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THE MORPHOLOGY AND VARIATION IN *RHACOPHYTON CERATANGIUM* FROM THE UPPER DEVONIAN AND ITS BEARING ON FROND EVOLUTION

BY

BRUCE CORNET*), TOM L. PHILLIPS**)
and HENRY N. ANDREWS***)

With 7 Plates and 6 Figures in the Text

Summary

More extensively preserved branch systems of *Rhacophyton ceratangium* have been studied from 40 selected specimens from the Upper Devonian (middle Famennian) Valley Head locality in West Virginia, U.S.A. Specimens of main axes (stems) are 75—77 cm long, sterile branch systems up to 44 cm long, and fertile specimens up to 50 cm long with lateral divisions up to 35 cm.

The stems of *Rhacophyton ceratangium* were up to 2 cm in diameter and were upwards of 1.5 m long with an erect to semi-erect habit. Degaging of type and new material established the stegotaxy of vegetative fronds as a two-rowed arrangement of paired rachises, with a common basal attachment, on opposite sides of the main stem. The paired arrangement, previously obscured by false spiralling of the clepsydroid stem anatomy, coincides with the quadriseriate, alternating paired arrangement of primary pinnae known on fertile frond portions. Quadriseriate pinna development distally on vegetative fronds is reported for the first time, and quadriseriate sterile to fertile development also occurs distally on some attached vegetative fronds. Three-dimensional quadriseriate branching, similar to that in *Protocephalopteris*, is regarded as the basic repetitive branching pattern of *Rhacophyton*. Vegetative frond portions show the greatest degree of specialization toward a planated frond, while still retaining the potential for indeterminate growth, and three-dimensional branching and secondary growth. Ultimate dichotomous non-laminate divisions (pinnule-like) vary in successive fossiliferous zones from markedly three-dimensional to essentially two-dimensional and planated. Single primary pinnae of biseriate frond portions and all higher pinna divisions, including ultimate pinnule-like units, in *R. ceratangium* are alternately arranged with basal and immediately opposed, minor dichotomous branchlets. These basal branchlets are interpreted as homologs of the potential second pinna of a pair which can be shown to develop as primary pinnae in quadriseriate pairs. Alternate development in the plane of the frond of only one member of potential pinna pairs was concomitant with planation up to the dichotomous ultimate divisions. Aphlebia-like structures subtend each branch order from rachis to penultimate pinna and are paired where branches occur in pairs. Fertile aphlebia-like structures occur in pairs below primary pinnae on quadriseriate fertile portions only. The occurrence of secondary xylem in all major axes suggests the cauline or axial nature of stems and rachises, as well as of some primary pinnae. All major axes appear to be parts of homologous branch systems by evidence of repetitive patterns, and the change from biseriate sterile to quadriseriate sterile and/or quadriseriate fertile in the same frond-like branch system indicates that the apparent frond-like dimorphism in *Rhacophyton* is not distinct at all. With the potential for indeterminate growth, the collective morphological data suggest that vegetative portions of *Rhacophyton ceratangium* represent a pre-frond stage, and that *R. ceratangium* can not be regarded as a fern.

Adventitious root systems with protostelic anatomy surrounded by radially aligned tracheids, and similar root-like structures up to 2 mm in diameter with unbranched laterals, occur on the main stem and at or between the bases of paired rachises.

Comparisons are made with *Protocephalopteris*, coenopterid (zygopterid) ferns and progymnosperms, and it is concluded that *Rhacophyton* exhibits characters shared by all these groups in addition to having some elements of the Trimerophytina. Speculation in the literature on the phylogenetic position of *Rhacophyton* heavily favors zygopterid ferns despite *Rachophyton*'s pro-

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Addresses of the authors:
*) Department of Geology and Geophysics, Pennsylvania State University, University Park, Pennsylvania.
**) Botany Department, University of Illinois, Urbana, Illinois.
***) Systematics and Evolution Section, Life Sciences, University of Connecticut, Storrs, Connecticut.

gymnosperm-like characters. The order Protopteridiales is resurrected here with a slightly emended diagnosis. *Rhacophyton* is returned to the Protopteridiales. *Rhacophyton, Cephalopteris,* and *Protocephalopteris* are assigned to the family Rhacophytaceae BARNARD & LONG. Biseriate planation in the branch system of *R. ceratangium* is emphasized as an incipient pre-frond stage of evolution, and restorations of representative portions of the reinterpreted branch systems are illustrated.

Contents

Introduction

Rhacophyton is an Upper Devonian (Famennian) lower vascular plant reported from Bear Island *(R. mirabilis* or *Cephalopteris*), Belgium *(R. condrusorum, R. zygopteroides)*, New York, the Perry Basin of Maine, the Donetz Basin and western Siberia *(R. incertum)*, and West Virginia *(R. ceratangium)*. The most completely known species are *R. zygopteroides* (LECLERCQ 1951, 1954) and *R. ceratangium* (ANDREWS and PHILLIPS 1968); these studies have emphasized *Rhacophyton*'s fern-like (zygopterid) and progymnosperm-like (aneurophytalean) morphology. *Rhacophyton* is a particularly significant genus in the study of frond evolution from branch systems because of its Upper Devonian age, its transitional morphology, repetitive branch orders of similar anatomy (including secondary xylem), and both biseriate and quadriseriate pinnate branching.

If *Rhacophyton* is not a fern, there would seem to be no known Devonian ferns at present. With our current knowledge of Upper Devonian and Lower Carboniferous pteridophytes, the recognition of the earliest ferns is dependent largely upon establishing the evolutionary sequence of frond morphology, because of the apparent lack of definitive sporangial characters in such plants. Frond morphology should separate ferns from other vascular plants (except pteridosperms) of the Upper Devonian-Lower Carboniferous. Our reinvestigation of *Rhacophyton ceratangium* has emphasized the branching patterns, frond-like morphology and their variations in order to re-evaluate the morphological interpretations of *Rhacophyton* and its natural affinities with ferns, progymnosperms and other lower vascular plants.

The revised description of *Rhacophyton ceratangium* is based on 40 selected specimens, many of which show larger intact portions of the plant than previously available, and on a re-examination and further degaging of some specimens described by ANDREWS & PHILLIPS (1968). All specimens are from the Upper Devonian (middle Famennian) of West Virginia.

As in previous descriptions of *R. ceratangium* (ANDREWS & PHILLIPS 1968) the terms stems, vegetative fronds and fertile fronds are used, but it should be clear that the branch systems lack clear-cut distinctions of an axial-appendicular system at the stem-frond level of differentiation. *Rhacophyton* represents a putative pre-frond stage, which is particularly significant because of the evolutionary developments which had already occurred, especially in the sterile branch systems and, in turn, because of the insight they seem to provide on the evolution of one type of frond.

The major branch axes corresponding most closely with a rachis or phyllophore in the sterile and fertile frond-like portions of *Rhacophyton* are interpreted as branch systems, which exhibit indeterminate apical growth and secondary growth. The sterile frond-like portions can change from two-dimensional to three-dimensional branching, and can be three-dimensionally sterile or become fertile distally. The fertile frond-like branch system is essentially homologous to a main axis or stem. There is, therefore, a strong basis for interpreting the three descriptive units, stems, fertile fronds and vegetative fronds as homologous branch systems with the vegetative fronds showing the greatest degree of specialization toward a planated frond, while still retaining the potential for indeterminate growth, three-dimensional branching and fertile morphology. If strictly cauline and foliar interpretations were applied to *Rhacophyton*, without further anatomical information, the most likely foliar portions would probably be the two to three (sometimes more) orders of dichotomously divided ultimate appendages which occur variously at the bases of branches (aphlebia-like and sterile or fertile), and; along pinnate branches of both sterile and fertile fronds (pinnule-like). The inference is that the sporangia are foliar-borne, and the presumptive transitional stage of pre-frond morphology exhibited by *Rhacophyton* presents a close parallel with progymnosperms in the potential evolution of a frond from pinnate branch systems with foliar appendages.

Material and Collecting site

Forty additional selected specimens of *Rhacophyton* were studied from hundreds collected at a road cut on the north side of State Route 15, two miles west of Valley Head, West Virginia; this is the same site from which *R. ceratangium* and two species of *Archaeopteris* have been reported (ANDREWS & PHILLIPS 1968; PHILLIPS, ANDREWS & GENSEL 1972). The zone is in the Hampshire Formation and the age is latest Cassadaga Stage to earliest Bradford Stage; in European terminology this is the middle Famennian of the Upper Devonian (OLIVER et al., 1967, 1969).

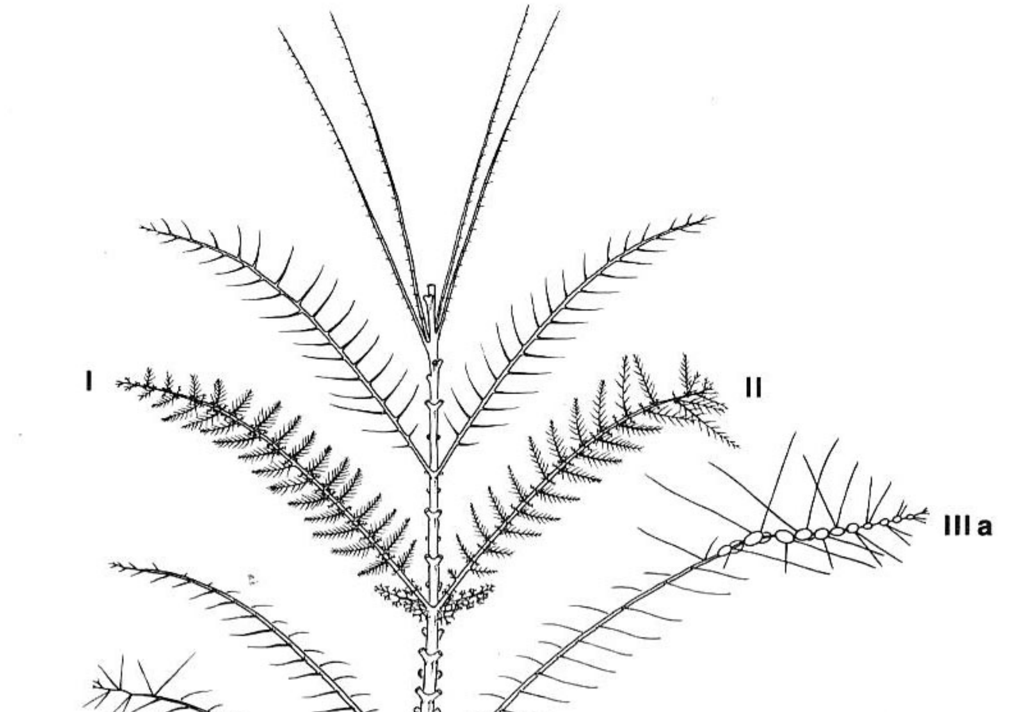
The quarry area in which we collected was about 1.6 x 3.1 m and was part of an originally exposed excavation made with the cooperation of WILLIAM H. GILLESPIE and the West Virginia State Road Commission in 1970. The fossil plants were excavated layer by layer through a depth of about 60 cm. Some specimens (Plate 1, fig. 1), which covered up to a m^2 area, were removed in pieces and reassembled in the laboratory.

The quarried deposits of plant material appear to represent an infilled channel that contained several logs, probably of *Archaeopteris,* and supported fish populations of arthrodires and crossopterygians, based on recovered ornamented bones and fish scales in the sediment.

Figured and described specimens and slide preparations are in the Paleobotanical Collections, Systematics and Evolution Section, Life Sciences, University of Connecticut, Storrs, Connecticut.

Methods

Degaging was extensively used to obtain details of all orders of branching. Small pieces of mudstone matrix containing branches were transferred from part to counterpart in order to mend breaks and provide continuity of major axes on a single exposed face. Both part and counterpart were degaged, although only one part is illustrated for a number of specimens. Water colors were employed to enhance contrast of a few weakly stained impressions for photographic purposes (Plate 3, fig. 7).



Text-fig. 1. Hypothetical, partial restoration of *Rhacophyton ceratangium* showing erect or semi-erect main axis (stem) about 1 m high with alternating pairs of vegetative rachises forming two rows on opposite sides of the stem. Adventitious roots are shown attached to stem. Four types of frond-like systems are shown (I—IV): biseriate vegetative system (I), biseriate vegetative system distally changing to quadriseriate vegetative system (II); biseriate vegetative with distal portion quadriseriate and fertile (IIIa) with sporangial masses represented by ovals; a combination of II and IIIa with the main rachis biseriate to distally quadriseriate and fertile with a large (pseudodichotomy) lateral sterile system (IIIb) — this branch system was not found attached to a larger axis; isolated fertile branch systems (lower left) which were not found directly attached to a main axis (IV). A pair of aphlebia-like branches subtend fronds I and II which are the only two illustrated in detail. Further descriptions are given in the text.

Petrified axes were studied with techniques described by Beck (1955) and Matten (1966) for limonitic petrifactions; Permount was substituted for Harleco Synthetic Resin. Pyritized axes, embedded in plastic, were studied, for the most part, directly from saw cuts. Ground thin sections of limonitic petrifactions were etched in oxalic acid to enhance detail when wet; dried sections were mounted in Permount or balsam.

