of spines on main axes compared to the paucity or lack of spines on lateral appendages. Many lateral appendages have only a few spines proximally and are naked distally (Plate 9, fig. 73) while some lateral appendages tend to be as spiny as main axes (Plate 6, fig. 50). All spines observed are pointed at their tips; most are undivided but some dichotomize or trifurcate (Plate 1, fig. 4). Spine bases are as wide as 1.[illegible] mm. Spine orientation is variable.

Plate 1, fig. 5 illustrates a multicellular spine in cross section. There is an outer zone of thick-walled cells identical to those of and in continuity with the outer cortex. A space is usually present inside the zone of thick-walled cells. The empty zone probably represents thin-walled parenchyma which has since deteriorated. Stomata have not been observed on spines, but crenulations sometimes occur on spine bases (Plate 1, fig. 7).

STOMATA

Although fertile and vegetative specimens are well preserved as coalified compressions, the paucity of stomata on these axes is enigmatic. As mentioned earlier, however, the primary preserving matrix might have been a hot volcanic ash that obliterated the epidermis. Specimens of *Psilophyton* from the Trout Valley Formation in northern Maine (Andrews et al. 1977, Kasper et al. 1974, Andrews et al. 1968) have no preserved stomatal or epidermal structures; Hueber's (1968) account of *P. princeps* from northern New Brunswick does not add any information about the epidermal structures of *Psilophyton*. Banks et al. (1975) report that the epidermis of *P. dawsonii*, from the Gaspé peninsula and Abitibi River, Ontario, is barely recognizable; they illustrate presumed guard cells in transverse section along with apparent substomatal chambers. Gensel (1979), however, does illustrate epidermal cells of *P. forbesii*. Plate 1, fig. 13 of the present report presents the first indisputable evidence of *stomata* on the axes of *Psilophyton*. The stomata are bounded by two guard cells which are 221 - 234 µm long; stomatal complexes are approximately 117 µm wide. Preservation did not allow elucidation of their distribution, but they have been observed on both vegetative and fertile axes.

VASCULATURE

Vascular strands, like the outer cortex, are occasionally preserved in three dimensions. This type of preservation has been observed only in wider axes. Strands in these axes exhibit centrarch maturation and range from approximately 400 µm to 1 mm in diameter (Plate 1, figs. 10 and 12, respectively). Metaxylem tracheids have diameters of 10 to 30 µm; their length is unknown. These tracheids have scalariform- and circular-bordered pits (Plate 1, fig. 11, arrows) with pit apertures being approximately 5 to 10 µm in diameter.

Plate 1, fig. 12 shows a vascular strand approximately 1 mm in diameter with an extensive amount of radially aligned metaxylem (no evidence of rays). Banks et al. (1975) have shown this type of metaxylem arrangement to occur in areas of profuse vegetative branching in P. dawsonii. It is unknown whether the strand in Pl. 1, fig. 12 came from a vegetative or fertile region.

DESCRIPTION OF THE FERTILE MATERIAL

The fertile branches are formed by the pseudomonopodial or dichotomous branching of main axes. Axes that bear fertile branches are 2.0 to 3.5 mm in diameter and spiny. The spines are identical to those previously described.

In my view, a fertile branch system of Psilophyton crenulatus consists of a primary branch and its branches that terminate in sporangia. Fertile branch systems are arranged in a loose spiral except when they terminate a dichotomous axis as in Plate 2, fig. 16. Primary fertile branches leave the main axis at an acute angle (approximately 45°) and are three dimensionally dichotomous with each successive division rotating through an angle of 90° (Plate 3, fig. 21). The overall length of a fertile branch system is approximately 2 cm.

The primary fertile branch is 1 to 2 mm wide as it leaves the main axis. Proceeding distally, a first dichotomy occurs 4.5 - 5.5 mm from the main axis, a second after another 2.0 - 5.0 mm from the first, a third after another 2.0 - 3.5 mm from the second, a fourth after another 1.5 mm, and the next one to three dichotomies are very closely spaced (Plate 2, figs. 19 and 20). Each branch produced by an ultimate dichotomy bears two sporangia (Plate 3, figs. 23 and 25).

Some specimens that bear mature sporangia have, attached to a common axis, terminal appendages that are paired, rounded or slightly elongated and exhibit a gradation in size (Plate 3, figs. 21, 22, 23 and 24 (arrow)). These terminations might represent vegetative branch tips or immature sporangia or possibly aborted sporangia. The isodiametric cells near the apices in Plate 3, fig. 22 (arrow) suggest that these tissues might have been immature at the time of preservation. Plate 3, fig. 24 illustrates a pair of mature, twisted sporangia and two smaller sporangium-like appendages (arrow) near their base. Mature, paired sporangia dehisce along a longitudinal slit on their inner facing surfaces (Plate 3, figs. 26 and 28). The longitudinal line on the inner facing surface of the upper termination in Plate 3, fig. 23 (arrow) resembles the dehiscence line found on mature sporangia. These data, in addition to the absence of associated vegetative branch tips suggest that Plate 3, figs. 21, 22, 23 and 24 (arrow) illustrate immature or possibly aborted sporangia. If this assumption is correct, then (since there is a gradation between immature/aborted and mature sporangia) this information represents the first documentation of sporangial ontogeny in Psilophyton. Plate 2, figs. 19 and [illegible] illustrate that sporangia of P. crenulatus are [illegible] primordia. The fertile branches, at maturity, are consistently recurved at the second or third dichotomy. This differs from P. dawsonii (Banks et al. 1975) where mature fertile branch systems are pendulous, horizontal or erect.

Mature sporangia are 1 to 2 mm wide, 3 to 5 mm long and fusiform with a small, slender distal beak (Plate 2, figs. 14-18; Plate 3, figs. 24-27). Each sporangium consists of an inner membraneous sac surrounding the spores (Plate 3, figs. 28 and 29, arrow) and an outer more resistant layer continuous with the outer cortex of the branchlets. The end walls of the cells in the outer layer are slightly oblique to perpendicular (Plate 3, fig. 24) and the cells are arranged obliquely to the long axis of the sporangium. It is, perhaps, the combination of these two characters that imparts, upon drying, a twisted configuration to the sporangium. In fact, the entire outer layer of the sporangium seems to act as a massive annulus. A calculated maximum of 128 sporangia can occur per fertile branch system. Fewer sporangia occur, in part, due to the presence of immature or possibly aborted sporangia (Plate 3, fig. 24, arrow) and/or the asymmetrical development of fertile dichotomies (Plate 3, fig. 25).

SPORES

In situ spores from attached sporangia of *P. crenulatus* are circular to subcircular in outline, trilete and range from 48 - 102 µm in diameter (average = 70 µm; N = 143). The sutures extend 1/3 to 2/3 along the spore radius, and a darkened area, due to a thickening of the spore wall (Plate 3, fig. 31), usually appears between the angle of the sutures (Plate 3, fig. 32; Plate 4, fig. 33). The spore wall is comprised of two layers; an inner wall which is smooth and an outer wall which is sometimes detached from the inner wall and is highly sculptured. The proximal surface of the inner wall is smooth with no visible curvaturae. The outer wall completely covers the distal surface of the inner wall and covers a portion of the proximal surface forming curvaturae that apparently represent the outer limit of tetrad contact areas (Plate 3, figs. 30 and 32). The sculpturing of the outer wall is uniformly distributed. Each element is 0.5 - 1.0 µm high, 0.1 - 0.3 µm wide at its base (Plate 4, figs. 36 and 37) and made up of several globules piled on top of each other. There is a reticulate network (perhaps representing sporopollenin) beneath the sculpturing (Plate 4, fig. 37). Some spores (Plate 4, fig. 35) have a trilete mark that appears to be on the distal rather than the proximal surface. This results from polar compression of the spore which causes the proximal surface to be pressed firmly against the distal surface giving the spore a cup-shaped appearance.

The spores of P. crenulatus most closely resemble the dispersed spore genus Apiculiretusispora (Streel) Streel. They compare very favorably with A. brandtii Streel as illustrated and described by McGregor (1973, pgs. 26-27; Plate 2, figs. 28-30) and Streel (1967).

DESCRIPTION OF VEGETATIVE MATERIAL

It seems appropriate to describe the vegetative characteristics in general terms so the significant features and overall variability of vegetative axes can be illustrated without a confusion of details. The essential details of the species will, however, be listed in the species diagnosis.

The main axes of Psilophyton crenulatus branch dichotomously and pseudomonopodially (anisotomously). Any one specimen, however, might illustrate a main axis with dichotomous branching exclusively (Plate 5, figs. 41, 43, 47 and 48), anisotomous branching exclusively (Plate 6, figs. 52, 53 and 55; Plate 8, fig. 62; Plate 9, fig. 69) or a combination of the two (Plate 6, fig. 49; Plate 7, figs. 60 and 61; Plate 10, figs. 76 and 77; Plate 11, figs. 78, 79, 82 and 83). Some axes branch profusely over a short distance (Plate 11, figs. 78 and 79) while other axes remain undivided for more than 10 cm (Plate 5, fig. 44) and still others fall in-between these two extremes (Plate 5, fig. 45; Plate 6, figs. 51 and 55; Plate 7, figs. 56 and 58; Plate 10, figs. 75 and 76). Profuse branching can produce as many as seven lateral appendages in a distance of 1 cm (Plate 9, figs. 69-71); in some specimens the areas of profuse branching occur shortly after a dichotomy in the main axis (Plate 11, figs. 78, 79, 82 and 83).

Main axes that branch anisotomously have lateral appendages arranged alternately (Plate 6, figs. 51, 52, 53, 55), spirally (Plate 9, fig. 72; Plate 11, figs. 79 and 82; Plate 12, fig. 85) or with no clear-cut organotaxy (Plate 7, figs. 59 and 60).

Lateral appendages vary in length from 2 mm (Plate 12, fig. 85, C) to 8.3 cm (Plate 4, fig. 38, arrow) and divide dichotomously in three dimensions (Plate 6, fig. 52), pseudomonopodially (Plate 12, figs. 85 and 87) or they appear to trifurcate (Plate 9, fig. 67; Text-fig. 15). Some of the longer lateral appendages are relatively undivided except in their more distal regions (Plate 7, figs. 56 and 60; Plate 8, figs. 62 and 65; Plate 9, fig. 68; Plate 10, figs. 73-77; Plate 11, figs. 79, 81 and 82; Plate 12, figs. 84-87). Some of the shorter lateral appendages are once or twice dichotomous (Plate 8, fig. 62; Plate 9, figs. 68 and 71; Plate 10, fig. 77; Plate 11, figs. 80 and 82) while others of intermediate size are twice to seven times dichotomous. Even a cursory examination of the specimens bearing these appendages, however, reveals that some specimens exhibit both extremes as well as intermediates and there is no perceived pattern to their occurrence.

The decrease in spine density in the more distal regions of lateral appendages has been referred to earlier (pg. 8), but it is a characteristic worth repeating and may have some bearing on the discussion and interpretation which follows. Examples of this characteristic are clearly illustrated in Plate 6, fig. 55; Plate 10, figs. 76 and 77 and Plate 12, fig. 85.

