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THE UNIVERSITY OF ALBERTA

A STUDY ON *BOTRYOPTERIS FORENSIS* AND *BOTRYOPTERIS TRIDENTATA* FROM THE WEST MINERAL, KANSAS AND WHAT CHEER, IOWA LOCALITIES

by

© MARK SHATTUCK BROSIER

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

AND RESEARCH IN PARTIAL FULFILLMENT OF THE

REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

IN

PALEOBOTANY

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

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 Study of *Botryopteris forensis* and *Botryopteris tridentata*, from the West Mineral, Kansas and What Cheer, Iowa Localities", submitted by Mark Brosier in partial fulfilment of the requirements for the degree of Master of Science.

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Date July 27, 1976

ABSTRACT

Numerous Middle Pennsylvanian specimens of *Botryopteris forensis* and *Botryopteris tridentata* from the West Mineral, Kansas and What Cheer, Iowa localities provide the basis for an examination of the vegetative features of *B. forensis* and *B. tridentata* and the reproductive features of *B. forensis*. The structure and anatomy of the plantlets (stems), petioles, roots and foliage of both species are elaborated. The fertile frond (fructification) of *B. forensis* is studied to determine its branching patterns and possible developmental sequence. The spores are studied to determine the variability in spore exine ornamentation and to relate that information in the evaluation of the criteria used to distinguish one fructification species, *B. forensis*, from the other, *B. globosa*. Implications of affinities between the Botryopteridaceae and extant ferns are discussed. Reconstructions of *B. forensis* and its fructification are also provided.

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INTRODUCTION

Botryopteris (Renault, 1875) is one of the more common coenopterid ferns encountered in Upper Carboniferous coal balls. Such notable paleobotanists as Renault (1875), Long (1943), Mamay and Andrews (1950), Surange (1952), Delevoryas and Morgan (1954), Corsin (1956), Murdy and Andrews (1957), Holden (1962), Phillips (1961, 1970, 1974), and Galtier (1967, 1969, 1971) have contributed greatly to our present understanding of the genus.

Botryopteris has a lengthy geological history extending from the Calciferous Sandstone Series, Lower Carboniferous of Scotland, to the Lower Permian of Germany. *Botryopteris* is known from North American horizons ranging from the Upper, Lower Pennsylvanian (Wesphalian B) to the Upper Pennsylvanian (Middle Stephanian).

Coal balls collected from Middle Pennsylvanian sediments near West Mineral, Kansas and What Cheer, Iowa have yielded vegetative organs assignable to *B. forensis* and *B. tridentata* as well as fertile organs (pinnae))assignable to *B. forensis*.

Vegetative organs were compared for the purpose of evaluating established criteria distinguishing between *B. forensis* and *B. tridentata*. Fertile pinnae were studied to reveal their branching patterns and possible developmental sequences, while the investigation of the spores provided information regarding the variability of spore ornamentation. This thesis relates new information obtained to our understanding of nomenclature for certain species of *Botryopteris*, relationships of the genus to other coenopterid ferns and to extant

ferns as well.

The History of the Genus *Botryopteris* and its Relationship to the Order Coenopteridales

The genus *Botryopteris* was established by Renault (1875). It was based on silicified plant parts including isolated petioles, stems with attached petioles, and a fertile frond, all of which were found in Middle Stephanian sediments (Upper Carboniferous) at Grand Croix, near St. Etienne, France. The character that united the above isolated plant parts and which unites all members of this genus, is the omega-shaped to trident-shaped strand found in the petioles.

Renault (1875) mentioned that Grand 'Eury had found, at Autun and St. Etienne, some isolated fragments of petioles and named them *Rachiopteris forensis*. The form genus *Rachiopteris* was earlier proposed by Williamson (1874) to include little understood fragments of supposed ferns. The name has its origin from Corda's (1845) vaguely defined family Rachiopterideae.