Description of Specimens — General Morphology

Rhacophyton ceratangium (Text-fig. 1) was erect to semi-erect, with the main axis or stem attaining more than 1.5 m in length and up to about 2 cm in width. The longest recovered stem specimens were 75—77 cm and incomplete (Plate 1, fig. 1; Plate 2, fig. 5). The apparent spiral phyllotaxy (stegotaxy) of individual sterile fronds reported by Andrews & Phillips (1968) is actually a false spiral of two vertical rows of fronds on both sides of the stem; the two rows on each side are formed by alternately arranged pairs of fronds. Each pair of sterile fronds has a common base with an angle of about 90° between the two rachises of a frond pair. There is a dichotomously branched aphlebia-like appendage laterally on each side at the common base of each pair of fronds (Text-fig. 5A). The sterile frond arrangement on the main stem is therefore quadriseriate or tetrastichous as are the sterile pinnae on the fertile fronds; fertile fronds have not been found attached directly to a larger stem or main axis.

The sterile or vegetative fronds were predominantly two-dimensional with three-dimensional tendencies primarily in ultimate dichotomous divisions; branching was reported by Andrews & Phillips (1968) as bipinnate and biseriate for fronds up to 30 cm long, but vegetative fronds 40 cm or longer, attached to stems, are bipinnate to tripinnate, and may also exhibit distally three-dimensional sterile and/or fertile morphology (Text-fig. 1).

The size of attached sterile and isolated fertile fronds differs consistently. Rachis diameters of vegetative fronds are up to 4—5 mm, while those of isolated fertile fronds are up to 6—8 mm. Most fertile frond portions encountered are within a 20 cm maximum length and incomplete (Andrews & Phillips 1968), but specimens up to 50 cm long with primary pinnae up to 35 cm long have been obtained in this study.

Among the frond specimens with rachises 40 cm or more in length are four intergradational types of fronds, which have been partially illustrated in Text-fig. 1 (I—IV): typical two-dimensional vegetative fronds, I; vegetative fronds which distally exhibit quadriseriate sterile pinnae, II, with the same three-dimensional construction as fertile fronds (Text-fig. 3); a vegetative type of frond which distally exhibits an abrupt transition to quadriseriate fertile frond morphology, IIIa, or a transition first to sterile quadriseriate and then to fertile frond morphology IIIb (Text-fig. 6) — this type of frond also possesses a false dichotomy of the rachis due to secondary bipinnate growth of a pinna originating just below the transition from biseriate to quadriseriate morphology; and the typical fertile frond, IV, which may be sterile basally but is quadriseriate throughout — no basal attachments of the typical fertile fronds have been established apart from the transitional forms IIIa and IIIb. In summary, there are gradational forms from two- to three-dimensional branching, and from sterile to fertile morphology. As previously mentioned, the isolated large fertile fronds appear to be homologous to main axes or stems.

The basic branching pattern of *Rhacophyton ceratangium* is one of paired or dichotomous branching, accompanied basally by a lateral pair of aphlebia-like appendages up to, but not including, the ultimate pinnate order, which bears similarly dichotomously branched appendages that may be characterized as pinnule-like but non-laminate. The principal distinction between aphlebia-like and pinnule-like appendages is position, and to some extent number of divisions and size, but it seems likely that these appendages also exhibited varying capacities to expand into more complex pinnate branches, which in turn have several orders of close, successive dichotomies.

Perhaps the most important aspect of the paired organization seen throughout *Rhacophyton*'s morphology is the pairing of a pinnate branch (primary pinna) with an opposite pinnule-like appendage in the two-dimensional sterile frond (Text-fig. 5C-E). This pair of unequally developed divisions seems to represent the significant reductional step from a three-dimensional quadriseriate sterile frond to a two-dimensional biseriate frond by the planate development of only one pinnate branch of a potential pair in a successively alternating sequence along the rachis.

The detailed branching of three types of ultimate, non-laminate, pinnule-like dichotomous divisions of the sterile frond are shown in Text-fig. 4. Only one type of pinnule has been found on a given frond, and only one type of frond on a given stem. No basic differences were otherwise found in the sterile fronds that bore them.

Roots 1.5 mm in diameter with a central primary xylary strand surrounded by radially aligned tracheids, occur on the main axes (Text-fig. 1, Plate 2, fig. 4) with sterile fronds. Roots or root-like structures also occur along narrow, vertical zones on the stem, close to but not on the same side as the fronds, and all departed in the same direction and were in the same compressional plane as the stem. Root-like structures also arise between some pairs of sterile fronds at their common base. All of these roots or root-like structures are interpreted as adventitious roots, and, while there is no evidence that *Rhacophyton* had a central root system, many root-like systems were encountered that could not be referred to any genus.

The fertile structures of *R. ceratangium* have been described in detail by ANDREWS & PHILLIPS (1968).

Main Axis or Stem

Three stem specimens of 75, 77 and 37 cm lengths respectively were compared dimensionally (stem width; internodal length) in order to reconstruct a larger segment of the main axis with reliable tapering, and to determine changes along the overlapping lengths; the node numbers given in the three figures indicate approximate matches of how we think the three specimens would overlap (Plate 1, fig. 1; Plate 2, fig. 5; Plate 3, fig. 7). The two longer specimens appear to be quite similar dimensionally over the length from nodes 6—20 with the same trends for increase and decrease in length (Plate 1, fig. 1; Plate 2, fig. 5); both exhibited evidence of 29 pairs of fronds; internodal lengths were 1.1—4.5 cm with an average of 2.5 cm. Frond pairs are more closely spaced vertically in the middle portion of the two stems. The stem diameters are 10—13 mm and 7—11 mm respectively. The third, shorter stem specimen (Plate 3, fig. 7), is either a more apical region and/or represents a younger plant. Its stem diameter is 5—9 mm with 11 pairs of fronds and internodal lengths of 2.5—4.5 cm and an average internodal length of 3.4 cm. Assuming that the overlapping portions of the three specimens give a fairly accurate indication of a more complete and larger stem, they would represent a composite length of 111 cm; with the established rate of tapering (1 mm per 14 cm), a stem 1.3 cm in basal diameter would reach a height of approximately 1.5 m, with a terminal diameter of about 2 mm.

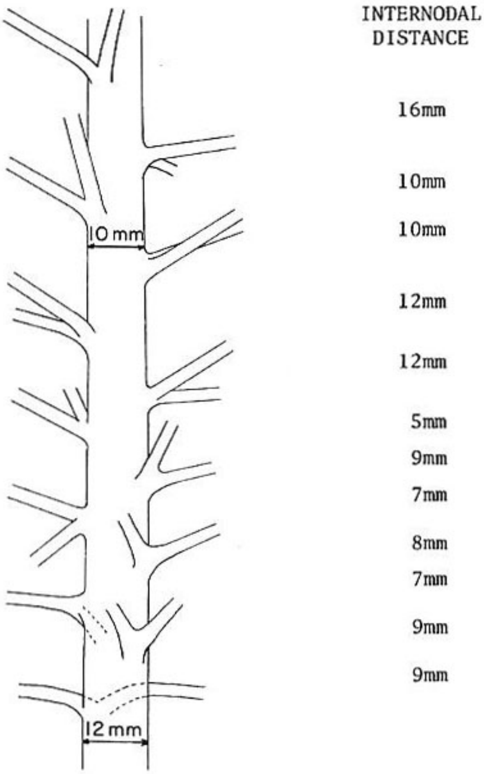
The occurrence of pairs of sterile fronds on the main axis was unexpected, since practically all informative splits of part and counterpart specimens revealed the main axis with alternating single fronds. Pairs of fronds at several nodes led to further degaging of parts and counterparts, confirming the regular occurrence of paired fronds on the main axis, usually found alternately in the part and then the counterpart as successive nodes were examined. Degaging of the sterile type specimen of *R. ceratangium* (USNM 42837, Fig. 1 in ANDREWS & PHILLIPS 1968) established the same quadriseriate arrangement formed by two rows of paired fronds (Text-fig. 2).

The two rows of paired fronds in the type specimen exhibit a false spiral, which apparently coincides with the internal twisting or slight rotation of the bilaterally symmetrical xylem strand of the main stem (Plate 2, fig. 3); this would logically place successive frond pairs next to the peripheral loop-like areas at each end of the bar-like primary xylem. This type of spiral is not a true phyllotactic pattern and should be designated as a false or pseudospiral.

False spiralling is gradual and persistent in some large stems (Text-fig. 2) and transient in others, occurring over short distances. In the specimen shown in Plate 3, fig. 7, the primary xylary bar of the stem rotated 180° between nodes 34 and 37; the spiralled positions of the frond pairs in the same region were consistent with observations of the rotation of the bilateral symmetry of the petrified xylem.

Roots and Root-like Appendages

Root-like appendages may occur in two areas on the main axes. Root-like structures are attached to the main stem (Plate 3, fig. 8) in a column, or in several groups, close to but not on the same side of the stem as the fronds. All radiate in the same general direction, and more than twenty may occur in a group. Root-like appendages also arise between a pair of fronds at their common base (Text-fig. 3, Plate 1, fig. 1; Plate 3,



Text-fig. 2. Diagram of portion of main axis (stem) of the sterile type specimen (USNM 42837, Fig. 1 in Andrews & Phillips 1968) of *Rhacophyton ceratangium* showing the false spiralling of two vertical rows of paired vegetative rachises with a common base revealed by degaging. See text for further detail. Natural size.

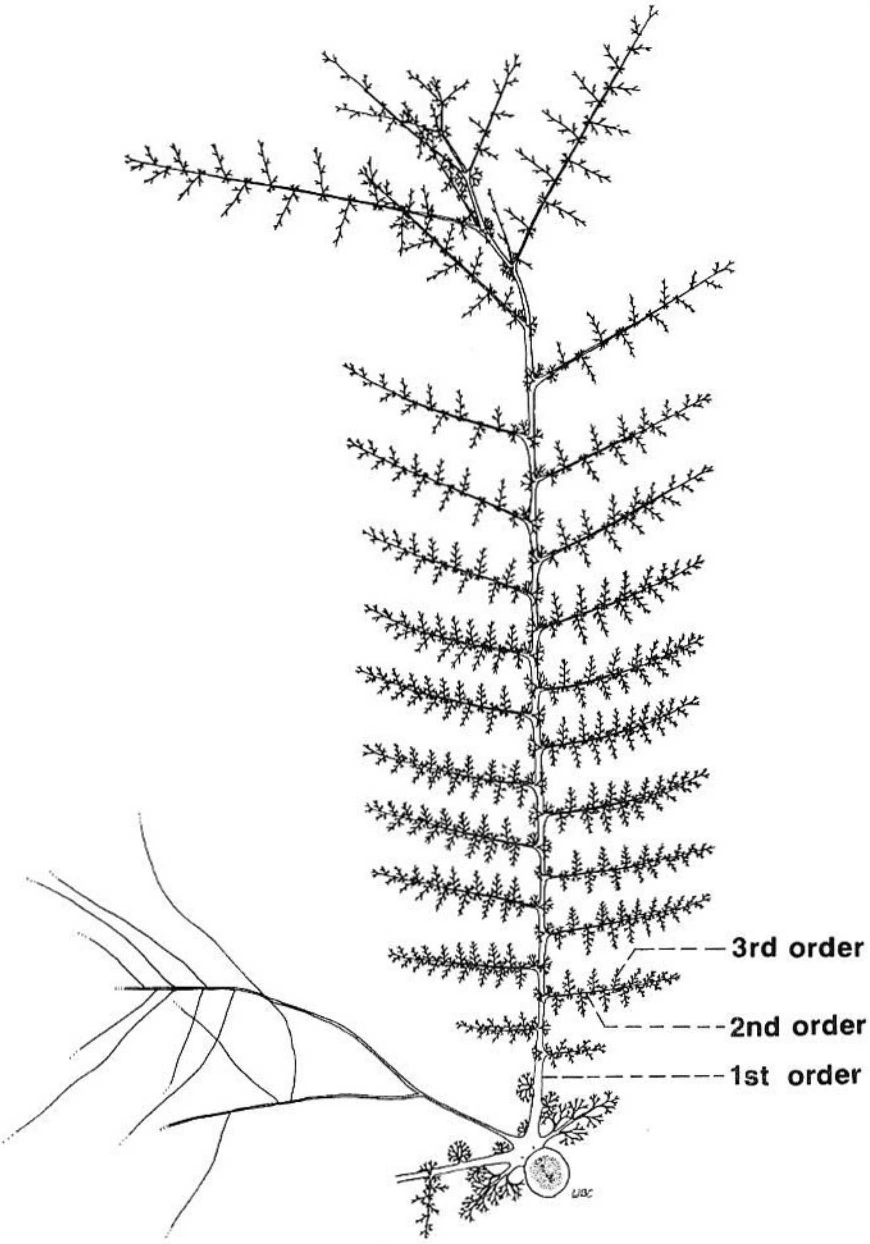
fig. 10). The root-like structure in Plate 3, fig. 10 is 2 mm wide with a central ridge 0.5 mm wide, and it has irregularly arranged unbranched laterals, which are 1 mm wide and similar to those root-like structures borne directly on the stem in groups.