Many specimens exhibit hair- or spine-covered presumed apical regions (meristems?) in the form of 1) blunt or circinate tips of dichotomously branching systems (Plate 5, figs. 41, 42 and 43), 2) central axes in double dichotomies (Plate 5, figs. 45, 46 and 48; Plate 7, figs. 58, 59, 60 and 61), 3) overtopped (aborted?, dormant?) portions of a lateral appendage (Plate 6, fig. 55; Plate 7, figs. 56 and 57; Plate 9, figs. 67, 69, 70 and 71) or 4) as circinately coiled lateral primordia (Plate 11, fig. 80; Plate 12, figs. 84 and 85.

The specimens in Plate 5, figs. 41, 43, 45 and 46 are dichotomous throughout, they resemble major axes in all respects, they are complete to their terminations, and the terminations are circinately coiled, blunt or dichotomous; the circinate and blunt terminations are covered with spines or hairs. These characteristics call to mind the hairy apices of many fern rhizomes as well as the dichotomous habit of the rhizome of some ferns (Bower 1923, 1926, 1928) and *Lycopodium lucidulum* (Primack 1973).

There are many specimens that illustrate double dichotomies similar to those described for *Psilophyton dawsonii* (Banks et al. 1975). The central axis of the double dichotomy varies in length from a few millimeters (Plate 5, figs. 46 and 48; Plate 7, figs. 58, 59, 60 and 61) to 2.5 cm (Plate 10, fig. 76). There are intermediate lengths as well (Plate 5, figs. 45 and 46; Plate 8, figs. 64 and 65; Plate 9, figs. 68, 69 and 71; Plate 10, fig. 75, Plate 11, fig. 81; Plate 12, figs. 84, 85, 86 and 87). The specimen in Plate 10, fig.

75 (Text-fig. 19) is particularly interesting because it bears three complete double dichotomies whose central axes range from 2 mm to 1.9 cm. One central axis (on lateral A-3, Text-fig. 19) is 1.4 cm long and densely covered with spines (proximally and distally) while the longest central axis (B-c, Text-fig. 19) has very few spines proximally and distally and, in fact, is nearly glabrous.

An example of epidogenesis (indeterminate growth) is illustrated in Text-fig. 4 (Plate 4, fig. 38) where axis A measures 1.5 mm after the separation of appendage 6 and increases to 2.5 mm before it dichotomizes. This increase in diameter is most likely accompanied by a similar increase in primary xylem diamter.

Apoxogenesis (determinate growth) was illustrated in P. dawsonii (Banks et al. 1975) where traces in all branches became successively smaller toward their apices. Concomitantly, a similar decrease in axial diameter occurred. Apoxogenesis in Psilophyton crenulatus can be similarly illustrated based on successively smaller measurements in the more distal regions of some lateral appendages. For example, lateral B-1 in Text-fig. 18 (Plate 10, fig. 73) is 1 mm as it separates from B, it dichotomizes three times and the ultimate axes taper to rounded tips 0.1 mm in diameter.

Menetogenesis refers to little or no change in primary xylem diameter and although the primary xylem could not be examined (except in a few cases), many axes show no change in diameter for as much as 10 cm (Plate 5, fig. 44).

DIAGNOSIS

GENUS Psilophyton Dawson, 1859.

Diagnosis of Banks, Leclercq and Hueber, 1975, emended.

Stems branch dichotomously and laterally, the latter in an irregular, close or extended spiral or alternate in zones of vegetative branching; fertile branches, in zones alternating with vegetative zones, more distant or terminal, alternate, distichous or spiral; lateral branches dichotomous with successive dichotomies each formed at right angles to the other, pseudomonopodial or trifurcate; axes naked or spinous, ridged or unridged, compressions may be marked by punctiform scars; sporangia elongate-elliptical, pendulpus, paired, and borne terminally on repeatedly dichotomized main axes or lateral branches, total number of sporangia per lateral branch or dichotomized main axis large (64-128); dehiscence longitudinal along facing surfaces of paired sporangia; xylem a solid strand, centrarch; outer cortex collenchymatous except in areas of substomatal chambers.

Psilophyton crenulatus Doran, sp. nov.

Main axes spinous, crenulate, 2-3 (rarely 4) mm wide; spines up to 6 mm long, undivided, dichotomous or trifurcate usually absent or less frequently encountered on distal-most segments of lateral branches. Vegetative lateral branches up to 8.3 cm long, 2-7 times dichotomous, occasionally crenulate, occasionally with double dichotomies; double dichotomies with central axis short (1 mm) and spine-covered, intermediate length (1 cm) and spine-covered or relatively long (2.5 cm), spiny or glabrous. Fertile lateral branches 5-7 times dichotomous, pendulous after second or third dichotomy, crenulate consistently. Sporangia in tight clusters, 3-5 mm long by 1-2 mm wide, fusiform with small slender distal beak, pairs twisted around one another consistently. Spores trilete, 48-102 μm in diameter, subcircular to circular in outline, with darkened triangular area in angle made by trilete rays; spore wall of two layers, outer layer covers distal surface and portion of proximal surface forming curvaturae, sculpturing elements conical, 0.5-1.0 mm high and 0.1-0.3 μm wide at base, made up of descrete globules, inner wall smooth, thickened in angle between trilete rays. Xylem a centrarch protostele, up to 1 mm in diameter; metaxylem tracheids with slarariform- to circular-bordered pits.

HABIT and HABITAT

The morphological similarities between P. crenulatus and certain ferns (e.g. Botryopteris (Phillips 1974) and Psalixochlaena (Holmes, 1977) along with the multitude of intertwined axes in Plate 1, fig. 2, the relatively small size of the vascular strand and the slender axes with profuse branching (Plate 9, fig. 69) suggest that P. crenulatus had a rhizome or stolon-like habit with occasional upright vegetative and reproductive shoots that were perhaps 30 cm tall (see Text-fig. 27).

It would appear, from an analysis of the preserving matrix and the thick mat of intertwined plant axes in Plate 1, fig. 2, that

P. crenulatus might have lived in a quiet water lacustrine or back levee flood plain environment in which individuals grew in dense communities.

COMPARISON WITH OTHER SPECIES OF *PSILOPHYTON*

Psilophyton crenulatus fits within the emended diagnosis of the genus *Psilophyton* (Banks et al. 1975) and the characteristics that have already been enumerated make it a unique species. There are seven reasonably well known species of *Psilophyton*; four species have enations and three are glabrous. *P. dawsonii* (Banks et al. 1975) and *P. crenulatus* are the best known species, but collectively, all seven species show varying degrees of complexity. Doran et al. (1978) and Gensel (1979) have listed the significant characteristics delimiting species in the Trimerophytina and the genus *Psilophyton*; the spiny nature of *P. crenulatus* necessitates a comparison with the other species of *Psilophyton*.

Psilophyton dapsile (Kasper et al. 1974), considered to represent the most primitive species, is characterized by small (up to 2.0 mm wide) naked, dichotomous axes and comparatively small (1.7 - 2.1 mm long and 0.5 - 0.9 mm wide), elliptical sporangia. Kasper et al. (1974) indicate that there is so[illegible] overtopping, but this species is essentially dichotomous throughout. There is overtopping to all degrees in *P. crenulatus*. Fertile branches of *P. dapsile* are occasionally six times dichotomous before a pair of sporangia are borne. As a result of a seventh dichotomy, a fertile branch could theoretically bear 128 sporangia.

Psilophyton forbesii (Andrews et al. 1968, Gensel 1979), a second glabrous species, displays a greater degree of complexity than P. dapsile in possessing a monopodial habit with main axes up to 9 mm in diameter; longitudinal ridges are characteristic on the larger axes and may be a result of longitudinal fiber bundles in the outer cortex (Gensel 1979). The fertile branches of P. forbesii are borne laterally, are three dimensionally dichotomous and bear terminal, paired sporangia. The sporangia are considerably larger than those of P. dapsile, being 3.5 - 5.0 mm long and 1.3 - 1.8 mm wide and they tend to twist about each other (Gensel 1979). Fertile and vegetative branches are distinctly lateral and five to six times dichotomous. The vascular strand of P. forbesii is a small, centrarch protostele that is up to 0.5 mm in diameter (Gensel 1979).

The discovery and description of P. dawsonii (Banks et al. 1975) has been a major advancement in our understanding of the genus Psilophyton and has afforded a realization, in part, of the morphological variability and presumed growth potential that seems to have been inherent among the species of this genus. The fertile branches of P. dawsonii are alternate and distichous, usually six times dichotomous (three dimensionally) and terminate in clusters of approximately 64 sporangia, 3.0 - 5.0 mm long by 1.0 - 1.5 mm in diameter. The first two divisions of the fertile system are two closely spaced dichotomies where one of the three resulting branches aborts. This is referred to as a double dichotomy. The authors feel that "in exceptional cases, there is no abortion and three branches develop from the double dichotomy" (p. 86). This latter suggestion has led Banks et al. (1975) to compare this type of branching with adventitious root production in *Botryopteris antiqua*. Vegetative branches of *P. dawsonii* are arranged in an irregular, close spiral where the amount of central protoxylem in the main axis increases substantially and is occasionally surrounded by a distinct zone of metaxylem. This condition is only found where the branches exhibit unequal vigor. The authors suggest that lateral organs of this sort might represent the origin of leaves or, in some cases, adventitious roots. *Psilophyton crenulatus*, although it is spiny and differs from *P. dawsonii* in this regard, exhibits a similar profusion of vegetative branches and, where not fully documented in *P. dawsonii*, double dichotomies occur in many states of development.

In summary, *P. crenulatus* differs from the three glabrous species of *Psilophyton* because of their lack of spines; however, all show phenotypic similarities inherent to the genus and, more importantly, they collectively illustrate the variable nature of this genus.

There are four spiny species of *Psilophyton* to which *P. crenulatus* can be compared. *Psilophyton princeps* (Hueber 1968) is the type species for the genus and has had a long and confusing history. In the time since Dawson's (1859) original description of *P. princeps* many workers have contributed to the confusion and final clarification of what a '*Psilophyton*' is supposed to look like and how *P. princeps*, in particular, is to be characterized (e.g. see Kasper et al. 1974 and Banks et al. 1975 for summaries). The most distinctive character attributed to *P. princeps* is its peg-like enations; the enations are 2 to 2.5 mm in length and their tips are slightly flared, discoid and depressed in the center forming a small cup-like termination (Hueber 1968, p. 818). These enations occur on all parts of the plant except the last three dichotomies. The spines of P. crenulatus are sharply pointed to hair-like and in this respect P. crenulatus is very different from P. princeps. There are, however, other differences. Fertile branch systems of P. princeps have longitudinal ridges, arise through a dichotomous division of the main axis and are decussate; their overall length is approximately 5 to 6 cm. The sporangia are 7.5 to 8 mm long by 1 to 2 mm wide. Fertile branch systems of P. crenulatus are borne laterally in a loose spiral, their overall length is approximately 2 cm, crenulations cover several orders of branches, longitudinal ridges are absent and the sporangia are considerably shorter than those of P. princeps. Main axes of P. princeps measure up to 10 mm in diameter and are 2 to 3 times larger than the main axes of P. crenulatus. Vegetative axes of P. princeps have been described, but in little detail. Hueber's (1968) specimens from New Brunswick do not show vegetative branching; Kasper et al. (1974) collected vegetative portions of this species from northern Maine, but never described them. Andrews et al. (1977), however, offer a reconstruction of a portion of a vegetative axis of P. princeps from northern Maine which depicts vegetative branches as lateral organs that dichotomize 5 to 7 times and terminate in small (1 mm in diameter) recurved tips. The peg-like emergences occur on all orders of branching, including penultimate and ultimate branchlets, and are shorter and more densely distributed than the peg-like enations on the northern New Brunswick plant.