Corda included in the Rachiopterideae isolated fern petioles that were hairy or naked and herbaceous or arborescent. They were grooved on the upper surface and rounded on the lower. The cortex was thick and cellular, while the pith was parenchymatous. The vascular bundle was either 1) single, moon-shaped or boot-shaped, inflexed or reflexed, or 2) doubled or tripled. One can conclude, as Williamson (1874) did, that this family was vaguely defined; thus, he rejected the family and proposed in its place the form genus *Rachiopteris*.

Renault (1874) described the attachment of *R. forensis* to a stem.

He then changed the name from *R. forensis* to *Botryopteris forensis*. Therefore, the first fossil species of the genus *Botryopteris* was *B. forensis*. Posthumus (1928) states that the name *Botryopteris* was applied by Presl (1825, 1848) to a species of the extant Ophioglossaceae. As recorded by Phillips (1961), those extant species assigned to the genus *Botryopteris* have since been placed in *Helminthostachys zelanica* by Christensen (1906). In *TAXON* (24: 69), under the heading "Report of the Committee for Fossil Plants", there appears a recommendation for the conservation of *Botryopteris* Renault.

Two other species of *Botryopteris* were described by Renault (1875). One was named *B. augustodunensis*, which Posthumus (1926) later transferred to *B. forensis*. Corsin (1937) believed that *B. augustodunensis* was a secondary petiole of *B. forensis*. The second species, *Botryopteris dubis*, based on isolated sporangia, was later transferred by Renault (1896) to the genus *Zygopteris*.

Williamson (1878) characterized a fern stem with attached petioles, which he called *Rachiopteris cylindrica*, from the Halifax Coal (Lower Carboniferous, Westphalian A) of Great Britain. Later, Gordon (1910) and Seward (1910) referred to this species as *Botryopteris cylindrica*. Bancroft (1915) retained the noncommittal generic name *Rachiopteris*, because the reasons given by others for transferring Williamson's species to the genus *Botryopteris* were unsubstantiated according to Bancroft's interpretation. Bancroft (1915) also divided *Rachiopteris cylindrica* into two morphological types. One she called *Rachiopteris cylindrica* (type *a*), the other she called *Rachiopteris cylindrica* (type *b*). The latter, she thought to be the aquatic form of *Rachiopteris cylindrica*. Holden (1960) was of the opinion that the two types of

R. cylindrica were in reality two distinct species. As a result, he renamed *R. cylindrica* (type α) as *Psalixochlaena cylindrica* and *R. cylindrica* (type β) as *Rhabdoxylon dicotomum*.

Grand 'Eury (1877) described two particular types of fern compression fossils from the Stephanian, near St. Etienne. He named the one *Schizopteris pinnata*, a sterile frond, and the other *Schizostachys frondosa*, a fertile frond. Later, Grand'Eury (1890) included *S. frondosa* in the genus *Botryopteris*, while Zeiller and Renault (1888) included both species under the name *Zygopteris pinnata*. Scott (1900, 1909, and 1920) apparently agreed with Zeiller and Renault as to the inclusion of *S. frondosa* and *S. pinnata* in the genus *Zygopteris*.

The Halifax Coal (Westphalian A, Lower Carboniferous) of Great Britain yielded *Rachiopteris robusta*, described by Williamson (1880). He illustrated *R. robusta* with a single cross section; therefore, the nature of the axis and of its possible affinities are quite uncertain. Nevertheless, Hirmer (1928) transferred *R. robusta* to the genus *Botryopteris*.

Williamson played an intermittant role in the history of the genus *Botryopteris*, describing *Rachiopteris hirsuta* in 1888 and *Rachiopteris ramosa* in 1891, both from the Westphalian A of Great Britain. Williamson (1891) stated that *R. ramosa*

> "...may prove to be merely a more fully developed and less hirsute form of *Rachiopteris hirsuta* described in Memoir, Part XV., in which case it may stand as *R. hirsuta*, var. *ramosa*."