A small main axis, 5 mm in diameter, with fronds had petrified anatomy in the main axis and in some lateral appendages (Plate 3, fig. 9; Plate 2, fig. 4), which can be regarded in this case as roots. The xylem of the main axis (stem) exhibits in cross-section the typical elongate bar of primary xylem with two protoxylem groups, or peripheral loop-like areas, surrounded by abundant secondary xylem, as previously described by Andrews & Phillips (1968). The attached roots are 1.5 mm in diameter and appear to depart in a single row without regular relationships to fronds. Cross sectional xylary anatomy of the root consists of a single group of primary xylem tracheids surrounded by radially aligned tracheids, probably secondary xylem (Plate 2, fig. 4). The main roots with such anatomy have numerous unbranched, lateral rootlets about 0.1 mm wide. In summary, the roots and root-like appendages are interpreted as adventitious roots. Many additional axes of undetermined nature were found to have densely radiating root-like structures, as have been reported by Kräusel & Weyland (1941) and by Andrews & Phillips (1968).

Morphological Variation of Vegetative Fronds

Two-dimensional Branching

Vegetative fronds occur in pairs on opposite sides of the main axis, and the adaxial angle between each frond rachis and the stem increases downwardly from the apex of the stem (Text-fig. 1; Plate 1, fig. 1; Plate



Text-fig. 3. View from above of a restoration of a complete vegetative branch system (sterile frond) of *Rhacophyton ceratangium* shown basally attached as one of a pair, subtended by aphlebia-like branches and with an adventitious root attached between rachis bases; this vegetative branch system shows distal transition from biseriate two-dimensional to quadriseriate three-dimensional branching. Stem anatomy is diagrammatically clepsydroid with secondary xylem. One half natural size. Specimen is illustrated in Plate 1, fig. 1 and counterpart in Plate 6, figs. 23, 24. Further details in text.

3, fig. 7) with angles of 10—50° in the upper part of the stem and 40—70° in the lower part. Each vegetative frond (branch system) has a lateral aphlebia-like structure at its base so that the common base of each frond pair is flanked by a pair of aphlebia-like structures (Text-fig. 5A; Plate 1, fig. 2). The aphlebia-like structure is 2—5 cm long and is less symmetrical than those subtending subsequent branch orders. It has an elongate primary axis with alternately arranged secondary branches, dichotomously divided.

The major branches along the rachis portion are alternately arranged in two rows (biseriate) with the following sequence of changes from the base of the rachis toward the distal end (Text-fig. 3): 3—4 alternating groups of dichotomously divided laterals, the first of which (Plate 2, fig. 6) is in a catadromic position (underside of rachis), and all of these resemble the ultimate pinnule-like divisions on pinnae, except for their markedly three-dimensional form; next are alternating pinnae of successively increased lengths (particularly the basal most 3 or 4; Plate 4, fig. 11, 16) up to a maximum length, which is then maintained to near the termination of the vegetative frond or to near the transition zone to three-dimensional and/or fertile morphology.

Understanding the significance of minor branchlets or dichotomously branched laterals (pinnule-like) on the two-dimensional, biseriate vegetative branch system in *Rhacophyton ceratangium* is dependent upon recognition that the vegetative frond exhibits the potential of being quadriseriate and three-dimensional (Text-fig. 3). These newly discovered, minor branchlet features are interpreted as vestigial, and derived from the quadriseriate branching pattern indicative of all the major branch orders of *Rhacophyton* from stem to pinnae. The anatomy is not known for any of the pinnae or dichotomously divided pinnule-like structures on the vegetative frond, and therefore our interpretations of major branchlets is dependent largely on their positional relationships.

At the base of and opposite to each pinna (first and second order) is a small dichotomously branched, pinnule-like development which is consistently either above or below the plane of the rachis or primary pinna (Plate 4, fig. 12—15); the position of this minor branchlet is comparable to that of a second pinna of a pinna pair. Various degrees of attained development of the branchlet observed in this position (Text-fig. 5, B—E) substantiate such an interpretation, especially where the two-dimensional vegetative frond becomes three-dimensionally quadriseriate with unequal sizes of the two members of a pinna pair (Text-fig. 3).

A second type of minor basal branchlet on the first and second order pinnae also occurs, but is lateral (catadromic); this dichotomously branched structure seems comparable to the aphlebia-like structures at the base of frond pairs (Text-fig. 5 A—E).

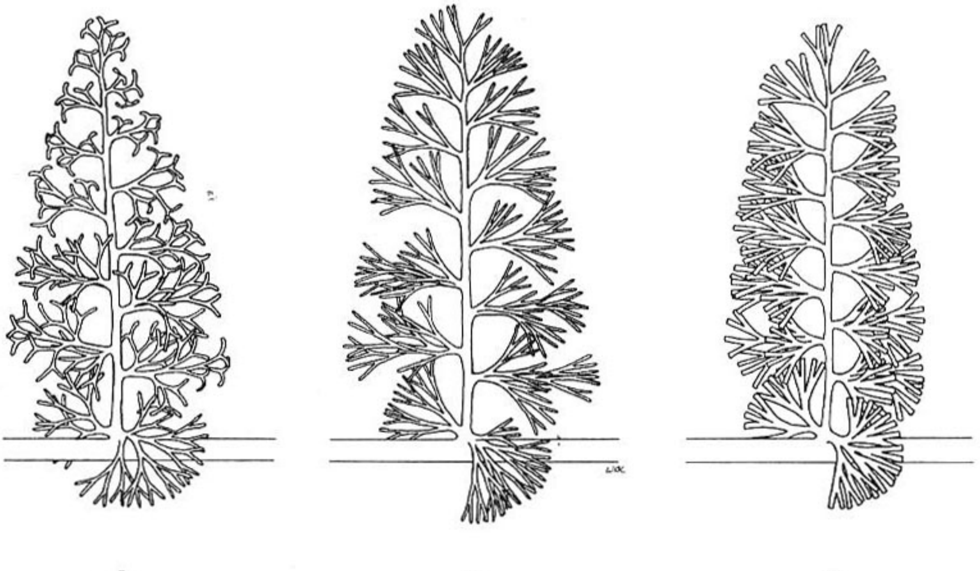
In both cases of minor branchlets (those homologous in position to one pinna of a pair and to aphlebia-like structures respectively) the dichotomous divisions are similar to ultimate pinnule-like divisions. While distinctions among all the pinnule-like, dichotomous ultimate divisions are positionally based for the most part, and they may not be significantly different in their external morphology, some differences have been noted. The basal and opposite branchlets comparable to the second pinna of a pair show gradationally larger forms, progressively up to distinct pinnae (Text-fig. 5 B—E); the same may be said for aphlebia-like structures, but usually this is applicable only to such structures at the base of a rachis and not at the bases of pinnae. Aphlebia-like (catadromic) divisions are usually symmetrical dichotomies with 3—5 orders of dichotomies, and frequently differ from other pinnule-like divisions of a pinna by their tendency toward isotomous dichotomy and their larger number of divisions (Text-fig. 4, 5 B—E; Plate 4, fig. 13, 15). There are exceptions.

It follows from the above descriptions and interpretations that both the primary and the secondary pinna orders of a two-dimensional biseriate frond in *Rhacophyton* represent modification of a primitively paired pinna organization, and that the biseriate condition is attained by the markedly unequal and greater development of one member of each potential pinna pair, with the developed pinnae alternating along the rachis in the same plane. In view of the approximate 90° angle between the two members of a frond pair, or a pinna pair on a three-dimensional sterile or fertile frond, the pattern in the biseriate portion of a frond would seem to have been established through geometrical rotation 45° from the original plane of bilateral symmetry of the clepsydroid rachis. Anatomical data on this are lacking.

The 3—4 alternating groups of dichotomously divided laterals (the first being catadromic) at the basal end of the vegetative rachis (Text-fig. 3) are 1.5—2.5 cm long with 5—6 orders of dichotomy. Each of these laterals may be interpreted as comparable to a potential pinna pair, the two members of which are separated by the first dichotomy, but not attaining development comparable to the progressively larger pinnae above them on the rachis. The discernment of aphlebia-like branchlets within already dichotomously divided branchlets, such as those basally on the rachis, is largely a theoretical exercise, but is possible in a number of specimens.

Pinnule-like Ultimate Divisions

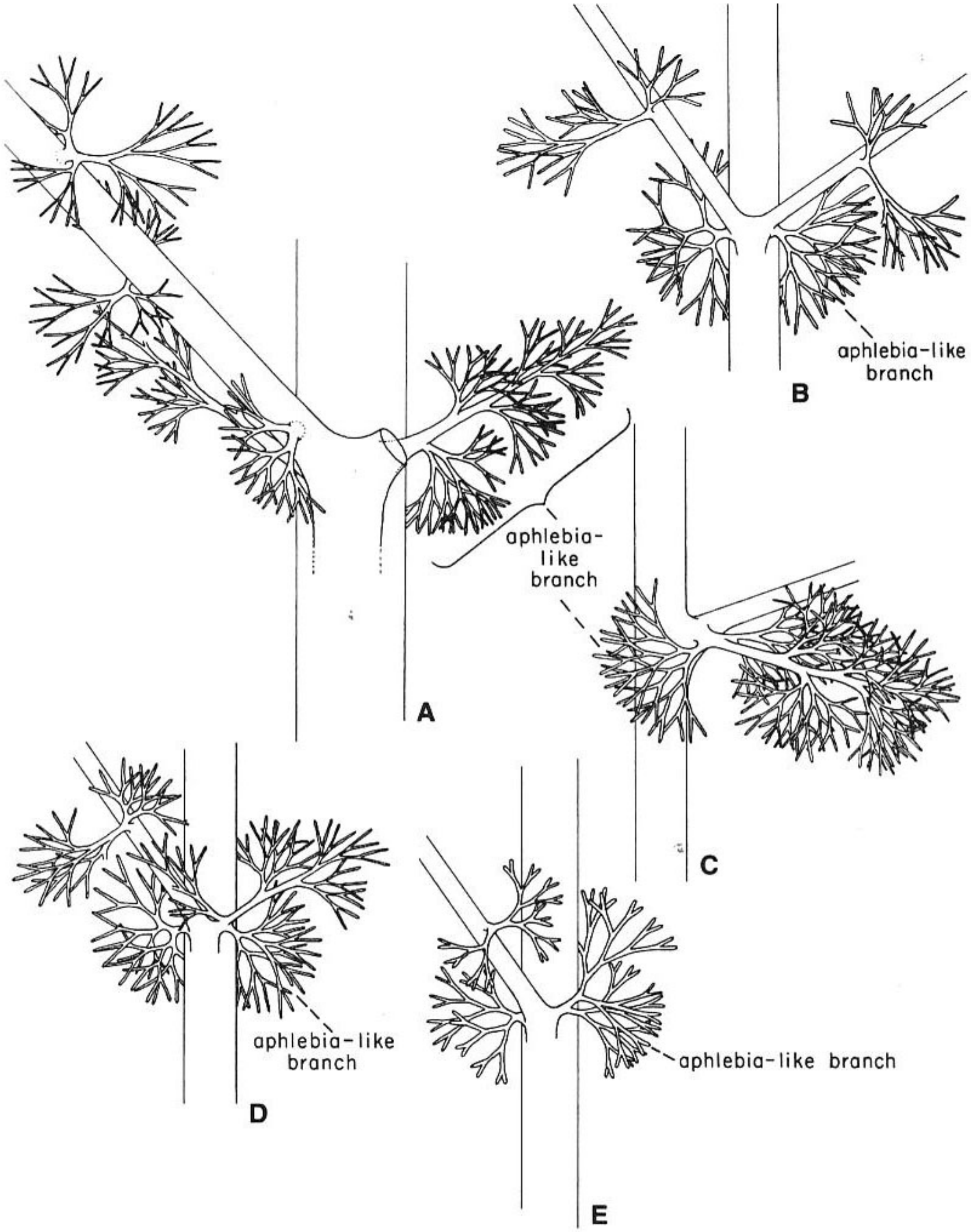
Ultimate, non-laminate, pinnule-like dichotomous divisions on the pinnae of sterile fronds are of three basic types (Text-fig. 4, A—C), which are restricted apparently to separate plants. Frequency of occurrence of these basic types differed markedly in the upper and lower portions of the 60 cm thick *Rhacophyton* zone. No basic differences were otherwise found in the vegetative fronds that bore them. Type A is the most three-dimensional, with recurved tips on all ultimate divisions, and was the most frequently encountered in this study (Plate 5, fig. 17, 18, 20). Type B is more flattened with straight tips and less divergent branches (Plate 5, fig. 21); this type was most abundant in the study by ANDREWS & PHILLIPS (1968). Type C is strictly two-dimensional with branches and ultimate divisions flattened in a single plane (Plate 5, fig. 19). Type C was rarest and usually associated with plant specimens bearing Type B pinnule-like divisions. Plants with Types A and B ultimate divisions were largely confined to separate zones with Type A being in the lower zones.



Text-fig. 4. Primary pinnae of *Rhacophyton ceratangium* each with a complete ultimate pinna bearing two rows of ultimate divisions; each of three different types of vegetative pinnules (A—C) has a symmetrical or nearly symmetrical fan-shaped aphlebia-like branch on the lower right, and a smaller aphlebia-like branch on the lower left. Type A pinnules are three-dimensional with recurved tips. Type B is essentially two-dimensionally branched with straight tips. Type C is markedly planated and flattened. See text for details of occurrence. x 2.6.