Psilophyton microspinosum (Kasper et al. 1974) has spines that are about 2 mm long and 0.4 mm broad at the base; they are not abundant and form an angle of 70° - 80° with the axis. In general, the spines of *P. microspinosum* are more delicate, much less abundant and less variable in size and shape (the spines of *P. crenulatus* divide) than spines of *P. crenulatus*. The more noticeable differences between *P. microspinosum* and *P. crenulatus* include alternately arranged fertile branch systems in *P. microspinosum* and helically arranged fertile units in *P. crenulatus*; sporangia of *P. microspinosum* are erect, elliptical and measure 3.5 - 4.0 mm long by 1 mm wide whereas those of *P. crenulatus* are pendulous, fusiform with a small, slender distal beak and measure 3 to 5 mm long by 1 to 2 mm wide. Fertile branch systems of *P. microspinosum* range from 2.0 cm to 4.5 cm in length and all are quite erect in appearance. The authors describe at least three dichotomies in these units, but suggest that there may have been one or two more divisions undetected. Each fertile unit of *P. crenulatus* is approximately 2.0 cm in overall length and there are six or seven dichotomies per unit. Fertile units of *P. crenulatus* have crenulations whereas those of *P. microspinosum* do not.

The details of *P. krauselii* are not well known but the sporangia are 2.0 - 2.5 mm long by 0.5 - 0.6 mm wide and, in comparison, are smaller than those of *P. crenulatus*. Also, *P. krauselii* is hairy whereas *P. crenulatus* has stout spines.

Psilophyton charientos, recently described by Gensel (1979) branches fairly profusely at 1.5 - 2 cm intervals. It has vegetative laterals that are borne at regular or irregular intervals, 1 mm to less than 0.5 mm wide and six to seven times three dimensionally dichotomous. Psilophyton crenulatus has variable branching, but can branch as many as seven times in a 1 cm distance; vegetative laterals are up to 2.5 mm wide, divide laterally and/or dichotomously and are up to 8.3 cm long. Spines of P. charientos are 2 - 2.5 mm long, 0.25 mm wide at the base, taper to very sharp points, are straight, slightly curved or curled and become smaller and fewer in number on the more distal portions of branches. Spines of P. crenulatus are up to 6 mm long, some are over 1 mm broad at their base, some divide dichotomously or trifurcate and some have crenulations on their bases. The tracheids of P. charientos have pit-like openings between the scalariform bars while the tracheids of P. crenulatus do not show this characteristic. Fertile branches of P. charientos are 2 - 3 cm long, 6 - 7 times dichotomous, 1.0 mm wide at their point of departure from the main axis, taper distally to less than 0.5 mm, are consistently recurved at the 4th or 5th dichotomy from the base of the lateral branch and bear spines on the basal segments only; crenulations are absent. Fertile branches of P. crenulatus are 1 - 2 cm long, 5 - 7 times dichotomous, 1 - 2 mm wide at their point of departure from the main axis, are consistently recurved at the 2nd or 3rd dichotomy from the base of the lateral branch and may have one or two spines on the primary branch; crenulations are abundant and cover several orders of branching. Sporangia of P. charientos are 3 - 4.5 mm long, 1.0 mm wide and only rarely seem to be twisted around one another. Spores of P. charientos are 48 - 74 μm in diameter whereas the spores of P. crenulatus are slightly larger. Psilophyton crenulatus is similar, in many respects, to P. charientos, but differs significantly from the latter to warrant a new species name.

DISCUSSION AND CONCLUSIONS

In fossil plant studies where anatomical data are available it is usually possible to determine stem-leaf-root relationships based on changes in symmetry or organization of the vasculature (Scheckler 1976). Anatomical studies of extremely primitive land plants are few in number, but data of this sort have become available (Kidston and Lang 1920, Banks et al. 1975) and where attempts to illustrate stem-leaf-root relationships have been made, there have been difficulties because of the simple (uniform?) organization of the anatomy involved. Nonetheless, investigators feel that certain primitive plants had begun to establish stem-leaf-root relationships by the late Emsian (Banks et al. 1975).

Whereas it is difficult to assess these relationships in an anatomical study, it is even more difficult when dealing with compression fossils due to the lack of three dimensionally preserved anatomy. Yet authors have made reference to this level of differentiation based mainly on the lateral position and comparative size of the appendages involved (Kasper and Andrews 1972). After studying many specimens of P. crenulatus one can see that there are differences between lateral appendages and main axes. A major difference is one of size; size distinction was made when defining the two terms (main axis, lateral appendage). Another difference is the presence and relative abundance of spines on main axes compared to the paucity or lack of spines on lateral appendages. The change in spine density is an interesting characteristic because this phenomenon occurs on other species of Psilophyton as well (Gensel 1979). Although the decrease in spine density might be related to apical volume or some other parameter and have no relationship with organ function, I feel that this characteristic (at least for P. crenulatus) might indicate a change in organ function from stem (where spine density is at a maximum) to leaf precursors or root precursors (where spines are either absent or at a minimum). The comparisons that follow, I believe, will help substantiate these claims and further our understanding of early land plant evolutionary pathways.

The origin of adventitious roots was, perhaps, partially elucidated when Banks et al. (1975) described the anatomy of Psilophyton dawsonii. They suggested that because changes in the size of the stele, during the production of certain appendages, were comparable to changes in the size of the stele of Botryopteris antiqua where it produced adventitious roots, the appendages of P. dawsonii might represent organs similar to the adventitious roots of B. antiqua. The authors suggested alternatively that these slender, flexuous appendages of P. dawsonii might represent aphlebiae. I would suggest that certain appendages of P. crenulatus, morphologically similar to the leaf-like and root-like appendages of P. dawsonii, might be interpreted as root-like and leaf-like organs as well. Some of these appendages are illustrated in Text-fig. 12, laterals A-2,3; Text-fig. 16; Text-fig. 17, laterals A-1,2 and D-1,2; Text-fig. 24, lateral 2/1 and Text-fig. 26, lateral 1/1.

The adventitious roots of Carboniferous ferns (e.g.

Botryopter[illegible]ceae, Anachoropteridaceae) are endogenous in origin and diarch; their cortex is composed of thick-walled cells in an outer zone and thin-walled cells that surround a centrally located vascular strand (Phillips 1970, 1974). Many of these adventitious roots are less than 1 mm in diameter, some divide and all seem to have an irregular arrangement. The spines of *P. crenulatus* have an outer zone of thick-walled cells and an inner zone of presumably thin-walled cells; they are undivided, dichotomous or trifurcate and they are irregularly arranged. The similarities between the data on spines of *P. crenulatus* and adventitious roots of some ferns such as *Botryopteris* and *Psalixochlaena*, along with the presence of spiny plants in the Upper Silurian (Edwards 1979), leads me to suggest that, if one applies the enation theory (Stewart 1964) to the evolution of adventitious roots in ferns, then the spines of *P. crenulatus* might be an early stage (pre-vascularization stage) in the evolution of these roots and a later vascularization and endogenous origin would be necessary to complete the sequence.

Many specimens illustrated in this report exhibit one or more double dichotomies where the central axis is either small and is represented by a short stump that is covered with spines (hairs?) (Text-figs. 6 & 10) or the central axis has grown out to varying degrees (Text-figs. 6, 7, 9, 13, 15, 16, 17, 19, 20, 22, 25). Double dichotomies have been found on other Devonian plants and the central axes have been referred to as stumps, bumps, axillary tubercles, arrested apices, axillary branches, etc. and in some cases have been compared to the rhizophores produced by extant selaginellas. Gensel's (1977) discussion of early land plant branching strategies makes reference to several fossil genera that exhibit these curious central axes and she suggests that "these occurrences seem to represent varying degrees or expressions of overtopping and to relate to or result from the influence of the shoot apex and differentiation of apices during ontogeny as plants evolved appendicular organs" (p. 26). The study by Cusick (1954) on morphogenesis in Selaginella willdenovii reveals that the absence or presence of growth regulators determines whether the angle-meristem of S. willdenovii produces a cauline system or rhizophore, respectively; a corollary to these findings is that the angle-meristem sometimes remains dormant for a long time and shows essentially no macroscopic growth. The primitive condition in the angle-meristem of S. willdenovii "is basically an embryonic shoot.... (and rhizophores occur as) a secondary change of growth pattern" (p. 180). It is tempting, therefore, to compare the angle-meristem (and its resultant axes) of S. willdenovii with the stumps, bumps, etc. that are found in Gosslingia (Edwards 1970), Psilophyton (Banks et al. 1975, the present report), Zosterophyllum (Lele and Walton 1961), Crenaticaulis (Banks and Davis 1969) and Renalja (Gensel 1976). In particular, the central axes of the double dichotomies in P. crenulatus illustrate many stages of development and, because of the morphological (developmental?) similarities between them and the embryonic shoot/rhizophore of S. willdenovii, I suggest that in some cases these central axes might represent extensions of the cauline system of P. crenulatus (perhaps representing an attempt at vegetative reproduction) while in other cases they might represent rhizophore-like structures for rooting or additional support.

The variable branching patterns exhibited by P. crenulatus are, in some cases, morphologically similar to the branching patterns of certain primitive ferns. For example, the Carboniferous fern Psalixochlaena cylindrica (Holmes and Galtier 1975, Holmes 1977) exhibits stems that produce a lateral branch where the lateral 1) divides to produce leaves, 2) may become dormant as an axillary or epipetiolar bud on a developed leaf (the leaf is defined as an axillant leaf when in constant association with an epipetiolar branch) or 3) may go undivided for a considerable length, attain a size that is similar to the main axis and function as such. Also, certain species of Botryopteris (Phillips 1961, 1970, 1974, Brosier 1976) have stem-branch-leaf relationships that are quite variable in nature; of particular interest are the foliar to cauline branching patterns in this genus. The comparisons that follow will be based on the external vegetative characteristics because of the poorly preserved internal anatomy of P. crenulatus.