This statement of Williamson's probably had some influence on Scott's opinion as to the validity of these last two species of *Rachiopteris*. Scott (1898) transferred *Rachiopteris hirsuta* Williamson and

Rachiopteris tridentata Felix (1886) to the genus *Botryopteris*. He wrongly credited Williamson with naming *Rachiopteris tridentata* and made no mention of *Rachiopteris ramosa*. Scott (1900) in his *STUDIES IN FOSSIL BOTANY*, comments on the two English species of *Botryopteris* (*B. ramosa* and *B. hirsuta*) by stating that "These two forms are very similar, and perhaps not really distinct.". Scott (1900) again gives credit to Williamson for naming *B. tridentata* and states that *Botryopteris tridentata* is the petiole of *Botryopteris hirsuta*. He concludes (1909, 1920) in later editions of *STUDIES IN FOSSIL BOTANY* that these two forms are very similar and not always easy to tell apart. Scott also gives Felix (1886) credit for the name *B. tridentata*, but he still insists that *B. tridentata* is the isolated petiole of *B. hirsuta*.

Felix (1886) described a petiole with an attached siphonostelic plantlet, and although he did not recognize the plantlet as such, he named the specimen *Rachiopteris tridentata*. Phillips (1970) verified the distinct identity of *B. tridentata* and suggested that *B. tridentata* came from the Katharina horizon, which is designated as the boundary between Westphalian A and Westphalian B.

From the beds of the Autun Series, a permineralized fossil plant was found and named *Grammatopteris rigollotti* by Renault (1891). *G. rigollotti* also has been referred to as *Botryopteris rigollotti* by Renault (1896), Bower (1908), and *Tubicaulis rigollotti* by P. Bertrand (1908). However, Bertrand (1909), Seward (1910), Scott (1920), Sahni (1932), Andrews (1961), Eggert (1964), and Miller (1974) continue to use the original name, *Grammatopteris rigollotti*.

The geologically oldest species of *Botryopteris*, *B. antiqua*, was described by Kidston (1908) from specimens found in the Calciferous

Sandstone Series (Culm), from Pettycur, near Burntisland, Scotland. In 1910, Pelourde described a French specimen of *B. antiqua* from the Lower Carboniferous strata of Esnost near Autun. Kidston (1908) notes that:

> "*Botryopteris antiqua* is a typical member of the genus, though perhaps its smallest species, and is easily distinguished by its minute size and the protoxylem elements of the leaf-trace being evenly distributed and not forming prominent teeth as in the other known species. The tracheae of the stem are scalariform, not porose."

He also observes the tendency for the petiole trace to become simpler in form as one traces it back into geological time.

Associated sporangia from the Lower Carboniferous of Scotland were first attributed by Scott (1910) to the species of *B. antiqua*. Pelourde (1910) found similar sporangia from the Lower Carboniferous (Culm) of France and noted their resemblance to sporangia described by Kidston. Galtier (1967) writes that the sporangia described by Renault (1896) under the names of *Hymenophyllites* and *Todeopsis*, as well as those figured by Pelourde (1910), should be attributed to *Botryopteris antiqua* from France. Holden (1962) and Phillips (1970) questioned whether the Scottish *B. antiqua* is identical to the French *B. antiqua*. The petioles from Burntisland, mentioned by Holden, are oval in transverse section, while those from Autun show a well marked adaxial groove. Phillips (1970) observes that foliar members from French localities are larger than any foliar members of *B. antiqua* from Scotland. Others who have described or figured associated sporangia assignable to *B. antiqua* are Surange (1952) and Corsin (1937). Surange's material came from the Lower Carboniferous of Scotland, while Corsin's came from the Lower Carboniferous of France.

In 1877 Grand'Eury described and figured a single specimen of *Rachiopteris forensis*. Later, Bertrand and Corneille (1910) erected a new species called *Botryopteris renaulti*. The species was characterized by the mode of petiole trace formation and, as can be seen in a petiole cross section, by the separation of the rounded or oval median arm from the rest of the arc-shaped vascular bundle. Corsin (1937) transferred Brand'Eury's (1877) *Rachiopteris forensis* to *B. renaulti*.