Three-dimensional Branching—Vegetative

Three-dimensionally branched, vegetative frond morphology is exhibited by some attached vegetative fronds, distally (Text-fig. 3), and this morphology may also be present in a frond region transitional to fertile frond morphology (Text-fig. 1, III A). Distally, the distinct development, but unequal lengths, of the two primary pinnae of a pinna pair occurs on the rachis of some vegetative fronds (Plate 6, fig. 22—24); an



Text-fig. 5. Restorations of basal portions of vegetative branch systems of *Rhacophyton ceratangium* with basal rachis pairs in A attached to stem and variously developed primary pinna pairs attached to quadriseriate vegetative rachis in B—E. A, pinna-like pair of aphlebia-like branches at the base of a rachis pair with three small paired dichotomous branchlets shown on the lower portion of one rachis. B, equally developed pair of primary pinnae subtended by pair of aphlebia-like branches and bearing dichotomous branchlets. C, inequally developed pair of primary pinnae with the shorter shown bearing pinnately arranged dichotomous branchlets and subtended by an aphlebia-like branch. D, inequally developed pair of primary pinnae with markedly smaller one on right; both pinnae are subtended by aphlebia-like branches. E, extremely reduced pinna development on right side compared to pinna member on left, both subtended by aphlebia-like branches. The gradational sequence in unequal development of one member of a pinna pair illustrates observed variation and is not a consecutive series on one branch system. x 2.

aphlebia-like branchlet occurs laterally on each side of the common base of the pinna pair. Subsequent, alternate pairs of sub-equally developed pinnae form a quadriseriate branch system. The angle between the two pinnae of a pair is about 90° where both are developed, but not necessarily the same length; their pinnule-like ultimate divisions are still oriented in a single plane. The pinnae of pinna pairs tend to be longer than in biseriate vegetative fronds, and the distances between alternating pairs of primary pinnae and between their secondary pinnae are usually greater and less uniform than in biseriate vegetative fronds.

In one specimen (Plate 1, fig. 1; Plate 6, fig. 23—24) distances between secondary pinnae progressively increased from 3—4 mm to 6—7 mm near the region of quadriseriate development. Distances between secondary pinnae rose to 11—12 mm in the quadriseriate portion of the frond, then diminished as did other dimensions in the distal-most part of the frond. Primary pinnae axes were 1.0—1.5 mm in basal diameter, tapering gradually. Axes of the distal-most paired pinnae were 0.5 mm in maximum diameter. Lengths of primary pinnae were 7.0 cm to about 10.0 cm in the biseriate portion, attained estimated lengths of up to 16 cm in the quadriseriate portion, and diminished in length down to 2.0 cm in the distal-most portion.

In a second vegetative frond, which exhibited the biseriate-quadriseriate change (Plate 6, fig. 22), and which was associated with the specimen shown in Plate 2, fig. 5, the primary pinna axes were 1.5—2.0 mm in basal diameter; primary pinna lengths were about 10.0 cm in the biseriate portion, 14.0 cm in the transitional region, and up to an estimated 25 cm in the quadriseriate portion. Distances between secondary pinnae increased more uniformly from the biseriate (5—6 to 8—9 mm) to the quadriseriate region (9—10 to 10—11 mm).

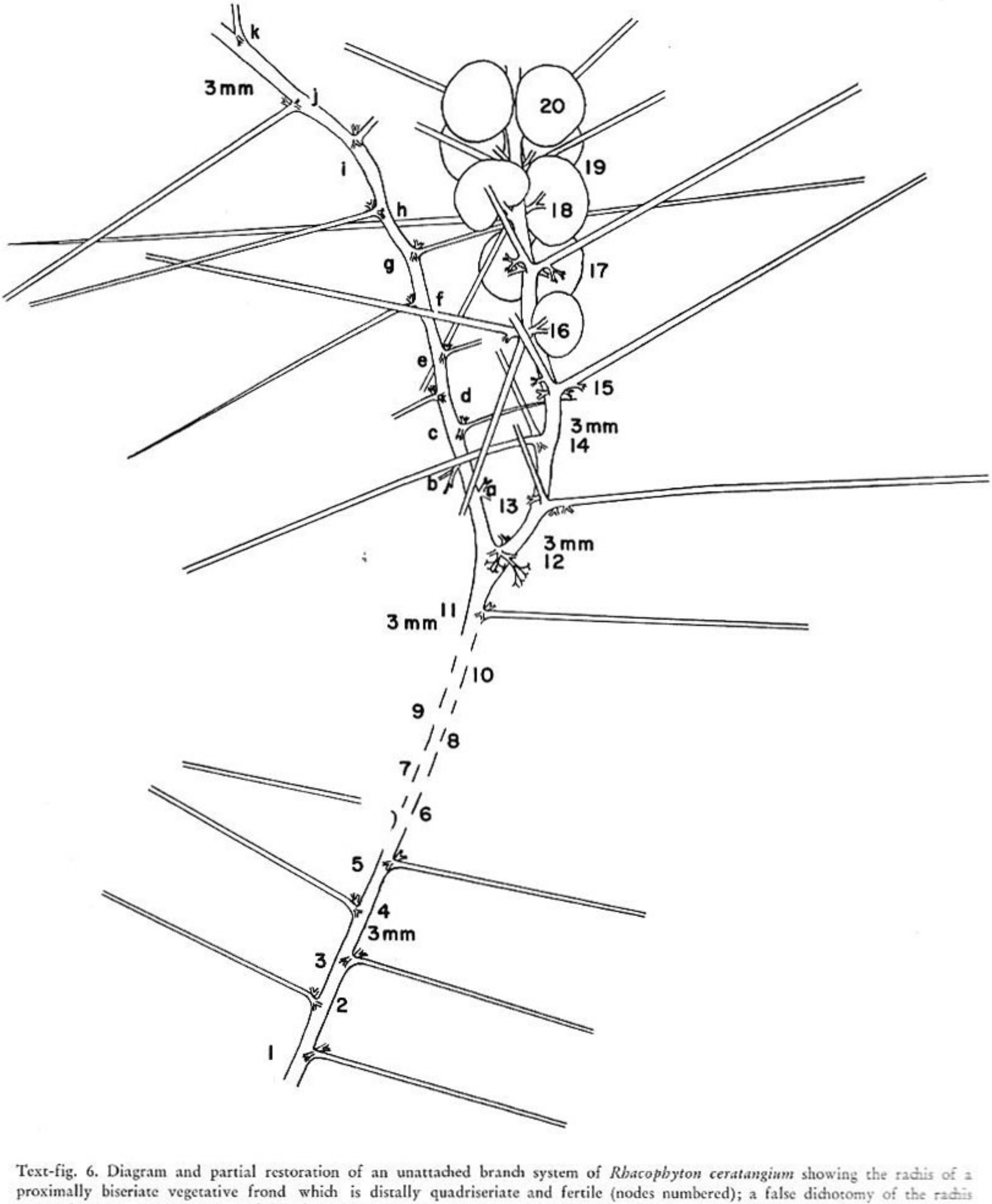
The pinnae of the two-dimensional frond portion are longest immediately below the three-dimensional portion, and the first pairs of pinnae on the three-dimensional portion are markedly unequal in length with the inequality less and less evident among successive pinna pairs. With one exception, vegetative fronds showing the change from biseriate to quadriseriate also exhibit a pronounced bending or twisting of the rachis just before or after the transition from two- to three-dimensional morphology.

Three-dimensional Branching—Fertile

One unattached frond specimen, predominantly vegetative and biseriate, had a major division at about its mid-length. This division is apparently a false dichotomy with one member, the apparent rachis of the frond, exhibiting a transition to quadriseriate sterile, and then to the fertile condition (Text-fig. 6; Plate 7, figs. 25—26); the other member continues with biseriate two-dimensional morphology. Pinna lengths on the biseriate branch increase rapidly from 3—4 mm near the base of the branch to over 11 cm distally. The main axes of both members of the false dichotomy are rather uniformly 3 mm wide throughout their preserved lengths. Below the false dichotomy inter-pinna distances are 13—17 mm, while in the quadriseriate portion, distances between pinna pairs increase slightly (15—20 mm). Axes of primary pinnae of the quadriseriate portion are up to 2.5 mm wide, and some pinnae can be traced for a length of 17 cm, while axes of primary pinnae below the false dichotomy are considerably smaller (1.0 mm wide).

The fact that the left biseriate branch of the false dichotomy is not the continuation of the rachis appears to be demonstrated when the right quadriseriate branch is omitted. An atypical frond is produced that has a disorganized arrangement of primary pinnae — the length of primary pinnae suddenly decreases just above the false dichotomy, and three successive appendages appear on the same side of the rachis at the position of the false dichotomy. If, however, the biseriate branch of the false dichotomy were removed, a typical biseriate frond would be produced that becomes quadriseriate-fertile distally.

The lower sterile quadriseriate portion of the above frond specimen is identical to previously described three-dimensional sterile fronds, and the existence of sterile nodes (Plate 7, fig. 25) on fertile fronds has been noted previously on *R. mirabilis*, *R. zygopteroides* (LECLERCQ 1951) and *R. ceratangium* (ANDREWS & PHILLIPS 1968). There is also a difference in the morphology between primary pinnae of biseriate vegetative fronds and those of quadriseriate vegetative and/or fertile fronds. The primary pinna pairs of the three-dimensional fronds are more distantly spaced and individual primary pinnae are wider, longer and have their secondary pinnae or pinnule-like divisions, as the case may be, more distantly spaced. Sterile three-dimensional vegetative frond portions seem to be quite homologous to fertile frond systems, but differ by lacking sporangia on the subtending aphlebia-like structures (Plate 7, fig. 27).



Text-fig. 6. Diagram and partial restoration of an unattached branch system of *Rhacophyton ceratangium* showing the rachis of a proximally biseriate vegetative frond which is distally quadriseriate and fertile (nodes numbered); a false dichotomy of the rachis occurs between quadriseriate and biseriate portions, with bipinnate development of left pinna (nodes lettered); fertile aphlebia-like structures with sporangia are represented by ovals; rachis remains uniformly 3 mm wide. x 0.7.

Discussion

Morphological Interpretations

Five morphological aspects of *Rhacophyton ceratangium* have been emphasized in the preceding descriptions: vegetative frond arrangements (stegotaxy) in pairs, previously obscured by false spiralling; quadriseriate pinna development distally on vegetative fronds; alternate arrangements of pinnae on biseriate vegetative fronds with basally associated minor branchlets; quadriseriate sterile to fertile development distally on vegetative fronds; and root anatomy with root-like structures attached to stems and at frond bases. These data permit a more coherent interpretation of the various axes and lesser branch systems which have been referred to descriptively as stems, and vegetative and fertile fronds with their attendant terminology.

The basic anatomical organization of *Rhacophyton ceratangium* consists of major branches (stems, rachises) with clepsydroid primary xylem and secondary xylem with rays (Kräusel & Weyland 1941, Andrews & Phillips 1968), and this type of anatomy may be inferred in the primary pinnae of quadriseriate fronds as established in *R. zygopteroides* by Leclercq (1951, 1954). The occurrence of secondary xylem in all the major axes suggests the cauline or axial nature of rachises of both sterile and fertile fronds as well as some primary pinnae.

Stegotaxy and Quadriseriate Branching

Recognition of the two-rowed arrangement of paired rachises on opposite sides of the main stem, with a common basal attachment of rachis pairs, now logically relates anatomy and stegotaxy. The false spiralling of the two opposite rows of paired rachises has, in turn, been correlated with rotation of the clepsydroid anatomy of the main stem. Particularly inconsistent with the bilaterally symmetrical anatomy in the main stem was the interpretation of closely spaced frond rachises as being spirally arranged (Andrews & Phillips 1968). The occurrence of quadriseriate (two rows of paired rachises), alternate branching on the main stem is identical to that in the quadriseriate fertile frond. Previously, the paired arrangement of primary pinnae on fertile fronds stood out as an exceptional feature in the overall branch pattern of *Rhacophyton.* Furthermore, with supposedly spiralled rachises, biseriate sterile fronds, and quadriseriate fertile fronds, the implied morphological levels of distinction among the stem and its dimorphic fronds seemed adequate to proceed with detailed homologies to fern organization. However, the repeated clepsydroid anatomy in stem, rachis and primary pinnae posed a persistent problem in fern comparisons, and also paralleled the type of repetitive anatomy now known in the progymnosperms.

Discovery of the occurrence of quadriseriate distal portions of otherwise biseriate vegetative fronds establishes the same quadriseriate (two rows of paired pinnae), alternate arrangement as on the stem and fertile frond. The potential in biseriate fronds for quadriseriate (three-dimensional) branching of the rachis, either exclusively sterile or sterile-transitional to fertile, emphasizes the basic similarities between biseriate and quadriseriate branch systems, and provides insight to what have been interpreted as basal sterile portions of fertile fronds. The stegotaxy of major branches therefore consists of opposite distichous rows of alternating paired branches with a common base (rachises or primary pinnae) and results in a repetitive quadriseriate morphology of successive branch orders with clepsydroid primary xylem surrounded by secondary xylem.