The stem of Psalixochlaena cylindrica sometimes divides to form a branch and an axillant leaf. The branch and leaf at first share a common trace, but then the two separate and the branch becomes situated in the 'axil' of the leaf; i.e., the branch is an axillary or epipetiolar bud on a developed leaf. The branch may later develop and bear leaves spirally, in which case the axillant leaf may appear as the first leaf on the lateral branch (compare Text-figs. 7, 9 and 15 in Holmes 1977). If we examine P. crenulatus for similar stem-branch-leaf relationships we do find similarities that might even be considered homologous; however, the 'leaves' of P. crenulatus are not laminated megaphylls (they might represent leaf percursors) and the changes in the vasculature of P. crenulatus are unknown. For example, in Text-fig. 18 (Pl. 10, fig. 73), lateral B-1 might represent the axillant leaf precursors and the once epipetiolar branch precursor, B, has developed and borne spirally arranged leaf precursors B-2, B-3 and B-4. Similarly, in Text-fig. 25 (Pl. 12, fig. 85), lateral 1/1 might represent the axillant leaf precursor and the once epipetiolar branch precursor, 1, has developed and borne the spirally arranged leaf precursors 1/2, 1/3, 1/4 and 1/5 (lateral 1/5 is still circinately coiled). If we consider axis A in Text-fig. 14 (Pl. 9, fig. 72), to be the epipetiolar branch precursor, then lateral 1 represents the axillant leaf precursor and laterals 2, 3, 4, 5, 6, and 7 represent the spirally arranged leaf precursors on the developed axis, A; lateral 7 is still a bit recurved.

Branches of Psalixochlaena may also go undivided for a considerable length, attain a size that is similar to the main axis and function as such. Psilophyton crenulatus has axes that remain undivided for more than 10 cm (Plate 5, fig. 44), they are very similar to main axes and would probably be considered as such if found isolated.

In Botryopteris antiqua (Galtier 1969, Phillips 1970) a shoot, originating in the proximal region of a pinna, produces five petioles of secondary fronds; the cauline structure and foliar member initially share a common trace. Other species of Botryopteris (Phillips 1961) have proximal and distal plantlets, borne on foliar members, that bear spirally arranged petioles; the foliar units of the plantlets in *B. forensis* (Phillips 1961, 1974) are both two and three dimensionally divided. The specimens of *P. crenulatus* that have previously been compared to *Psalixochlaena* might also be compared to those species of *Botryopteris* where (e.g. *B. forensis*) there are three dimensionally divided foliar units of plantlets and major axes bearing spirally arranged lateral appendages.

Relationships between trimerophytes and some Carboniferous ferns have been largely based upon the similarities in their reproductive structures (Kasper and Andrews 1972). The discovery of *Psilophyton dawsonii* (Banks et al. 1975), however, illustrates that there are similarities in anatomy and variability in branching as well. The similarities in vegetative branching and in the reproduction structures of *P. crenulatus* and certain Carboniferous ferns further suggest that *Psilophyton* was, indeed, ancestral to some primitive ferns and that cauline and foliar (megaphyllous) differentiation had begun by the lower Emsian.

The presumed relationships between trimerophytes and progymnosperms have been discussed by Banks et al. (1975) and Andrews et al. (1975). Andrews et al. (1975) suggest that the progymnosperms might be related to trimerophytes via plants like *Oocampsa* and certain species of *Psilophyton*. The variable branching patterns found in *P. crenulatus* do not shed any light on presumed evolutionary pathways leading to the progymnosperms, but do illustrate the plasticity of trimerophyte taxa and support the suggestion that, because trimerophytes exhibit such a variety of branching patterns, they might have had a part in the evolution of progymnosperms (Banks 1968, Banks et al. 1975). The addition of Petrica dalhousii (Doran et al. 1978) to the list of known trimerophytes opens speculation that the spirally arranged branches and loosely arranged terminal clusters of sporangia found in this plant might represent an initial step toward the evolution of some progymnosperms (e.g. Rellimia). Andrews et al. (1975) suggest that Pertica, because of its compact clusters of sporangia, is in a line of evolution leading to Carboniferous ferns such as Botryopteris and Anachoropteris; the spirally arranged branches and loosely arranged terminal clusters of sporangia just described for P. dalhousii, however, in addition to its relatively larger size (compared to Psilophyton), leads me to suggest that certain species of Pertica (namely P. dalhousii) may have been evolving toward a progymnosperm morphology as well. The discovery of anatomically preserved Pertica will, in my opinion, be an important addition to our understanding of early land plants and their evolution.

Psilophyton is a widespread genus having been found in Ontario, northern Maine, northern New Brunswick, the Gaspe peninsula, Scotland, Norway and Siberia (Banks et al. 1975). It ranges stratigraphically from the late Siegenian (Croft and Lang 1942) to the Emsian-Eifelian (Lower-Middle Devonian) boundary. Banks et al. (1975), after careful study, report no valid evidence of Upper Devonian Psilophyton, but suggest [illegible]at it persisted into later Middle Devonian; most species of Psilophyton are known from the late Lower (= upper Emsian) Devonian (Gensel 1979).

The oldest plant remains belonging to the Trimerophytina (Banks 1968) are fragments, referable to Dawsonites arcuatus, described from the late Siegenian of Wales (Croft and Lang 1942). Banks et al. (1975) and Gensel (1979) note that there are abundant remains of *Psilophyton* from the Emsian-Eifelian boundary, yet no examples of *Psilophyton* have been found from the strata between (i.e., lower Emsian). The discovery of *Psilophyton crenulatus* fills that gap in the stratigraphic range of *Psilophyton* and provides valuable information about trimerophytes and plant evolution during the Lower Devonian.

The Trimerophytina (Banks 1968) has been proposed as the plexus from which certain younger plant groups evolved. This assumption was based, in part, on the level of complexity and plasticity (variable morphology) exhibited by trimerophytes as a whole. *Psilophyton crenulatus*, I think, exemplifies these characteristics in its possession of dichotomous and pseudomonopodial main axes, lateral appendages that demonstrate a morphologic variability unprecedented among known trimerophytes, terminal [illegible]ters of sporangia that dehisce longitudinally and a centrarch vascular strand. Doyle and Hickey (1976), in their discussion of the transition flora from pre-angiosperm taxa to early angiosperms of the Lower Cretaceous, describe what they think the characteristics and environment of the earliest angiosperms might have been. Their characterization of early angiosperm taxa is of particular interest because it suggests a gradual change in form and function from pre-angiosperms to true angiosperms. They write, in a paraphrase of Boch's (1965) work, that "the shift from one zone to another occurs in a transitional adaptive zone where, under new selective pressures, structures which had arisen under different selective pressures in the ancestral adaptive zone....take on new functions" (p. 184). Using this information in an analogy with early land plant evolution, I would designate the rhyniophytes, characterized by dichotomous, three dimensional axes, terminal sporangia and slender centrarch vascular strands, as the ancestral stock. Banks et al. (1975) suggest that "the trimerophytes can only be regarded as an elaboration of the rhyniophyte level of evolution resulting from the interplay of overtopping and elaboration in both anatomy and morphology." They state further that "the trimerophytes represent a natural plexus at an evolutionary level whence such groups as coenopterids and progymnosperms might evolve" (p. 112). Clearly, from the previous discussion and description, *Psilophyton crenulatus* and the other known trimerophytes represent a transitional plexus where, under new selective pressures, the morphology and anatomy of rhyniophytes have been modified to perform new functions (i.e., primitive leaves and roots) in trimerophytes and, in turn, the trimerophytes provide the foundation for subsequent changes found in more highly evolved taxa.

GENERAL SUMMARY

The new species *Psilophyton crenulatus* is a unique species of fossil plants because of its variable vegetative branching systems, crenulations and fertile units. Its mode of preservation has allowed the recovery of numerous plant axes that illustrate a heretofore unprecedented degree of variability in branching among known Lower Devonian plant fossils; the variable branching found in *P. crenulatus* has allowed a more complete circumscription of the 'whole-plant' characteristics of the species and has provided a strong basis for comparison with other trimerophytes and more highly evolved plants, namely some Carboniferous ferns and progymnosperms. This information further emphasizes the suggestion (Banks 1968) that the trimerophytes were an important group of early land plants, most likely ancestral to several more highly evolved groups, and that <u>Psilophyton</u> was not only a major component of the early land flora, but was indeed a very important element in the subsequent evolution of vascular plants.

As we accumulate more data we find that although the present systems of early vascular plant classification are useful they are artificial in the sense that they do not reflect the intergradation of taxa that results from gradual evolutionary changes.

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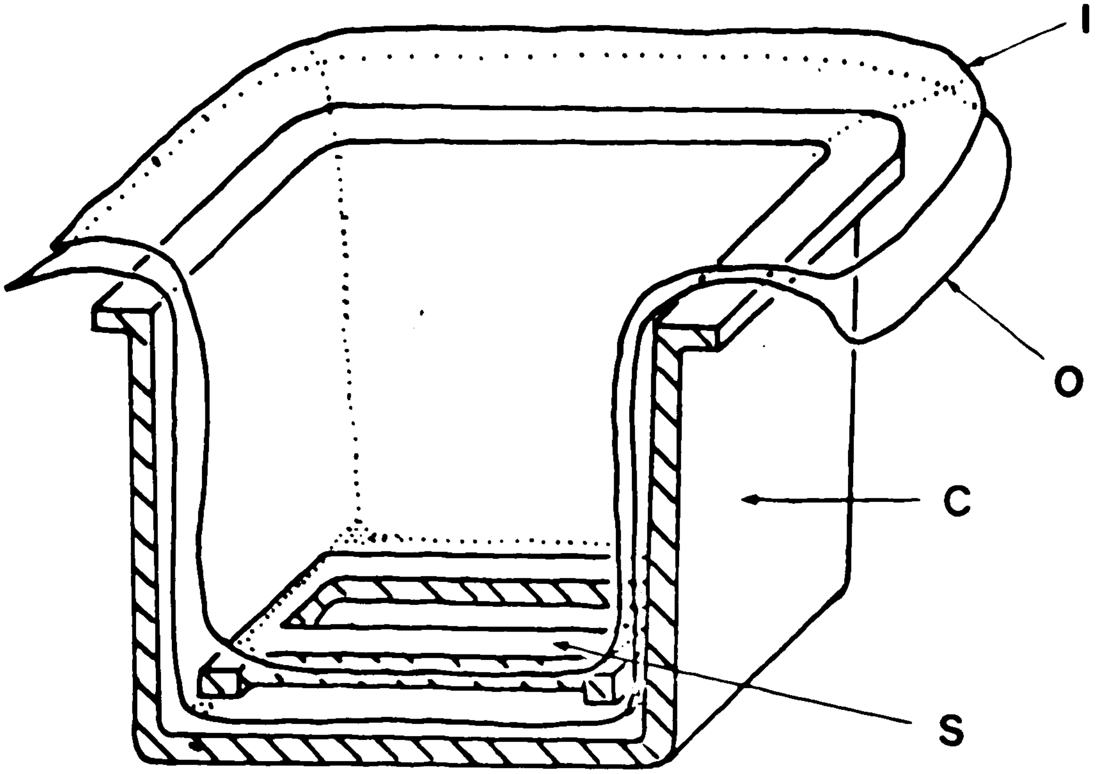
Text-figure 1.