Adding to the number of species of *Botryopteris*, Leclercq (1927) described a new species *B. fraiponti* from Belgium Westphalian A coal balls. Darrah (1941), from material of the Des Moines Series, Middle Pennsylvanian of Kansas, characterized *Botryopteris radiata*. Later, Fry (1954) transferred both species, *B. fraiponti* and *B. radiata*, to his new lycopod genus *Paurodendron*. It was clear to Fry that *Paurodendron* was not a fern.

Material from the Bouxharmont stratum, an age equivalent of the Halifax Coal of Great Britain, provided the specimen which Kraentzel (1933) named *Botryopteris mucilaginosa*. This species possesses diagnostic stem cortex and petiole bundles.

C. Bertrand and Cornaille (1910) presented a detailed hypothesis explaining the sequence of changes necessary to produce a lateral trace in *Botryopteris forensis*. This scheme was later adopted by P. Bertrand (1913), Corsin (1937), and Darrah (1941).

Graham (1935) described *Botryopteris americana* in coal-balls from the McLeansboro Group of Illinois (uppermost Carboniferous). Graham (1935) explained that vascular bundles in the petioles of *B. americana* produced lateral traces in a manner different from that hypothesized by Bertrand and Cornaille (1910) for *B. forensis*. Delevoryas and Morgan

(1954) raised the point that since Bertrand's scheme (1913) was hypothetical, Graham's use of this character for species distinction had no validity. Graham (1935) also differentiated *B. americana* from *B. forensis* on the basis that the former does not have intraxylary sclerenchyma or gum canals in the cortex, while the latter does. Delevoryas and Morgan (1954) further suggested that variable characters, such as intraxylary sclerenchyma or gum canals, should not be used to distinguish *B. americana* from *B. forensis*. As a result, they came to the conclusion that there was no sound basis for distinguishing between these two species. Associated sterile and fertile sporangia, similar to those described by Graham (1935), were noted by Delevoryas and Morgan (1954).

Several fertile specimens were described by Darrah (1939) from the Des Moines Series, Middle Pennsylvanian of Iowa. He called these *Botryopteris globosa*. Darrah distinguished between this and the fructification of *Botryopteris forensis* because of the smaller spore size of *B. globosa*.

Fertile and sterile organs were first found attached by Phillips (1966) when he ascertained that,

> "....three previously established American species, *Botryopteris trisecta*, *B. globosa*, and *B. americana*, are parts of a single species which has, in turn, been referred to *Botryopteris forensis*."

Phillips (1970), after reexamining material described by Graham (1935), Darrah (1939), Delevoryas and Morgan (1954), Mamay (1950) and Murdy and Andrews (1957), and studying new material from Illinois, Kansas, and Iowa, came to the conclusion that there were two species of *Botryopteris* fructifications. The two species differ in the

character of spore ornamentation. He designated one *B. americana* Graham which possesses spores with a predominately verrucate pattern; the other, *B. globosa*, which possesses spores with a predominately rugulate pattern. Reexamining the Renault type material, Galtier (1971) came to the conclusion that the spore ornamentation of *B. forensis* and *B. americana* was identical. According to Phillips (1974), Galtier's study of the type material of *B. forensis* allows the identification of the same species in America, but described under the names of *B. americana*, *B. trisecta*, and in part specimens assigned to *B. globosa*.

In an extensive study of the Coenopteridales, Corsin (1937) established a new species of *Botryopteris*, which he called *B. minor*. Snigirevskaya (1962) as translated by Phillips (1964), hints that *B. minor* may be a small branch of *B. forensis*. Snigirevskaya writes,

> "This author [Corsin] brought in the new species of *B. minor* which, however, was represented only by a trivial branches of the type of *B. forensis*."

Surange (1954) characterized *Botryopteris elliptica* and separated it from *B. hirsuta* and *B. ramosa* by supposed differences in petiolar structure. In his monograph on the European species of *Botryopteris*, Phillips (1970) suggested that *B. elliptica* should be regarded as a synonym of *B. hirsuta*.