Biseriate Branching

The major exceptions which now stand out are the biseriate primary pinnae portions of vegetative fronds as well as all higher orders of division of primary pinnae on both vegetative and fertile fronds up to the dichotomous ultimate divisions. Once the quadriseriate potential of the sterile frond was established, recognition of the fundamentally quadriseriate plan of the biseriate primary pinnae of vegetative fronds and all higher pinna orders relates to the consistently alternate arrangement of single pinnae. Minor dichotomous branchlets (or ultimate divisions) at the base of and immediately opposed to each of the alternately developed primary and secondary single pinnae suggested the vestigial occurrence of structures which constituted the second, potential pinna of a pair. These ultimate-dichotomous divisions are separated from similar basally attached aphlebia-like structures by their basally opposite attachment, not lateral and catadromic, and by the fact that they are consistently above or below the rachis-pinnae plane. In viewing the biseriate frond from above as in portions of Text-fig. 3, the pattern of single pinna development from a potential pair apparently requires consistent development of, for example, the lower pinna members or the upper pinna members, but not alternate development above and below the plane of the frond as might be expected; the opposed and perpendicular minor branchlet representing the vestigial second member of a pinna pair will be consistently above or below the frond plane. The strongest supportive evidence for this interpretation of the opposed basal branchlet as a vestigial second member of a potential pinna pair is the change from biseriate to quadriseriate where the proximal most pinna pairs are quite unequal in development, and a pair of aphlebia-like structures occur at their common base.

Aphlebia-like Structures

Aphlebia-like structures occur singly in catadromic positions subtending each order of branching from rachis to ultimate pinnae and are strictly sterile except those below the primary pinnae of fertile fronds. Their actual nature is problematic and probably in part foliar, but those at rachis bases clearly had the potential for pinna-like development and so they too are branch-like in character. Aphlebia-like structures occur in distinct pairs, where branches occur in obvious pairs such as rachises and quadriseriate pinnae, thus adding to the overall repetitive pattern of the branch system of *Rhacophyton.*

Comparisons of Sterile and Fertile Portions of a Common Branch System

The more extensive lengths of rachises of sterile fronds, up to 44 cm, and those of fertile fronds, in excess of 50 cm with some primary pinnae of more than 35 cm in length, coupled with transitions from biseriate to quadriseriate sterile and fertile branches, raise doubt concerning even the determinate nature of the frond-like branch systems. While the evidence is not clear cut, data on very gradual tapering of rachises and pinnae, the near terminal portions of some frond specimens (Text-fig. 3), and others with secondary growth of primary pinnae (Text-fig. 6), suggest the likelihood that the rachises and perhaps some primary pinnae of the frond systems were not determinate in growth, or at least still retained the potential for indeterminate growth under certain conditions.

The marked differences in size of quadriseriate fertile portions, particularly rachis diameter and primary pinnae length compared to biseriate fronds, reflect some significant differences in growth of the two systems. Fertile fronds and, in general, quadriseriate branch systems seem to attain larger diameters and more extensive apical growth (rachis and pinnae) than do the biseriate vegetative portions. This is further evident in frond specimens exhibiting biseriate-quadriseriate changes, sterile or fertile. In both fertile and sterile branch systems the primary pinnae in the quadriseriate portion are markedly longer and somewhat larger in diameter; often the primary pinnae immediately below the quadriseriate-change are the longest on the biseriate part of the frond. Maximum diameter for sterile frond rachises is 4—6 mm, while that of isolated fertile (entirely quadriseriate) rachises is 6—8 mm. In one specimen showing secondary bipinnate growth of a primary pinna (Text-fig. 6), the rachis appears to divide (false dichotomy). The axis of the bipinnate primary pinna is the same diameter (3 mm) as the rachis of the quadriseriate fertile portion. However, the pinnae on the fertile portion of the false dichotomy are markedly longer than the pinnae on the sterile portions of the frond.

The organic attachment of entirely quadriseriate fronds to the main stem has not been established in *R. ceratangium,* although the direct attachment of a quadriseriate sterile portion of a frond is known in *R. zygopteroides* (see discussion later). Vegetative portions of the branch system are biseriate and/or quadriseriate; fertile portions occur more distally in some attached and isolated frond systems. Failure to discover attachment of fertile frond systems directly to a main axis among the numerous specimens examined seems to suggest that the tentative arrangement of fertile fronds shown by ANDREWS & PHILLIPS (their Text-fig. 4, 1968) is less likely, and that strict dimorphism of the sterile and fertile branch system is an over-simplification based on the assumption that there was a greater degree of frond differentiation and dimorphism than actually existed. The branch systems were clearly capable of changing from biseriate to quadriseriate, either sterile or fertile; there might have been distal reversions to sterile and biseriate unless mature fertile branch systems were selectively abscissed or by their different growth rates became transformed into what we might later interpret as main stems with two rows of alternating paired rachises.

In *Rhacophyton ceratangium* the stem with paired rachises, the vegetative rachis with paired or alternate, single, primary pinnae, and the fertile rachis with paired primary pinnae (each with aphlebia-like structures) — all appear to be homologous branch systems by evidence of repetitive patterns and, in the case of fronds, by transformation from one type to the other. *Rhacophyton* was a relatively complex and repetitive system of branch systems, closely paralleling progymnosperm branch morphology, but in the vegetative fronds a significant evolutionary level of biseriate development and planation had been achieved throughout extensive portions (up to 40 cm long). The development of only one member of potential pinna pairs was carried out with planation up to the dichotomous ultimate divisions.

Pinnule-like Ultimate Divisions

The pinnule-like ultimate divisions of the sterile fronds of *Rhacophyton ceratangium* differ largely according to fossiliferous zones (Text-fig. 4, A—C). The markedly three-dimensional pinnules tend to have more tip recurvation, resembling an *Aneurophyton*-type of ultimate division; this type, designated A, occurs in the lower zones. Type B is more flattened, and the ultimate tips are fairly straight. This form characterized the type material of *R. ceratangium* from the upper zone. The third and rarest, Type C, is strictly two-dimensional with the flattened ultimate divisions in a single plane. The occurrence of essentially two-dimensional pinnule-like forms in the upper zone and markedly three-dimensional forms in the lower suggests several possible interpretations — evolutionary planation, dimorphism, taxa differences or just natural variation. We are inclined to regard the sequence as one of variation which is critically needed for other *Rhacophyton* species if real distinctions are to be maintained among species based on pinnule morphology.

Pinnules similar to Type C are common in Upper Devonian plant assemblages. Some from the Upper Devonian of Belgium have been identified as *Sphenopteris modavensis* STOCKMANS, *S. maillieuxi* STOCKMANS, and *S. flaccida* CREPIN; *R. condrusorum* is from that flora (STOCKMANS, 1948).

Adventitious Root System

Evidence from *R. ceratangium* and *R. zygopteroides* (LECLERCQ 1951) indicates there was an adventitious root system developed from the main stem and/or between the bases of rachises; root-like structures have not been reported for other species. In *R. ceratangium* the larger roots are 1.5—2 mm in diameter with unbranched laterals, 0.1—1.0 mm in diameter. The cross-sectional anatomy of one root attached to a petrified main axis bearing fronds exhibited a single group of primary xylem tracheids surrounded by radially aligned tracheids. In *R. zygopteroides*, LECLERCQ (1951) reported diarch roots up to 6—7 mm in diameter with scalariform tracheids. One very stout one was found attached to the stem, and roots were described as unbranched except for one bifurcate specimen. The occurrence of adventitious roots was particularly noted to occur in *R. zygopteroides* specimens which exhibited coherent masses of vegetative fronds apparently extending from a main stem.

Comparisons with Other Species of *Rhacophyton*

From more recent detailed studies of *Rhacophyton* (STOCKMANS 1948, LECLERCQ 1951; ANDREWS & PHILLIPS 1968) and our descriptions, the generic concept of *Rhacophyton* has become more coherent, assuming certain aspects we have described are actually exhibited by all the other species. The actual bases for species separation have become more tenuous because of insufficient comparable data or emphasis on relative dimensions, particularly of preserved lengths of structures. Diagnoses of the genus and the species will have to be revised when such information becomes available for other assemblages of *Rhacophyton*. Detailed comparisons among the species have been made most recently by ANDREWS & PHILLIPS (1968) and, with the exception of *R. condrusorum* (CREPIN 1875; GILKINET 1922; STOCKMANS 1948), detailed summaries of each species is given in ANDREWS & BOUREAU (1970).

A comparative feature previously lacking in *R. ceratangium* and deduced in *R. zygopteroides* is the quadriseriate sterile morphology apparently found below the fertile portion of the frond. This type of morphology does occur in *R. ceratangium* distally in a strictly vegetative frond, in a transition from biseriate to quadriseriate fertile frond morphology, and at the base of a predominately fertile, completely quadriseriate frond. Because quadriseriate morphology was previously known in *R. zygopteroides* only in the fertile frond, LECLERCQ (1951) deduced that the basal part of the fertile frond was probably quadriseriate sterile, as had been briefly mentioned for *R. mirabilis* (NATHORST 1902), when she discovered the lower portion of an attached frond that was sterile and quadriseriate. This was the basis for interpreting the attachment of an associated fertile frond to the main stem of *R. zygopteroides* which was carefully shown disconnected in the often reproduced restoration by LECLERCQ (1951). Contrary to NATHORST's (1902) suggestion that the lower portion of fertile fronds of *R. mirabilis* were quadriseriately sterile, SCHWEITZER (1968) reported that all the specimens he had examined were either sterile or fertile, but their dimensions were not given. Our data indicate that quadriseriate sterile morphology can be transitional to fertile morphology; however, the existence of strictly dimorphic frond systems is not supported.

The occurrence of paired rachises on the stem of *R. zygopteroides* can be ascertained by further degagement, but one curious feature discerned by LECLERCQ (1951, p. 14), but not included in her restoration, was the occurrence of an aphlebia-like or catadromic pinnule at the base of the vegetative frond. It is not clear whether this was an aphlebia-like structure laterally subtending the rachis or the catadromic vestigial "pinna pair", both of which occur on vegetative fronds of *R. ceratangium*.

Stems (larger axes) have not been reported for *R. mirabilis* or *R. condrusorum;* however, the relative dimensions and supposed tripinnate branching of *R. condrusorum* suggest that the rachis, which is 35 cm long, 1 cm in diameter with primary pinnae 30 cm long and 4 mm in diameter, might be the main stem with frond rachises instead (ANDREWS & PHILLIPS 1968). In view of our reinterpretation of *Rhacophyton ceratangium* as a repetitive branch system with similar axial cauline anatomy in the major branches, this is somewhat of a moot question now, but the specimen in question (STOCKMANS 1948; Plate II, fig. 8) has spacing between successive alternating lateral branches quite similar to some stems of *R. ceratangium* (Plate 3, fig. 7); it may represent the more apical portions of the stem-frond system, and the upper-most pair of "rachises" appear to be subopposite.

SCHWEITZER (1968) has rejected LECLERCQ's assignment of *Cephalopteris mirabilis* NATHORST to the genus *Rhacophyton,* and while he presented a restoration of the frond system of *C. mirabilis,* based on newly discovered specimens from Bear Island, a detailed description and documentation has not yet been published.

The fusiform sporangia of *Rhacophyton* species are quite similar with the elongate sporangial tip being most pronounced in recovered specimens of *R. ceratangium.* Homospory for the genus is deduced from the trilete spores with a perispore and diameters of 40 x 52μ to 42 x 70μ in *R. ceratangium* (ANDREWS & PHILLIPS 1968) and 45—68μ in *R. incertum* from the Upper Devonian (Torcha suite) of the Russian platform (ISCHENKO & SOROKINA 1968).

Comparison with *Protocephalopteris*

Protocephalopteris praecox (HØEG) ANANIEV from the Middle Devonian of Spitsbergen (HØEG 1942, SCHWEITZER 1968) and the Minusinsk Basin of western Siberia (ANANIEV 1960) has been compared with *Rhacophyton* by the above authors. Data from the reinvestigation of *R. ceratangium* bring the comparative morphologies of *Protocephalopteris* and *Rhacophyton* into closer basic similarities consistent with the proposed phylogenetic morphological trends of these genera from Middle to Upper Devonian (ANANIEV 1960, SCHWEITZER 1968).

HØEG's Discovery

HØEG (1942) originally discovered *Protocephalopteris (Cephalopteris)* (?) *praecox* along the beach of Wijdefjorden, Spitsbergen, and illustrated a large bipinnate frond-like specimen (HØEG 1942, Plate 17) with a rachis 18 cm long and 5—7 mm wide at the base. The pinnae, 2—3 mm wide, were alternately arranged, and the surface of all the branches was markedly striated, a character corroborated by ANANIEV (1960) and by SCHWEITZER (1968). The pinnae, in turn, bore either sterile or fertile pinnule-like divisions; the sterile pinna divisions were alternate and the lower-most sterile pinnule-like structures occurred on the abaxial side of the primary pinna. Non-laminate ultimate sterile divisions were divided three times with recurved tips; such structures were 1.5 cm long and dichotomously to pseudomonopodially branched. The fertile divisions were opposite in pairs and occurred at regular intervals of about 2.5 cm.