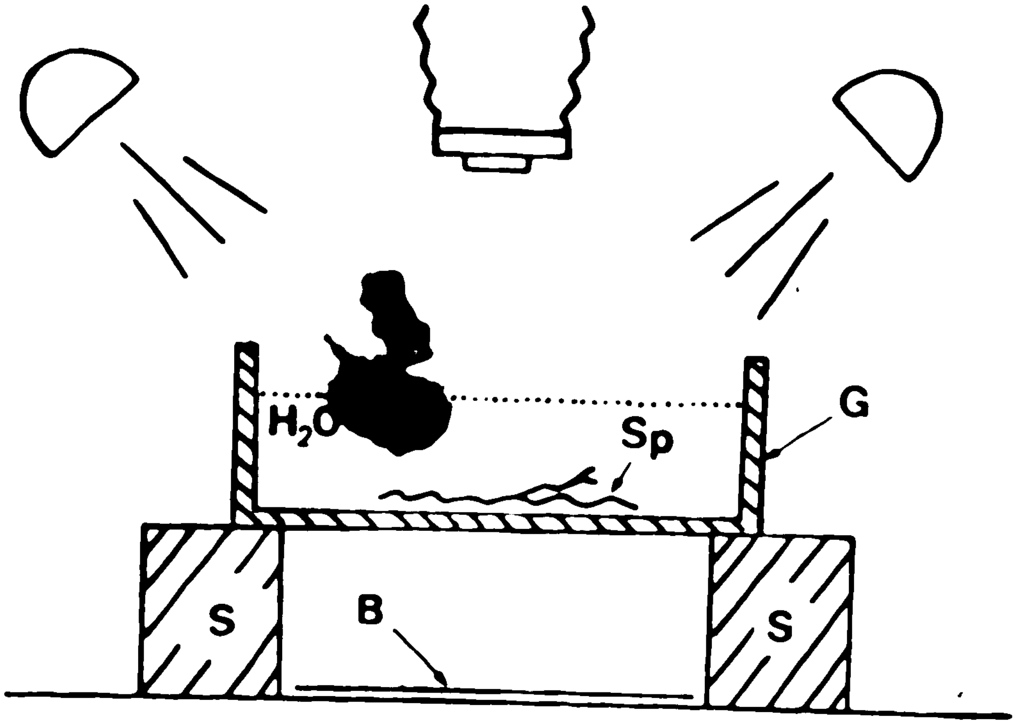
The rock specimen, when placed in the container (C), is supported by inner (I) and outer (O) nylon screens that are separated by a perforated piece of sheet plastic (S). The sheet plastic and the inner nylon screen are the principle supports when the freed axes are lifted from the acid bath (by lifting the outer screen); the sheet plastic prevents the inner screen and carbonized plant axes from bending or breaking while the mesh and perforations allow sludge to be sifted from the axes.



Text-figure 1.

Text-figure 2.

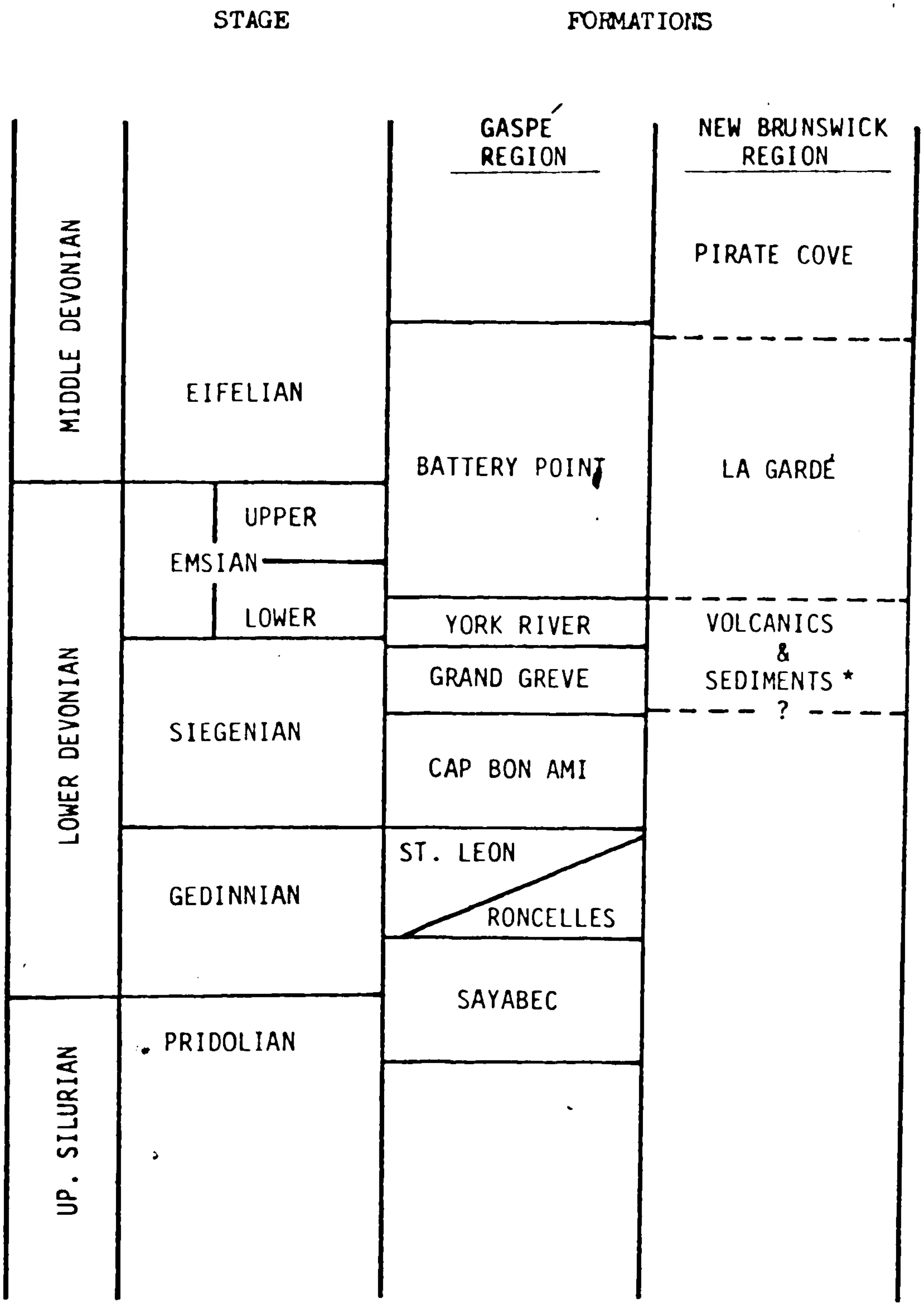
Photographic apparatus for eliminating shadows; Sp = specimen, G = glass container fashioned from plate glass, B = black construction paper to reduce reflection, S = 8-10" supports.



Text-figure 2.

Text-fig. 3

Correlation chart showing the position of the volcanics and sediments at Atholville and the York River Formation in the Gaspe region. Asterisk denotes beds in which Psilophyton crenulatus occurs. Modified from McGregor (1977) and Dinely and Williams (1968).



Text-figure 3.

Most spines have been omitted from Text-figures 4-26.

Text-figures 4-8

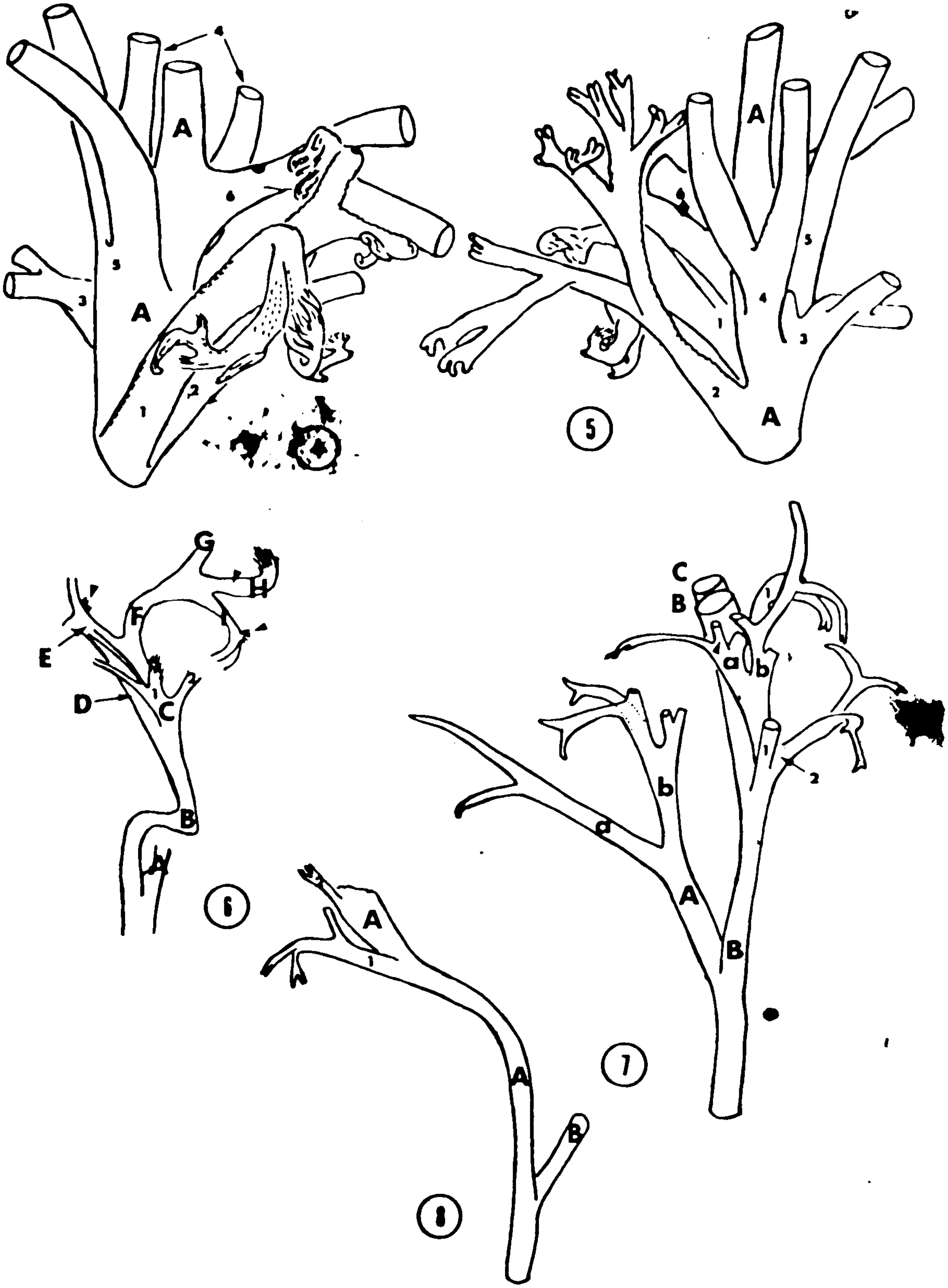
Text-figure 4. Tracing of Plate 4, fig. 39 showing arrangement of laterals (numbers) on a main axis (A).

Text-figure 5. Tracing of Plate 4, fig. 40 showing arrangement of laterals (numbers) on a main axis (A).

Text-figure 6. Tracing of Plate 5, fig. 45 showing resultant axes of dichotomies (letters, except H), laterals (1) and central axes of double dichotomies (diamonds and H).