In 1950 Mamay and Andrews described *B. trisecta*, now known to be the main rhizome of *B. forensis*. Because Phillips (1966) had found organic connections between *B. forensis* and *B. trisecta*, and because *B. forensis* has priority, then *B. trisecta* should be placed in synomony.

The next three species of *Botryopteris* were sporangia species and

were described by Mamay (1950). *B. fecunda*, *B. illinoensis*, and *B. spinosa* were diagnosed by sporangial dimensions, spore sizes, spore morphology, and spore ornamentation. Holden (1962) noted the similarity between the spores of *B. illinoensis* and the spores of *B. antiqua*.

Based on the foregoing summary of the genus *Botryopteris* it is possible to present the following chronological list of valid species of the genus:

1. *Botryopteris forensis* Renault (1875)
2. *Botryopteris hirsuta* (Williamson) Scott (1898)
3. *Botryopteris tridentata* (Felix) Scott (1898)
4. *Botryopteris ramosa* (Williamson) Scott (1900)
5. *Botryopteris antiqua* Kidston (1908)
6. *Botryopteris renaulti* Bertrand and Cornaille (1910)
7. *Botryopteris mucilaginosa* Kraentzel (1933)
8. *Botryopteris globosa* Darrah (1939)
9. *Botryopteris illinoensis* Mamay (1950)
10. *Botryopteris fecunda* Mamay (1950)
11. *Botryopteris spinosa* Mamay (1950)

This thesis deals with vegetative structures of *B. tridentata* and *B. forensis* and reproductive structures of *B. forensis*.

The description and classification of Paleozoic ferns have long captured the attention of paleobotanists, who have grouped them under various comprehensive names such as Botryopterideae Renault (1875), Inversicatenales Bertrand and Cornaille (1904), Primofilices Arber (1906), Coenopterideae Seward (1910) and Paleopteridales Bertrand (1933).

For each of the names of the groups listed above there has been at least one system of classification developed. Such schemes of classification have been porposed by Renault (1875), Scott (1900, 1908, 1920), Bertrand (1912, 1933, 1941), Seward (1910), Posthumus (1926), Delevoryas and Morgan (1954), Eggert (1964), Emberger (1968), Andrews and Boureau (1970), and Phillips (1974).

The classification used here is that of Delevoryas and Morgan (1954), who divide the Coenopteridales into four distinct families, Anachoropteridaceae, Botryopteridaceae, Stauropteridaceae, and Zygopteridaceae. The basic elements of this have been adopted by Eggert (1964), Andrews and Boureau (1970), and Phillips (1974). Delevoryas and Morgan (1954), Eggert (1964), and Phillips (1974) agree that *Botryopteris* is best placed in a monotypic family, Botryopteridaceae. At first authors such as Scott (1900, 1908, 1920), Delevoryas and Morgan (1954), Eggert (1964) considered the Coenopteridales too specialized to have been the ancestors of modern ferns. Later Phillips (1965, 1974), Eggert and Taylor (1966), Eggert and Delevoryas (1967) however, considered some Coenopteridales as true ferns or possible paleophytic representatives of later groups.

This later interpretation, indicating possible relationships between coenopterids and true ferns is based, in part, on studies of sporangial characteristics. It reveals an important change in the thinking of paleobotanists about interrelationships among the extinct and extant Pteridophyta. Obviously, any speculation of phylogenetic relationships has to be based on every bit of available information; therefore, it is indeed encouraging to see an increasing amount of new information being presented concerning this group of plants.

Collecting Localities and Stratigraphy

The material investigated in this study was collected at two coal ball (carbonate petrifation) localities, one near West Mineral, Kansas and the other near What Cheer, Iowa. West Mineral coal balls, Middle Pennsylvanian in age, occur in the Fleming or Westmineral coal, Cabaniss Subgroup, Cherokee Group, Desmoinesian Series. What Cheer coal balls are also Middle Pennsylvanian in age and also occur in the Cherokee Group of the Desmoinesian Series.