Fertile Branch Systems of *Protocephalopteris*

ANANIEV (1960) has described the fertile portions of *Protocephalopteris* in greater detail from four localities in the southeastern part of western Siberia in the Ilemorovskay Fm. which is stratigraphically in the Givetian. There is apparently no identifiable main stem in the assemblages of *Protocephalopteris* and the specimens of branch systems described, both fertile and sterile, are entirely quadriseriate with paired and once or twice dichotomously divided ultimate divisions (see restorations in SCHWEITZER 1968). The hypothetical fertile restoration of ANANIEV (1960, fig. 2) depicts a rachis with alternating pairs of oppositely arranged primary pinnae (the members of a pair are separated from each other by about 90°), which are subtended by a pair of catadromic, dichotomously branched (up to 5 times) aphlebia-like fertile structures with terminal sporangia, an arrangement basically similar to *Rhacophyton*. However, the number of divisions and abundance of sporangia are markedly less and all the branches of the catadromic system seem to be in one plane. *R. (Cephalopteris) mirabilis* exhibits fewer divisions and sporangia than other *Rhacophyton* species. The ultimate appendages on the primary pinnae are alternate in pairs and also fertile with each member of a pair terminating with a pair (or small clusters according to ANANIEV) of almost sessile, elongate, exannulate sporangia (1.4—2.0 mm) which are identical to those in the catadromic fertile structures below the primary pinnae. The ultimate divisions on the primary pinnae with paired sporangia appear to be bent downward. A major distinction between *Protocephalopteris* and *Rhacophyton* is the quadriseriate branching of the ultimate appendages which are fertile. It is not certain whether all such ultimate appendages of primary pinnae were fertile, and the distal extremities of primary pinnae as well as the main rachis are not known. ANANIEV described twice bifurcated branchlets which were apparently sterile but did not establish their actual attachments. No dimensions for *Protocephalopteris* are given by ANANIEV (1960).

Sterile Branch Systems of *Protocephalopteris*

The relationship of fertile branch systems to the sterile branch systems described and reconstructed by SCHWEITZER (1968) are uncertain, but the details of sterile branch systems are largely derived from his study and are consistent with the descriptions of fragmentary specimens reported by HØEG (1942) and by ANANIEV (1960). The sterile branch system of *P. praecox* is based on specimens from the Wijde Bay Series of northwest Spitsbergen, which in European terminology is approximately Middle Eifelian to Middle Givetian in age (SCHWEITZER 1968). The sterile branch system is identical in organization to the fertile ones with the important exceptions that the alternating paired ultimate appendages of primary pinnae are about 1.4 cm long, uncurved, and twice bifurcated with the short tips recurved; this feature is also exhibited by the ultimate tips of the sterile, catadromic pair of aphlebia-like structures subtending each primary pinna pair. It should be noted that all known paired, ultimate, sterile appendages on primary pinnae are identical, and subtending aphlebia-like structures occurred only at the base of paired primary pinnae. Rachis lengths were up to 24 cm with a basal width of 1.0 cm; there were 7—16 cm between primary pinna pairs which were 3 mm wide and up to 18.5 cm long. The adaxial angle of primary pinnae with the rachis was 35—50° and both pinnae of a pair exhibited the same size with maximum diameters about 1/3 that of the rachis. The subtending catadromic, sterile aphlebia-like structure was up to 4 cm long and exhibited 5 successive orders of dichotomies. An interesting observation made by SCHWEITZER emphasized that the sterile primary pinnae of *Protocephalopteris* were consistently larger in diameter than fertile ones.

Morphological Differences and Hypothetical Changes of *Protocephalopteris* to *Rhacophyton*

The frond-like branch systems of *Protocephalopteris* are quadriseriate to the extent that they are known and this basic arrangement coincides with that of *Rhacophyton ceratangium* with the important exceptions of the biseriate, sterile branch system and the secondary sterile pinnae of both sterile and fertile branch systems.

Evidence has been given to support an interpretation of biseriate planation by the alternate development of only one member of a pinna pair in *Rhacophyton* and the potential for development of both has been demonstrated. *Protocephalopteris* is an ideal representative of an ancestral condition that is primitively quadriseriate throughout. In the hypothetical derivation of *Rhacophyton* morphology from that of *Protocephalopteris*, an additional pinna order has developed, each pinna order has a subtending aphlebia, more extensive dichotomies of the ultimate appendages have developed, and only one member of alternating pinna pairs and pinnule-like structures develop in typical biseriate fronds. The occurrence of some quadriseriate primary pinnae on sterile fronds and on all fertile fronds is in close agreement with *Protocephalopteris.* However, sporangia-bearing has become restricted in *Rhacophyton* to catadromic three-dimensionally branched aphlebia-like structures below primary pinnae, and all primary pinnae are sterile. The differences in sizes of sterile and fertile primary pinnae in *Protocephalopteris* is paralleled in *Rhacophyton* by the generally larger dimensions of all sterile primary pinnae in quadriseriate branching compared to primary pinnae of biseriate frond portions, but the main axes (rachis) of fertile portions of *Rhacophyton* are larger than those of sterile portions.

The morphological similarities between *Rhacophyton* and *Protocephalopteris* in the context of geologic time strongly suggest phylogenetic changes between these Devonian representatives which have led to some rather subtle modifications of branch systems toward frond-like structures. Much remains to be known about the anatomy and the gross morphology of *Protocephalopteris* as well as *Rhacophyton* species.

Comparisons with Coenopterid Ferns and Progymnosperms

The concepts of coenopterid ferns have changed considerably over the past half century but their taxonomy does not seem to have kept pace with current ideas. These small Permo-Carboniferous ferns represent figuratively the cross-roads of late Paleozoic fern evolution (PHILLIPS 1974) and they should be separated into at least two main groups: the Coenopteridales sensu stricto with the Botryopteridaceae, Grammatopteridaceae (?), and Anachoropteridaceae, which do not appear until Visean (*Botryopteris, Grammatopteris* ?), Namurian or even later, and which apparently grade into the Filicales; and the Zygopteridales with the Clepsydroideae and Etapteroideae which consistently appear earlier in the Mississippian and in greater diversity than the Coenopteridales sensu stricto. The recognition of the zygopterid ferns as real ferns in the fullest sense and as a unique late Paleozoic dead-end phylogeny is appropriate in discussions of possible fern-relationships with *Rhacophyton, Protocephalopteris* or any Devonian precursor. If one considers what a general morphological concept fern is along with its lower vascular plant life cycle, it seems clear that we should continue to have difficulty separating fern-like and progymnosperm-like plants in the Devonian-Mississippian strata. A fern does in general have morphologically distinct stem, roots and fronds with sporangia and, with the exceptions of roots, any of the structures may suggest a plant of fern-like characters but none as decisively as the combination of frond with sporangia. With such general characters it seems desirable to acknowledge that the concept of a fern represents both a level of organization as well as a life cycle; fern should be an acceptable polyphyletic concept as are the gymnosperms and by inference the progymnosperms.

While zygopterid-like phyllophore specimens *(Clepsydropsis)* have been reported from the Upper Devonian of East Germany, there is insufficient data to assess the existence of distinct frond morphology for any putative Devonian fern. The repeated occurrence of clepsydroid phyllophore-like specimens in the earliest known Mississippian plant localities tends to support the likelihood of a markedly earlier appearance of zygopterid ferns. This is strongly supported by the report of BÖHM (1935) of *Metaclepsydropsis*-like specimens from the basal Visean (Lyciennes horizon) of the Montagne Noire of France; the specimens have been described in detail as *Clepsydropsis leclercqii* and GALTIER (1966) has emphasized its transitional or intermediate morphology between the Clepsydroideae and Etapteroideae with clepsydroid xylem, permanent peripheral loops, crescent-shaped pinna traces and quadriseriate with quite a long undivided pinna trace below the dichotomy to a pinna pair. Some of the earliest known fern sporangia with annuli are those assigned to *Musatea* (GALTIER 1968, CHAPHEKAR & ALVIN 1972) from the Visean of France and Scotland and attributed to the etapteroid genera *Diplolabis* and *Metaclepsydropsis.* Frond branching and the attachment of *Musatea duplex* to *Metaclepsydropsis* has been well established in this Visean fern (CHEPHEKAR & ALVIN

1972). There is no evidence of distinct laminate foliage among these early ferns of the Mississippian Period. In summary, zygopterid ferns do occur quite early in the Mississippian. While earlier reports of such from the Devonian are too fragmentary to evaluate, the sequence of occurrence of *Protocephalopteris* and *Rhacophyton* are not inconsistent with an ancestral role to zygopterid ferns. One important aspect which should not be overemphasized in such a tentative phylogeny is the occurrence of secondary xylem in a strictly reductional sequence. While secondary xylem is a feature of *Zygopteris,* the occurrence of such growth in zygopteris may be quite variable and other suggestions as to the development of secondary growth in the Etapteroideae should be considered (DENNIS 1974).

The repetitive branch system morphology of *Rhacophyton,* without a reasonably clear cut frond, relegates this genus as well as *Protocephalopteris* to a level below that of ferns. In drawing comparisons between *Rhacophyton* and the Zygopteridales it should be ncted that *Rhacophyton*'s main axes, which correspond most closely with a rachis or phyllophore in *Rhacophyton*'s sterile and fertile frond-like portions, are interpreted as branch systems. Some of these were still indeterminate in nature, and consequently *Rhacophyton* represents a putative pre-frond stage morphologically. *Rhacophyton* could be regarded as a prefern in the phylogeny toward biseriate and quadriseriate zygopterid ferns but it does not meet the criteria required of the zygopterid or coenopterid fern status attributed by ANANIEV (1960) or SCHWEITZER (1968). The last two authors would, however, probably agree with LECLERCQ (1954) that *Rhacophyton* may be representative of the ancestral group from which the Zygopteridales have evolved.

Detailed comparisons of *Rhacophyton* and zygopterid ferns have already been made (LECLERCQ 1951, 1954; ANANIEV 1960; ANDREWS & PHILLIPS 1968; SCHWEITZER 1968). The important points of similarity between *Rhacophyton* and various zygopterid ferns are the combined biseriate and quadriseriate branching of the phyllophore or main axis of the frond-like branch system, its clepsydroid anatomy, the presence of secondary xylem, the orientation of primary pinnae orders and aphlebia or aphlebia-like structures.

Rhacophytons's progymnosperm-like characters have been given by ANDREWS & PHILLIPS (1968 p. 61): "three-dimensional branch systems terminating in dichotomized ultimate appendages, mesarch protostele, repetition of the same primary strand along with secondary xylem in one or two orders of branching and terminally borne fusiform sporangia on a highly divided branch system. The differences between *Rhacophyton* and genera of the Aneurophytales are largely limited to the clepsydroid primary strand with peripheral loops; these are characters that occur in Coenopteridales and Cladoxylales."

The implications of *Rhacophyton,* with its progymnosperm-like characters, as an ancestral prefern representative in the phylogeny leading to zygopterid ferns are (1) a return to the phyletic thrust embodied by the original Protopteridiales of HØEG (1942), (2) a consistently earlier geologic appearance of zygopterid-like fossils compared to the other main groups of Carboniferous ferns and (3) a reasonable explanation for the unique morphology of certain Permo-Carboniferous zygopterid ferns because they were probably derived from quite a different evolutionary line of Devonian plants than other ferns. Such phylogenetic alignment of *Rhacophyton* and probably *Protocephalopteris* as ancestral prefern types leading to the zygopterid ferns would be consistent with derived explanations of the phyllophores, secondary growth, biseriate and quadriseriate pinnae, aphlebia, clusters of sporangia (but not sporangial complexity) and at the same time there is very close parallel with the progymnosperms in the potential evolution of a frond from pinnate branch systems.

Taxonomic Affinities

Rhacophyton, in representing characters of both progymnosperms and preferns with some elements of the Trimerophytina (BANKS 1968), should be returned to the Protopteridiales with some modifications of the original circumscription of HØEG (1942, p. 178) and with the recognition that there is need for a taxon of at least ordinal rank for Devonian-Mississippian lower vascular plant forms transitional between the ancestral and generalized Trimerophytina and the highly differentiated taxa such as ferns and seed ferns which exhibit fronds. This apparently was the motivation in the establishment of the Protopteridiales as well as the Aneurophytales by KRÄUSEL & WEYLAND (1941). Since the phylogenetic recognition of progymnosperms (BECK 1960), the Protopteridiales have become entirely vacated by the transfer of all genera to the progymnosperms, largely to the Aneurophytales, and the only exception has been repeated assignments of *Rhacophyton* to the Zygopteridales or equivalent. In view of the historical difficulties in disttinguishing between the frond foliage of ferns and pteridosperms in Carboniferous strata, the taxonomic problems in Middle Devonian to Mississippian frond-like branch systems seems particularly acute with little recourse to progymnosperm assignments except new monotypic orders or a growing incertae sedis category. There will no doubt be some conflicting overlap between a resurrected Protopteridiales and the now revised Aneurophytales (progymnosperms) with plants such as *Rhacophyton* which exhibit secondary growth; however, the Protopteridiales offer a necessary taxonomic option for plants with frond-like branch systems or frond-like structures whose anatomy are not sufficiently known to allow precise morphological interpretations. The Protopteridiales may serve as a focal point for fern-like plants which may have progymnosperm characters but are apparently not in a direct line of gymnosperm evolution; primitive ancestors of pteridosperms may well fit this criteria. The Protopteridiales may parallel the progymnosperms in many external morphological characters but probably have closer fern-like affinities to the Zygopteridiales, Coenopteridales, Cladoxylales or other groups (see SCHECKLER 1974) which are either so heterogeneous or poorly known at present as to be too vague to recognize at a higher taxonomic rank.

Protopteridiales, HØEG (1942, p. 178), emended.

Plants of a more or less fern-like habit with branch systems, frond-like, but with slight differentiation between axes and frond-like branch systems. The ultimate ramifications of the branch systems may resemble pinnules but no broad laminae are found. Sporangia are borne terminally on ultimate non-laminate divisions.

Rhacophytaceae, BARNARD & LONG (1975, p. 240) emended.