Text-figure 7. Tracing of Plate 6, fig. 49 showing arrangement of laterals (numbers) on main axes (capital letters) and dichotomies in axes (small case letters). Diamond indicates central axis of double dichotomy.

Text-figure 8. Tracing of Plate 6, fig. 54 showing arrangement of laterals (numbers) on main axes (letters).



Text-figures 4-8.

Text-figures 9-15.

Text-figure 9. Tracing of Plate 7, fig. 56 showing arrangement of laterals (numbers) on a main axis (A). Arrow indicates spine-covered arm of dichotomy; diamond indicates central axis of a double dichotomy.

Text-figure 10. Tracing of Plate 7, fig. 58 showing arrangement of laterals (numbers) on a main axis (A)., Diamond indicates central axis of a double dichotomy.

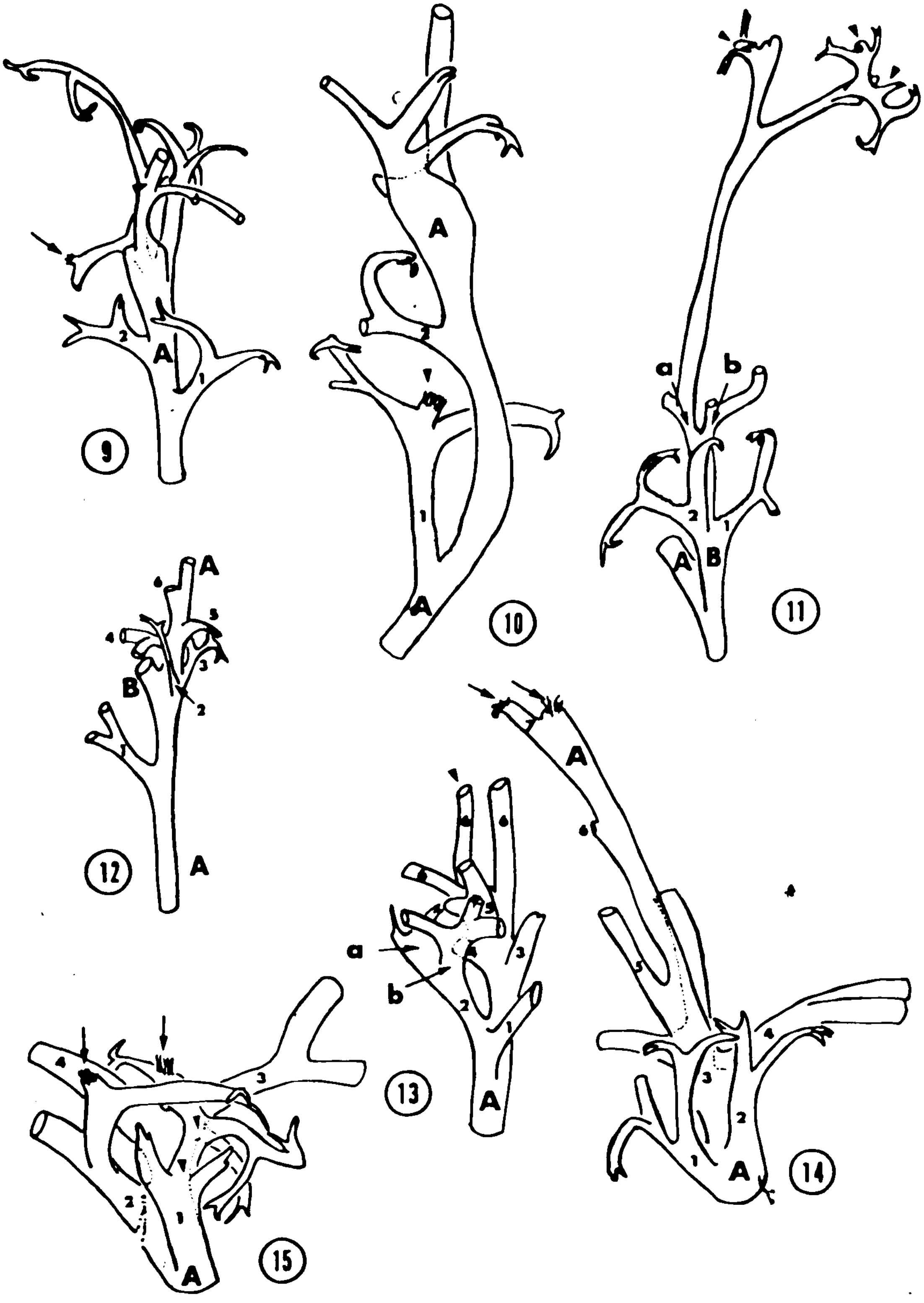
Text-figure 11. Tracing of Plate 7, fig. 60 showing arrangement of laterals (numbers). A & B = main axis; B dichotomizes to form a & b. Diamonds indicate central axes of double dichotomies.

Text-figure 12. Tracing of Plate 8, fig. 63 showing arrangement of laterals (numbers) on main axes (letters).

Text-figure 13. Tracing of Plate 8, fig. 64 showing arrangement of laterals (numbers) on a main axis (A). a & b indicate dichotomy in lateral 2. Diamond indicates central axis of double dichotomy.

Text-figure 14. Tracing of Plate 9, fig. 72 showing arrangement of laterals (numbers) on main axis (A). Arrows indicate spine-covered presumed apical regions.

Text-figure 15. Tracing of Plate 9, fig. 67 showing arrangement of laterals (numbers) on main axis (A). Arrows indicate spine-covered presumed apical regions; diamonds indicate trifurcations on lateral 1.



Text-figures 9-15.

Text-figures 16-21

Text-figure 16. Tracing of Plate 9, fig. 71 showing arrangement of laterals (numbers) on main axis (A). Diamond indicates central axis of double dichotomy on lateral 5.

Text-figure 17. Tracing of Plate 9, fig. 68 showing arrangement of laterals (numbers) on main axes (letters). Diamonds indicate central axes of double dichotomies.

Text-figure 18. Tracing of Plate 10, fig. 73 showing arrangement of laterals (numbers) on main axes (letters).

Text-figure 19. Tracing of Plate 10, fig. 75 showing arrangement of laterals (numbers) on main axes (capital letters). Small case letters (a,b,c) indicate axes in double dichotomy; c is central axis.

Text-figure 20. Tracing of Plate 10, fig. 77 showing arrangement of laterals (numbers) on main axes (capital letters). B ultimately undergoes a double dichotomy to produce a, b and central axis c (diamond). Arrow indicates primordia.

Text-figure 21. Tracing of Plate 11, fig. 79 showing arrangement of laterals (numbers) on main axes (A, B).

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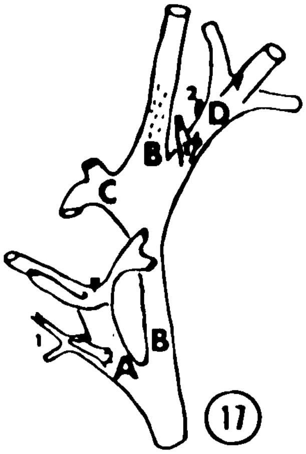

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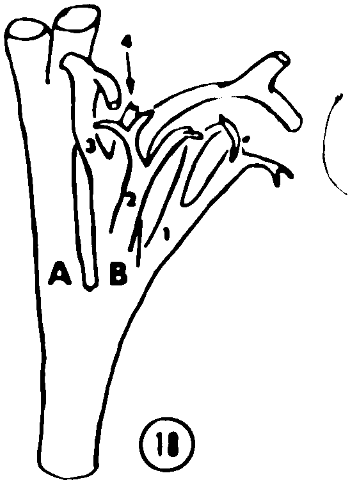

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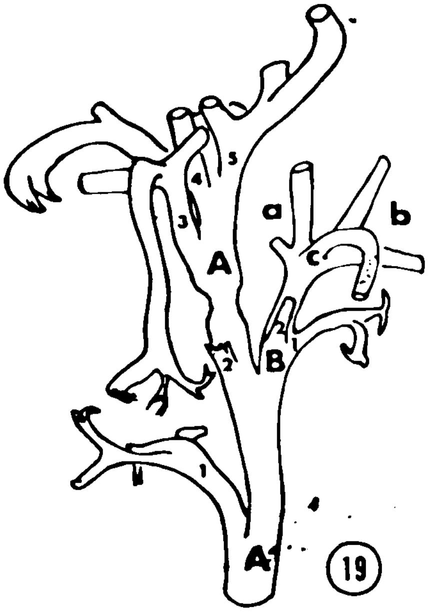

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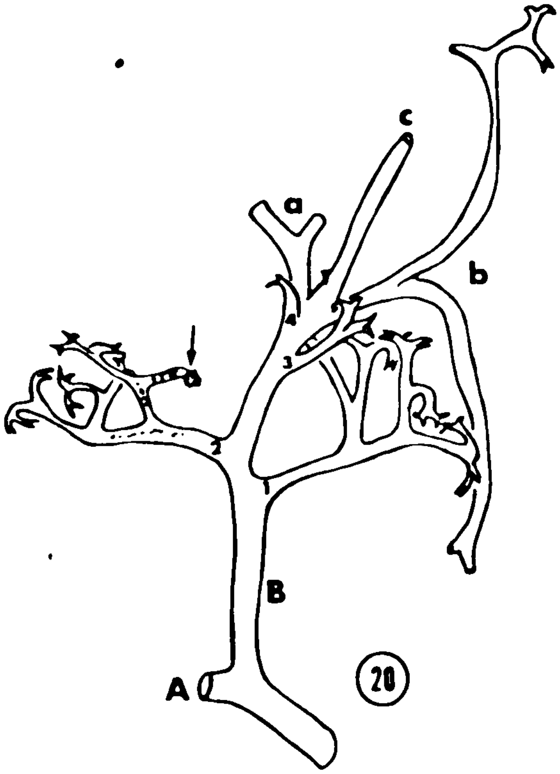

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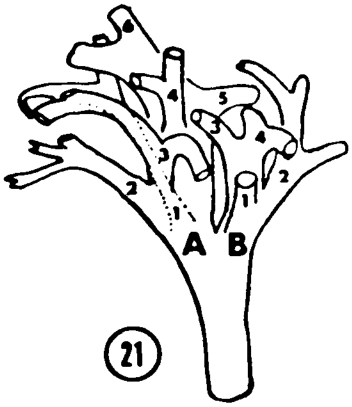

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Text-figures 16-21.