Plants with repetitive alternately arranged quadriseriate to biseriate pinnate branch systems, subtended by aphlebia-like structures, sterile or fertile, and with dichotomously divided, non-laminate ultimate appendages. Axial anatomy clepsydroid with peripheral loop-like areas; secondary xylem present. Sporangia elongate, elliptical to fusiform, exannulate; homosporous.

Root system adventitious.

Habit, semi-erect to erect branch system, suffrutescent.

Genera assigned to the Rhacophytaceae (known stratigraphic range-Middle and Upper Devonian):

Type Genus: *Rhacophyton* CREPIN 1875; Generitype *R. condrusorum* CREPIN.

Other Genera:

Cephalopteris NATHORST 1902; Generitype *C. mirabilis* NATHORST.
Protocephalopteris ANANIEV 1960; Generitype *P. praecox* (HØEG) ANANIEV.

Frond Evolution

The alternately pinnate branch systems of *Rhacophyton ceratangium* provide insight into the evolution of a planated biseriate morphology suggesting a significant pre-frond stage from a three-dimensionally branched quadriseriate system. Our study has clearly removed the frond-like portions of *Rhacophyton* from the frond category by adding to the already established repetitive axial anatomy with secondary xylem — the apparently indeterminate nature of some axial elements (rachis-like), the lack of distinct dimorphic (sterile and fertile) branch systems, and the same basic arrangement of frond-like systems on the largest axes (stems) as seen in the frond-like systems themselves. With a clearer understanding of the basic quadriseriate organization in first order branching (rachis-like elements on the main stem) and secondary order branching (primary pinna-like elements) the deduction was made that the remaining orders (except ultimate dichotomous divisions) are also derived from a quadriseriate organization with development of only one member of each potential pinna pair. The ancestral, completely quadriseriate arrangement is exemplified by *Protocephalopteris.*

The essentially planated pinna systems of *Rhacophyton,* particularly in the biseriate branch systems, indicate differential development in a very systematic pattern. These may have evolved under selective pressures of changing habitat and habit, and/or a tendency toward developing specialization of vegetative and fertile portions of the branch systems which are impressive in their differences but are not distinct entities in their occurrences within the plant's organization. The varying degree of three-dimensional to two-dimensional arrangement of pinnule-like ultimate divisions may also reflect the tendency toward planation and specialized photosynthetic function. The least tendency toward planation is found in aphlebia-like structures and the 3—4 basalmost dichotomously branched units on the vegetative rachis. The degree of planation of the primary pinna orders in biseriate branches of *Rhacophyton* differs from the comparably positioned branches of *Archaeopteris* which are in opposite pairs and bear laminate leaves in a spiral or decussate arrangement.

Some of the persistent problems in anatomical-morphological interpretations of the branch systems of *Rhacophyton* are the lack of anatomical information for some higher orders of branching to complement the data of Leclercq (1951) and the bilaterally symmetrical, clepsydroid anatomy of all major branches including the largest axes. Leclercq (1951) has reported a stellate pattern in a partial cross-section of the main stem of *R. zygopteroides* and this apparently different stem anatomy has not been resolved with the anatomy of *R. ceratangium*. The evolution of fronds from branch systems in ferns and pteridosperms generally results in anatomical differences between stem and leaf which are essentially of radial and bilateral symmetry respectively. Axial anatomy in such phylogenies is generally regarded as primitively radial (Rhyniophytina) with a tendency toward an elliptical shape in some Trimerophytina. In the last group, Bierhorst (1971) has also pointed out the slight indication of radial alignment of metaxylem tracheids in the *Psilophyton* described by Hueber & Banks (1967) and more recently by Banks, Leclercq and Hueber (1975). In *Rhacophyton* the primary xylem of all major branches was bilaterally symmetrical at the pre-frond stage and this may be exceptional in that bilateral symmetry clearly preceded putative frond differentiation and that bilateral symmetry may also be evident in later stem differentiation where fronds are borne laterally in two rows along a prostrate rhizome as in a number of Etapteroideae genera.

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Brenda Carter, an independent artist, rendered the composite restoration in Text-fig. 1.

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Addendum

Since the time this manuscript was submitted for publication more recent evaluations of the taxonomic affinities of *Rhacophyton* have been given by Barnard & Long (1975), Bonamo (1975) and Beck (1976). All are in essential agreement that *Rhacophyton* should be excluded from the Progymnospermopsida and that the genus is probably most closely allied with zygopterid ferns: *Rhacophyton* was assigned to the Zygopteridaceae by Leclercq (1951; see Leclercq & Bonamo, 1971, p. 109—110; Bonamo, 1975); "*Rhacophyton, Protocephalopteris* and *Childanophyton* may well be primitive members of the Zygopteridaceae (Coenopteridales)." (Beck, 1976, p. 8); and assignment of *Rhacophyton* to the Rhacophytaceae fam. nov. Barnard & Long (1975, p. 240) along side the Zygopteridaceae in the Coenopteridopsida.

In this manuscript we had inadvertently duplicated part of the intent of Barnard & Long (1975) in proposing a new family, and have therefore accepted their family name, Rhacophytaceae. However, their brief circumscription has been emended in order to provide a broader basis for inclusion of other genera, and the Rhacophytaceae was placed in the Protopteridiales — hence, the element of our different opinion at present is the morphological concept of a true fern.

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Explanation of Plates

Plate 1

Figs. 1—2. *Rhacophyton ceratangium* Andrews & Phillips.

Fig. 1. Part of a stem measuring 75 cm in length. Twenty-four of thirty nodes are shown. Numbers indicate position of established nodes or frond attachments. The lower part of the stem was exposed on the underside of rock slab. Arrows indicate frond reconstructed in Text-fig. 3 and enlarged in Plate 6, fig. 23. Specimen UC-1007. Scale is 15.6 cm.

Fig. 2. Part of the largest aphlebia-like branch (and shorter catadromic pinna at base of frond) found attached to stem shown in Plate 4, fig. 15. The position of the catadromic pinna indicates a possible relationship to the aphlebia-like branch. Specimen UC-1011A.

Plate 2

Figs. 3—6. *Rhacophyton ceratangium* ANDREWS & PHILLIPS.

Figs. 3—4. Cross-sections of petrified xylem.

Fig. 3. Stem xylem from specimen shown in Plate 3, fig 9, with clepsydroid arrangement of primary xylem. Secondary xylem is radially arranged around the ends of both loops, but it is perpendicularly arranged on both sides of the median constriction. Specimen UC-1013. x 2.3.

Fig. 4. Stele of main root shown in Plate 3, fig. 9, with secondary xylem radially arranged around a small primary area. Specimen UC-1013. x 3.4.

Fig. 5. Part of a stem measuring 77 cm in length. Twenty-nine nodes are shown and indicated by numbers. One nearly complete, bent frond is attached at node number 3, arrows. Root-like appendages occur on stem near node 17, R. Specimen UC-1009. Scale 15.6 cm.

Fig. 6. A typical and symmetrical catadromic pinna at the base of a frond; base of a second catadromic pinna (arrow) is partially exposed. Specimen UC-1010. x 1.2.

Plate 3

Figs. 7—10. *Rhacophyton ceratangium* ANDREWS & PHILLIPS.

Fig. 7. Part of a stem measuring 37 cm in length with 11 numbered nodes. The specimen may represent a more apical region of the stem. Specimen UC-1008. Scale 15.6 cm.

Fig. 8. Unbranched root-like appendages, R, attached to stem, S, in a vertical row. A frond, F, is overlain by the root-like appendages. Specimen UC-1017A. Scale on photograph.

Fig. 9. A rhizome-like stem, S, bearing fronds on the underside and roots, R. The anatomy of both the stem and main roots was partially preserved (Plate 2, fig. 3, 4) and demonstrates a distinction between stem and root in *Rhacophyton*. Many slender lateral roots arose from the larger roots. Specimen UC-1013. x 1.

Fig. 10. An adventitious main root, MR, with a lateral root, R, from between a pair of fronds (node 17, Plate 1, fig. 1) on the stem, S. The root extends below one frond before being broken. Part of the base of one frond has been removed to reveal attachment of the root, MR. Specimen UC-1015. x 1.4.

Plate 4

Figs. 11—16. *Rhacophyton ceratangium* ANDREWS & PHILLIPS.

Fig. 11. Part of a large stem showing the aphlebia-like branches at the bases of fronds. The basal four pinnae on one frond are exposed, arrows; two additional pinnae are preserved higher on the counterpart. One frond (lower left) apparently failed to develop normally. Specimen UC-1011A. x 0.8.

Figs. 12—15. Paired part and counterpart of two frond portions demonstrating the two branches departing from the base of each pinna. One branch is larger than the other; the smaller branch is the aphlebia-like branch to the developed pinna (figs. 13, 15, arrows). The undeveloped pinnae have aphlebia-like branches that are always directed laterally and cross back under the rachis. Not all of each undeveloped pinna is visible, but the first "pinnule" or branch of an undeveloped pinna is sometimes large and is usually directed in the same general direction as the developed pinna (figs. 12, 14, arrows).

The aphlebia-like branches to the developed pinnae can be seen to be over-topped (fig. 13 and 15), a characteristic which was frequently encountered when the undeveloped pinnae were large and elongate. The undeveloped pinnae were found consistently on the part or counterpart (figs. 12 and 14), and did not alternate above and below the frond.

A root-like structure can be seen attached to the base of a pinna in fig. 12 (third node from bottom).

Figs. 12, 13. Specimen UC-1012A & B. x 1.8.

Figs. 14, 15. Specimen UC-1019A & B. x 1.2.

Fig. 16. A pinna (second from base) of a frond with each half of the first dichotomy a mirror image of the other. A lateral aphlebia-like branch is distinguishable near the base of each half, arrows. x 1.9.

Plate 5

Figs. 17—21. *Rhacophyton ceratangium* ANDREWS & PHILLIPS.

Figs. 17, 18. Part and counterpart of Type A pinnule-like divisions showing two lateral branches near or at the base of one pinnule axis. The branch at the base of the pinnule is interpreted as a reduced or undeveloped pinnule (fig. 18, arrow). An aphlebia-like branch to that branch appears after crossing beneath the pinna axis. The aphlebia-like branch to the developed pinnule arises slightly higher on the pinnule axis (fig. 17). Each branch is positioned slightly above and below the plane of the pinnule. Specimen UC-1016A & B. Scale in mm.

Fig. 19. Pinnules of Type C with flattened branch tips shown attached to two pinna axes. An aphlebia-like branch at the base of one pinna is shown extending under the removed rachis portion, arrow. Specimen UC-1014. x 1.9.

Fig. 20. A large pinnule from the frond in Plate 7, fig. 26, with recurved tips of Type A. Specimen UC-1018A. Scale in mm.

Fig. 21. Pinnae from a frond figured by ANDREWS & PHILLIPS (1968, Plate 4, fig. 12) with pinnules showing straight branch tips. Specimen USNM 42842. Others shown in Plate 4, fig. 11. x 1.4.

Plate 6

Figs. 22—24. *Rhacophyton ceratangium* ANDREWS & PHILLIPS.

Fig. 22. Part of a sterile frond associated with the plant in Plate 2, fig. 5, showing a transition from single to paired developed pinnae. One of the first pinnae of the three-dimensional portion of this frond is almost complete and about two times the length of pinnae on the two-dimensional portion of the frond. The first node with two developed pinnae occurs before the rachis bends, arrow. Specimen UC-1015B. Scale on photograph.

Fig. 23. A complete frond attached to node 24 of the stem in Plate 1, fig. 1. The end of this frond has been restorted by using a reversed photograph of the counterpart (fig. 24). Sections of the rachis have been repaired. Three pinnae are damaged on both part and counterpart and missing. Text-fig. 3 is a restoration of this frond, showing the unusual "pairing" of pinnae at the distal end. Specimen UC-1007. Scale is 15.6 cm.

Fig. 24. The distal end of the frond in fig. 23 and Plate 1, fig. 1, showing single, then paired developed pinnae. The very tip of the frond is concealed, as is one pinna of two pairs. Aphlebia-like branches and undeveloped pinnae are visible. Specimen UC-1007. Scale is 4 cm.

Plate 7

Figs. 25—27. *Rhacophyton ceratangium* ANDREWS & PHILLIPS.

Fig. 25. Part of a frond showing a transition from single to paired developed pinnae, and then to a fertile condition. The last "unpaired" pinna (arrow) is enlarged and produced one more branch order. No true dichotomy of the rachis occurs. Part of the rachis is missing. The frond was not found attached to any stem. A partial restoration of this illustrated in Text-fig. 6. Specimen UC-1018B. Scale is 15.6 cm.

Fig. 26, 27. Counterpart to the frond in fig. 25 showing in more detail the fertile rachis and the bipinnate pinna. The union of these two branches is not present on the counterpart. Fertile aphlebia-like branches are not present at the first three nodes (arrows) with paired, developed pinnae. One sterile aphlebia-like branch with seven dichotomies has been enlarged in fig. 27. Only one pinna of a pair is clearly visible. The second pinna is buried in the matrix (alternately) in the part or counterpart. Along with the equal development of both pinnae of a pair, the first pinnule shifts close to a catadromic position. Specimen UC-1018A. Fig. 26. x 0.7.