Text-figures 22-26

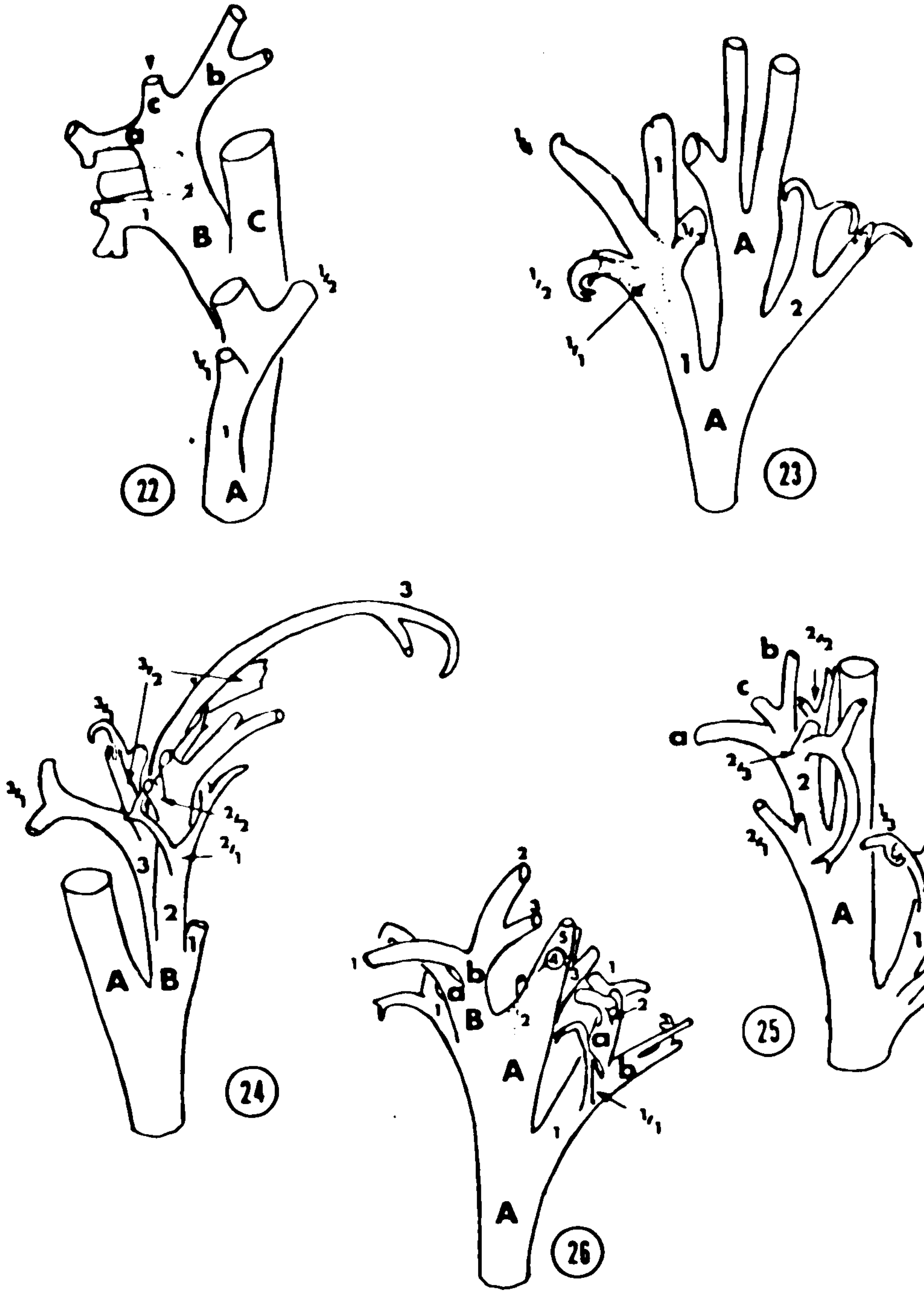
Text-figure 22. Tracing of Plate 11, fig. 81 showing arrangement of laterals (numbers) on main axes (A,B,C). B ultimately undergoes a double dichotomy to produce a, b and central axis c (diamond).

Text-figure 23. Tracing of Plate 11, fig. 80 showing arrangement of laterals (numbers) on a main axis (A). Lateral 1 divides laterally.

Text-figure 24. Tracing of Plate 11, fig. 82 showing arrangement laterals (numbers) on main axes (A,B). Note laterally divided laterals 2 and 3.

Text-figure 25. Tracing of Plate 12, fig. 85 showing arrangement of laterals (numbers) on main axes (A,B). A-1 divides laterally and dichotomizes to form a and b. B dichotomizes to form a and b.

Text-figure 26. Tracing of Plate 12, fig. 87 showing arrangement of laterals (numbers) on a main axis (A). Both laterals (1 and 2) divide laterally; lateral 2 ultimately undergoes a double dichotomy to produce a, b and central axis C. Note the circinately coiled 1/5.



Text-figures 22-26.

Text-figure 27.

Reconstruction of Psilophyton crenulatus based on vegetative and reproductive structures screened from the plant mat in Plate I, fig. 2 and another mat of axes presently under study. Fertile branches are spirally arranged or terminate a dichotomizing axis; vegetative laterals are alternately or spirally arranged or show no definite organotaxy. Some of the smaller vegetative laterals depict presumed adventitious root precursors or leaf precursors. The presumed habit of P. crenulatus is rhizomatous or stoloniferous with the central axis of double dichotomies representing rhizophore-like structures (extensions of the cauline system or root-like structures). Approx. X1.

Text-figure 27.

EXPLANATION OF PLATES

Important details not readily visible in the following figures are best seen in the Text-figures referred to in the figure captions.

PLATE I

Fig. 1. General appearance of P. crenulatus on rock surface. X0.8.

Fig. 2. Mat of intertwined axes after dissolution of rock matrix. X0.3.

Fig. 3. SEM of flattened axis showing thick walled cells of the outer cortex. UAPC S7144. X68.

Fig. 4. SEM of a trifurcate spine. UAPC S7145. X41.

Fig. 5. SEM of a spine in cross section near spine base. UAPC S7145. X105.

Fig. 6. SEM of marginal and submarginal crenulations. UAPC S7146. X80.

Fig. 7. SEM of crenulations on main axis and spine base. UAPC S7147. X38.

Fig. 8. SEM of oval crenulations. UAPC S7148. X115.

Fig. 9. SEM of round crenulation. UAPC S7146. X254.

Fig. 10. SEM of slightly flattened vascular strand in cross section. UAPC S7149. X100.

Fig. 11. SEM of metaxylem tracheids with circular-bordered pit (upper arrow) and scalariform-bordered pits (lower arrows). UAPC S7150. X875.

Fig. 12. SEM of radially aligned metaxylem tracheids. UAPC S7150. X50.

Fig. 13. Light micrograph of two stomata from fertile axis. UAPC SL5715. X100.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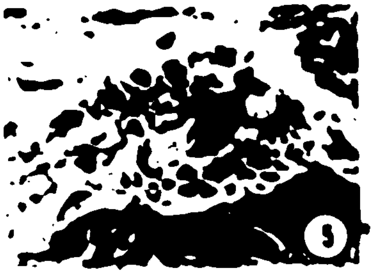
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PLATE 2

Fig. 14. Most complete fertile specimen with seven lateral branches. C delimits area with visible marginal crenulations. UAPC S7109. X2.9.

Fig. 15. Obverse view of the specimen in Fig. 14. UAPC S7109. X2.9.

Fig. 16. Dichotomous fertile specimen from distal-most portion of fertile axis. C denotes area with visible marginal crenulations. UAPC S7110. X2.

Figs. 17 & 18. Two views of one fertile specimen. Specimen in Fig. 17 broke during preparation for Fig. 18; sporangia in Fig. 18 (obverse of Fig. 17.) represent lower-most clusters in Fig. 17. UAPC S7111. X2.1.

Fig. 19. Fertile specimen showing pendulous orientation of young sporangia. UAPC S7112. X1.6.

Fig. 20. Close up of obverse side of Fig. 19 showing sporangial primordia, dichotomous divisions in a fertile unit and boat-shaped appearance of dehisced lowermost sporangium. UAPC S7112. X10.

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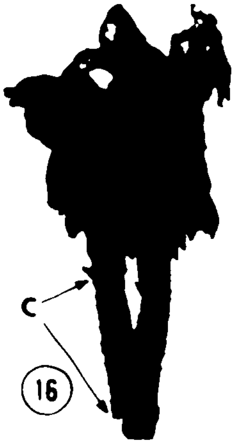

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PLATE 3

Figs. 21-28. Sporangial ontogeny.

Fig. 21. SEM of eight pairs of sporangial primordia; note that each dichotomy is at an angle of 90° to the previous division. UAPC S7151. X30.

Fig. 22. SEM of two young sporangia; note isodiametric cells of apical region (arrow). UAPC S7152. X75.

Fig. 23. SEM of two young sporangia; note incipient longitudinal line of dehiscence on inner facing wall of upper sporangium (arrow). UAPC S7152. X74..

Fig. 24. SEM showing two mature (twisted) sporangia and two immature sporangia (arrow). UAPC S7153. X11.

Fig. 25. SEM of six pairs of mature sporangia. UAPC S7154. X7.1.

Fig. 26. SEM showing two dehisced sporangia that have twisted around each other. UAPC S7155. X17.

Fig. 27. SEM of distal beak. UAPC S7156. X66.

Fig. 28. SEM of one mature, longitudinally dehisced sporangium revealing multitude of isospores. UAPC S7157. X38.

Fig. 29. SEM showing spores in sporangium, inner membraneous sporangial sac (arrow) and thick outer sporangial wall. UAPC S7158. X190.

Fig. 30. SEM of spore showing proximal surface, trilete mark and detachable outer layer. UAPC S7157. X750.

Fig. 31. SEM of proximal surface of spore and trilete mark. UAPC S7157. X710.

Fig. 32. Light micrograph of spore showing darkened area in angle of trilete rays. UAPC SL5714. X600.


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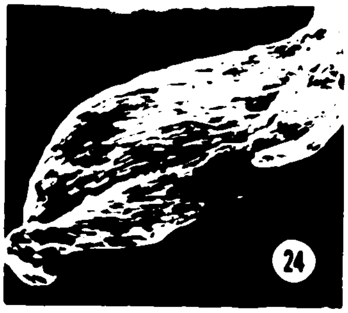
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PLATE 4

Fig. 33. Light micrograph showing darkened area in angle of trilete rays. UAPC SL5715. X580.

Fig. 34. Light micrograph of ornamentation on distal surface of spore. UAPC SL5716. X600.

Fig. 35. SEM showing trilete mark pushing up distal surface. UAPC S7157. X600.

Fig. 36. SEM showing normal, ornamented distal surface of spore. UAPC S7157. X650.

Fig. 37. SEM close up of spore ornamentation. UAPC S7157. X11,520.

Fig. 38-40. Fertile and vegetative axes on same specimen.

Fig. 38. Entire specimen with two (basal-most) fertile branches and four (upper-most) vegetative ages; arrow indicates 8.3 cm lateral. UAPC S7113. X1.2.

Fig. 39. Close up of fertile branches (see Text-fig. 4) and vegetative axes; arrows indicate sporangia. UAPC S7113. X3.3.

Fig. 40. Obverse side of Fig. 39 (see Text-fig. 5). UAPC S7113. X3.3.

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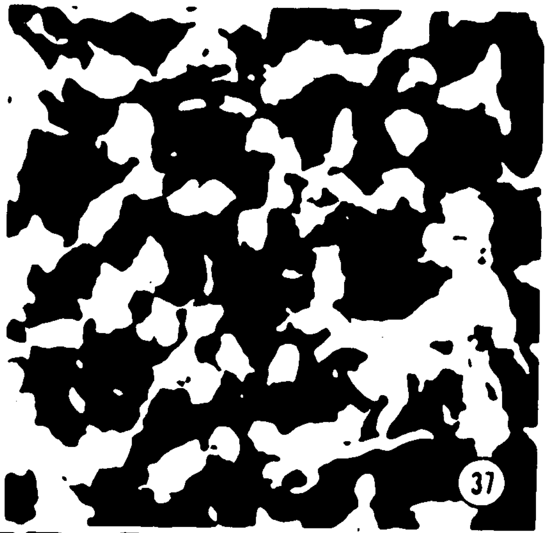

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VEGETATIVE AXES

PLATE 5

Fig. 41. E[illegible]ly dichotomous specimen; note spines and terminations. UAPC S7114. X1.7.

Fig. 42. Close up of spines and terminations (arrows). UAPC S7114. X3.2.

Fig. 43. Dichotomous specimen. UAPC S7115. X1.2.

Fig. 44. Two specimens with long, sparsely divided axes. UAPC S7116. X0.7.

Fig. 45. Specimen illustrating several double dichotomies (see Text-fig. 6); this specimen might represent either a vegetative terminal-most portion of P. crenulatus or a ground-level portion of the rhizome with dichotomous adventitious roots. UAPC S7117. X3.3.

Fig. 46. Obverse side of Fig. 45; arrows indicate central axis of respective double dichotomies. UAPC S7117. X3.3.

Fig. 47. Incipient dichotomy resulting in two determinate appendages (arrows). UAPC S7118. X2.7.

Fig. 48. Specimen similar to Fig. 47, but with double dichotomy and slightly longer, more developed appendages. UAPC S7119. X2.3.


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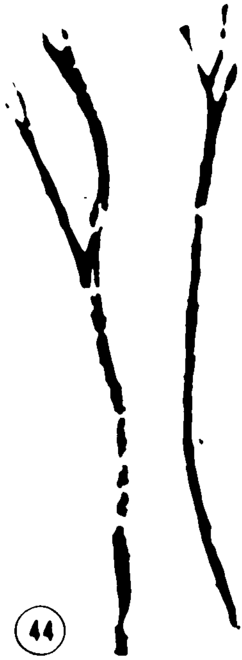
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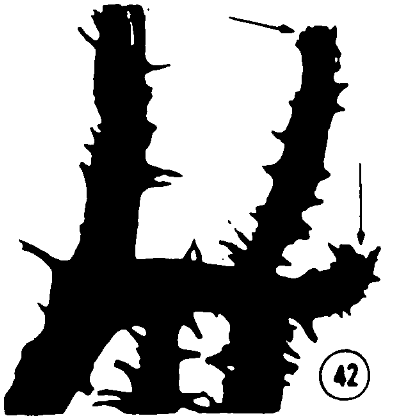
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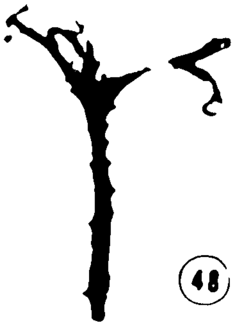
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VEGETATIVE AXES

PLATE 6

Fig. 49. Dichotomous and pseudomonopodial branching on same specimen (see Text-fig. 7). UAPC S7120. X1.5.

Fig. 50. Dichotomous and pseudomonopodial branching on same specimen; A = main axis, 1 & 2 = laterals. UAPC S7121. X1.3.

Fig. 51. Relatively long (5.5 cm), alternately disposed lateral branch. UAPC S7122. X1.4.

Fig. 52. Relatively short (1.3 cm), alternately disposed lateral branches. UAPC S7123. X1.6.

Fig. 53. Relatively short (1.3 cm), alternately disposed lateral branches. UAPC S7124. X1.7.

Fig. 54. Dichotomous and pseudomonopodial branching on same specimen (see Text-fig. 8). UAPC S7125. X1.7.

Fig. 55. Alternate but unevenly spaced lateral branches; note spine covered apex (arrow). UAPC S7126. X1.2.

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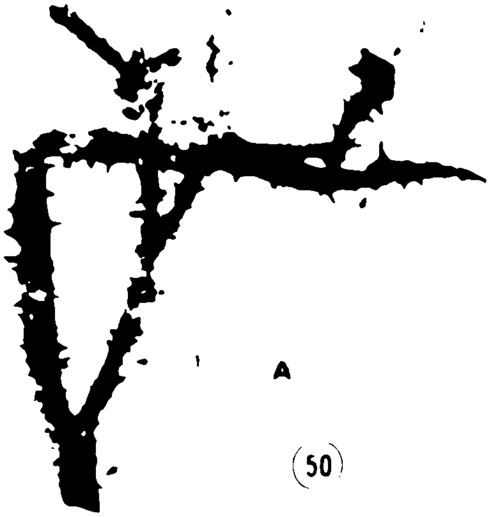

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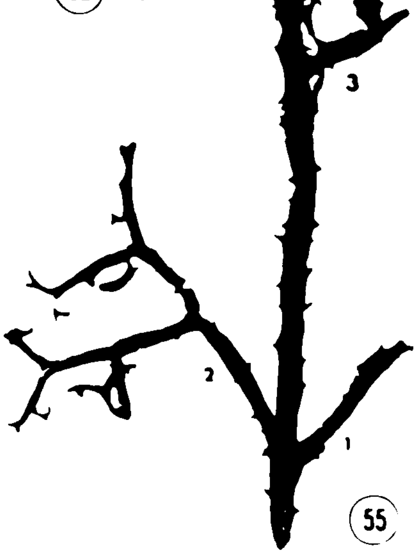

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VEGETATIVE AXES

PLATE 7

Fig. 56.	Two alternately arranged laterals on a terminally dichotomous main axis (see Text-fig. 9); note spine covered apex (a) and central axis of double dichotomy (C). UAPC S7127. X3.2.
Fig. 57.	Obverse side of Fig. 56. UAPC S7127. X3.2.
Fig. 58.	Specimen showing less patterned laterals and central axis (C) of double dichotomy. UAPC S7128. X2.1.
Fig. 59.	Obverse side of Fig. 58. UAPC S7128. X2.1.
Fig. 60.	Terminal dichotomous specimen with double dichotomies; arrows indicate central axis of respective double dichotomies. UAPC S7129. X1.8.
Fig. 61.	Obverse side of Fig. 60. UAPC S7129. X1.8.

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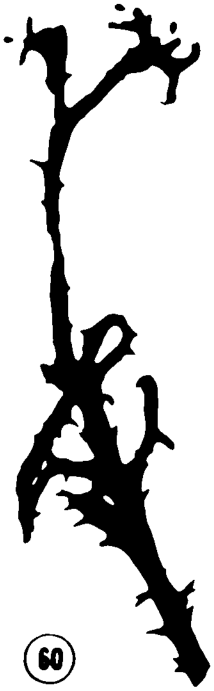

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VEGETATIVE AXES

PLATE 8

Fig. 62. Specimen with relatively small (about 1 cm) lateral appendage (arrow). UAPC S7130. X2.4.

Fig. 63. Obverse side of Fig. 62. UAPC S7130. X2.4.

Fig. 64. Specimen with relatively long, sparsely divided laterals (see Text-fig. 13). UAPC S7131. X1.5.

Fig. 65. Obverse side of Fig. 64. UAPC S7131. X1.5.

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VEGETATIVE AXES

PLATE 9

Fig. 66. Specimen with presumed twice trifurcate lateral. UAPC S7132. X2.5.

Fig. 67. Close up of apparent trifurcations (white arrows) in Fig. 66; the apparent trifurcation at the upper white arrow occurs on the obverse side and the central axis of this trifurcation is indicated by the black arrow. UAPC S7132. X3.8.

Fig. 68. Specimen showing central axis (c) of double dichotomy and small lateral appendages (arrows) that might represent root precursors. UAPC S7133. X1.8.

Fig. 69. Specimen showing area of profuse branching and undivided continuation of main axis. UAPC S7134. X1.

Fig. 70. Close up of Fig. 69 showing branching. UAPC S7134. X1.6.

Fig. 71. Obverse side of Fig. 70. (see Text-fig. 16). UAPC S7134. X1.6.

Fig. 72. Specimen with spirally arranged laterals (see Text-fig. 14). UAPC S7135. X2.6.

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VEGETATIVE AXES

PLATE 10

Fig. 73. Specimen showing presumed 'axillant leaf precursor' (arrow) epipetiolar branch precursor (B) relationship (see text and Text-fig. 18). UAPC S7136. X2.3.

Fig. 74. Obverse side of Fig. 73. UAPC S7136. X2.3.

Fig. 75. Large specimen (4.8 cm) illustrating three double dichotomies where the central axes (arrows) are complete and vary in length from a few millimeters (a) to 2.5 cm (b). See Text-fig. 19, A-1, A-3 and B-c. UAPC S7137. X1.7.

Fig. 76. Specimen illustrating double dichotomies, small lateral appendages and primordia (see Text-fig. 20); UAPC S7138. X1.6.

Fig. 77. Obverse side of Fig. 75. UAPC S7138. X1.6.

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VEGETATIVE AXES

PLATE 11

Fig. 78. Specimen showing dichotomy in main axis followed by area of profuse branching (see Text-fig. 21). UAPC S7139. X2.4.

Fig. 79. Obverse side of Fig. 78. UAPC S7139. X2.4.

Fig. 80. Specimen showing dichotomously (D) and pseudomonopodially (P) divided laterals (see Text-fig. 23). X3.1.

Fig. 81. Specimen showing lateral branch (l) that divides pseudomonopodially (see Text-fig. 22). UAPC S7140. X3.

Fig. 82. Specimen showing pseudomonopodially divided laterals (see Text-fig. 24). UAPC S7141. X2.5.

Fig. 83. Obverse side of Fig. 82. UAPC S7141. X2.5.

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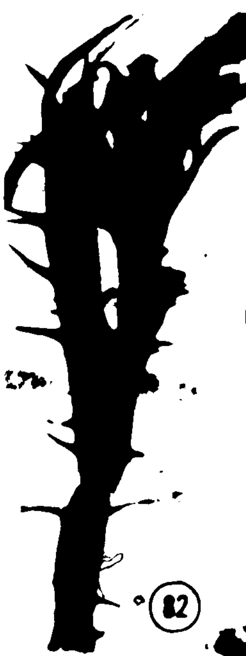

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VEGETATIVE AXES

PLATE 12

Fig. 84. Specimen illustrating pseudomonopodially divided laterals (1 & 2) and apparent 'axillant leaf precursor' relationship; A = 'axillant leaf precursor', B = epipetiolar branch precursor. UAPC S7142. X2.1.

Fig. 85. Obverse side of Fig. 84 (see Text-fig. 25); note circinately coiled, 2 mm appendage (c). UAPC S7142. X2.1.

Fig. 86. Specimen illustrating dichotomously and pseudomonopodially divided lateral (1). UAPC S7143. X2.6.

Fig. 87. Obverse side of Fig. 86 (see Text-fig. 26). UAPC S7143. X2.6.

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