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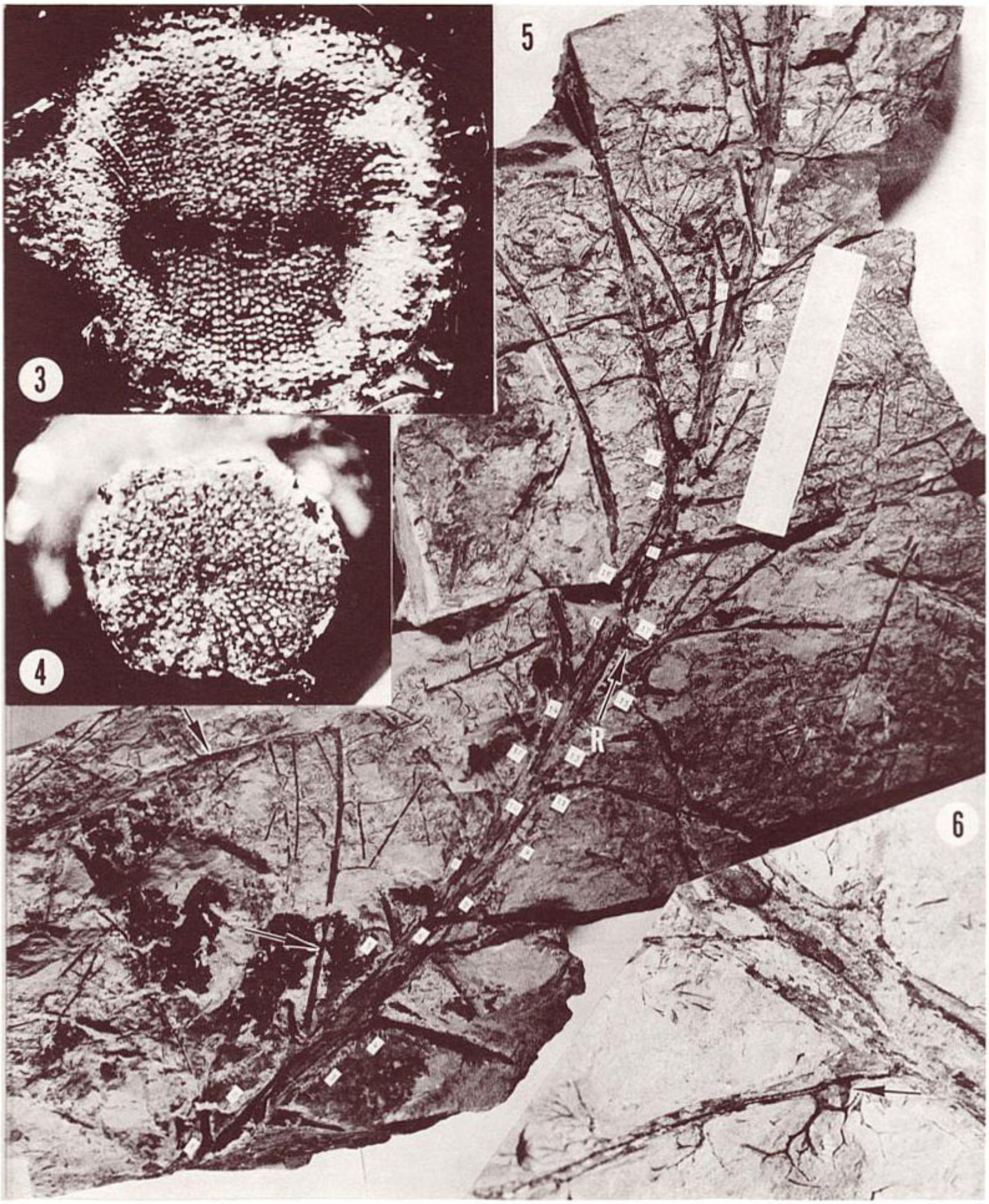

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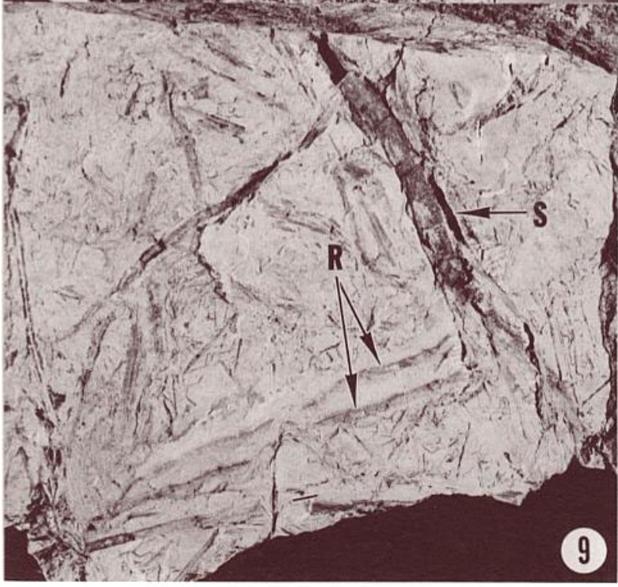
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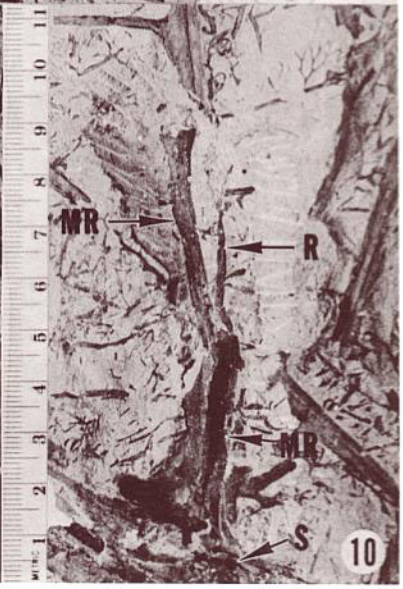
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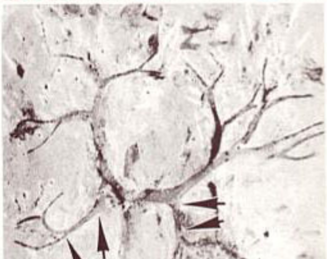
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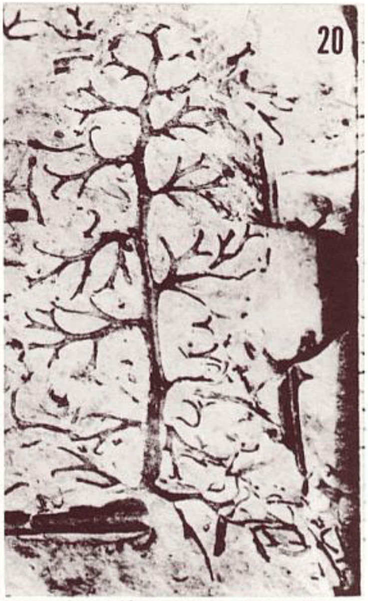
17



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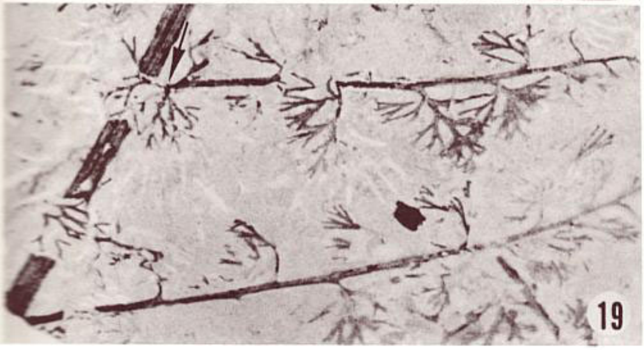

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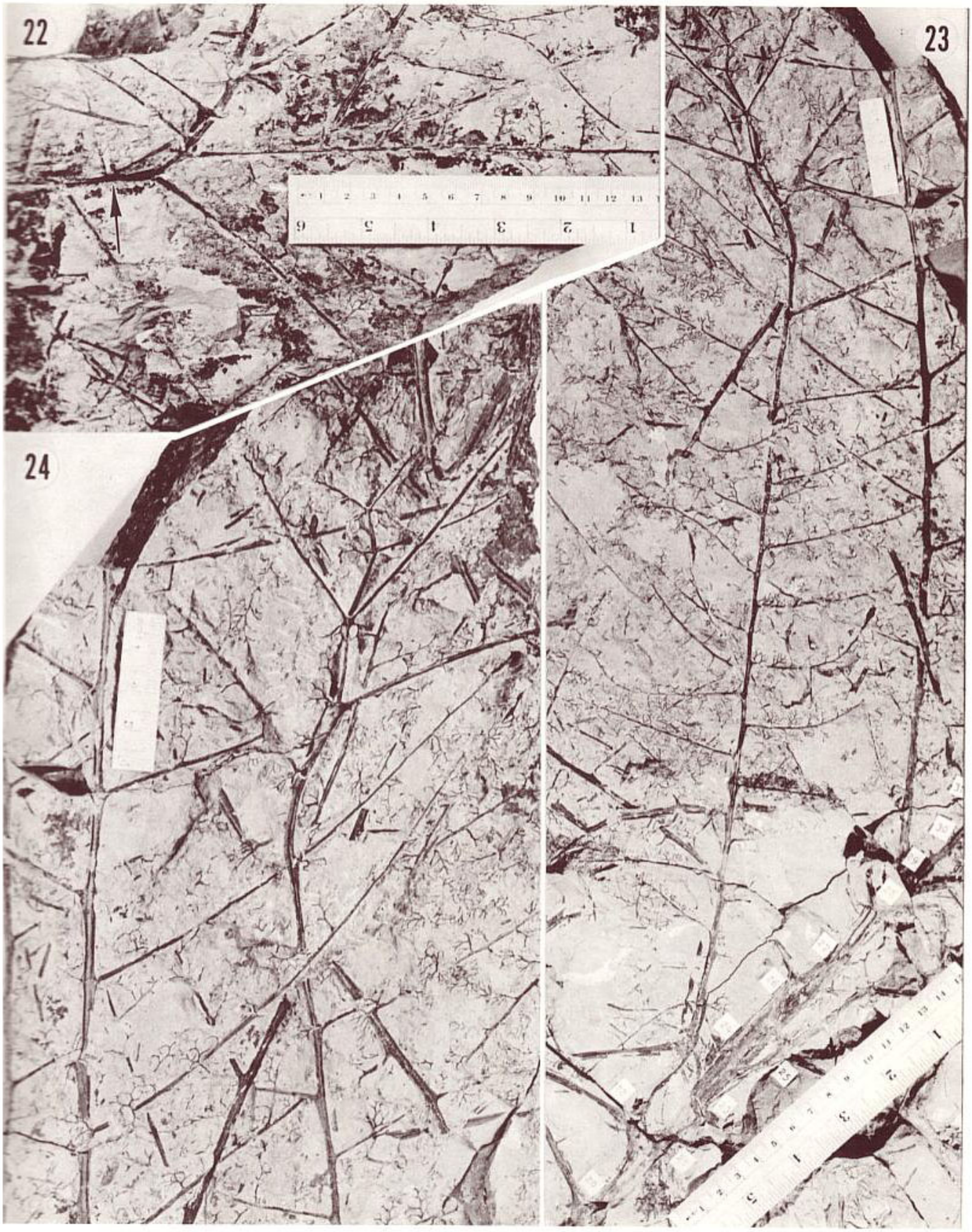

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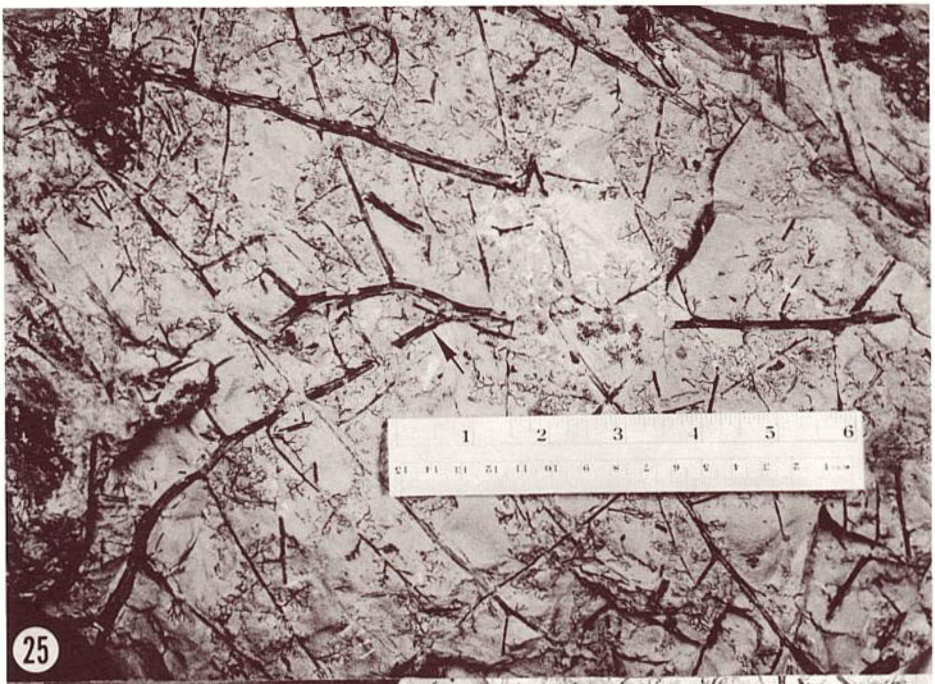

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