Directory of Specimens

Each specimen has been arbitrarily assigned a letter to facilitate ease in referring to the specimens in this study. With one exception, all specimens are from the West Mineral, Kansas locality and are in the paleobotanical collection of the University of Alberta. The exception is coal ball #A240 which is from the What Cheer, Iowa locality. The coal ball number for each specimen follows:

Potryopteris forensis

Specimen A- Coal ball 38-a

Specimen B- Coal ball 38-b

Specimen C- Coal ball 38-f-g

Specimen D- Coal ball 265

Specimen E- Coal ball 328

Specimen F- Coal ball 328

Specimen G- Coal ball 328

Specimen H- Coal ball 328

Specimen I- Coal ball 335

Specimen J- Coal ball 467

Specimen K- Coal ball 552

Specimen L- Coal ball 552

Specimen M- Coal ball 552

Specimen N- Coal ball 577

Botryopteris tridentata

Specimen A- Coal ball 240

Specimen B- Coal ball 265

Specimen C- Coal ball 265

Specimen D- Coal ball 265

Specimen E- Coal ball 265

Specimen F- Coal ball 303

Specimen G- Coal ball 311

Specimen H- Coal ball 328

Specimen I- Coal ball 380

Specimen J- Coal ball 552

Specimen K- Coal ball 575

Specimen L- Coal ball 577

Techniques

Standard paleobotanical procedures as outlined by Stewart and Taylor (1965) were followed in preparation of serial peels and slides. Spore samples were obtained and prepared according to procedures employed by Taylor and Eggert (1969), Zimmerman and Taylor (1970), and Phillips and Rosso (1970). After locating *Botryopteris* sporangia and spores in the coal ball specimen, the spore-containing area was surrounded by a low wall of paraffin, which restricted the action of

the dilute hydrochloric acid (2%) used to release the spores from the rock matrix. The spores were then washed in distilled water, dehydrated by alcohol (50%, 70%, 90%), and stored in 90% alcohol. Portions of the spores sampled were mounted in Harleco Synthetic Resin for light microscopic examination. Other portions were spread on specimen stubs while in suspension, and allowed to dry. These stubs were then prepared for examination with the scanning electron microscope (SEM). An additional spore extraction technique utilized gummed tape, which was applied to the dry, deeply etched coal ball surface where the spores could be extracted after the initial sampling (see above). The gummed tape was then pulled from the surface bringing with it the desired spores. This tape was subsequently cut to fit an SEM stub, which was further prepared for observation.

DESCRIPTION OF MATERIAL

General Features

Of the several known species of *Botryopteris*, I have considered only two in detail in this study. They are *B. forensis* and *B. tridentata*. Anatomically and morphologically, *B. forensis* is the most completely known species. The parts of *B. forensis* that have been identified and described are rhizomes, petioles, roots, plantlets, foliage, and the fertile pinnae. Although *B. tridentata* is not as completely known, the anatomy and morphology of its petioles, plantlets, roots and foliage have been described.

Botryopteris forensis

B. forensis has a stratigraphic range extending from the Des Moines Series, Middle Pennsylvanian (middle Westphalian C) of the U.S.A. to possibly the Lower Permian of Germany. The best description of the form and growth habit of *B. forensis* is presented by Phillips (1974). He describes the plant as follows:

> "The habit in the *B. hirsuta* line (based on *B. antiqua B. forensis*) is a prostrate rhizome with a semi-erect apex, as in *Osmunda*, with fronds spaced less closely than in *Tubicaulis*."

He also states that:

> "In *B. forensis* (*B. trisecta* of Mamay and Andrews, 1950; Phillips, 1961, 1966) the occurrence of lateral stems on petiolar bases results in a dense "false stem" composed of hundreds of foliar members, their division and parent stems around the main rhizome and its fronds. This aggregation is up to 15 cm across."

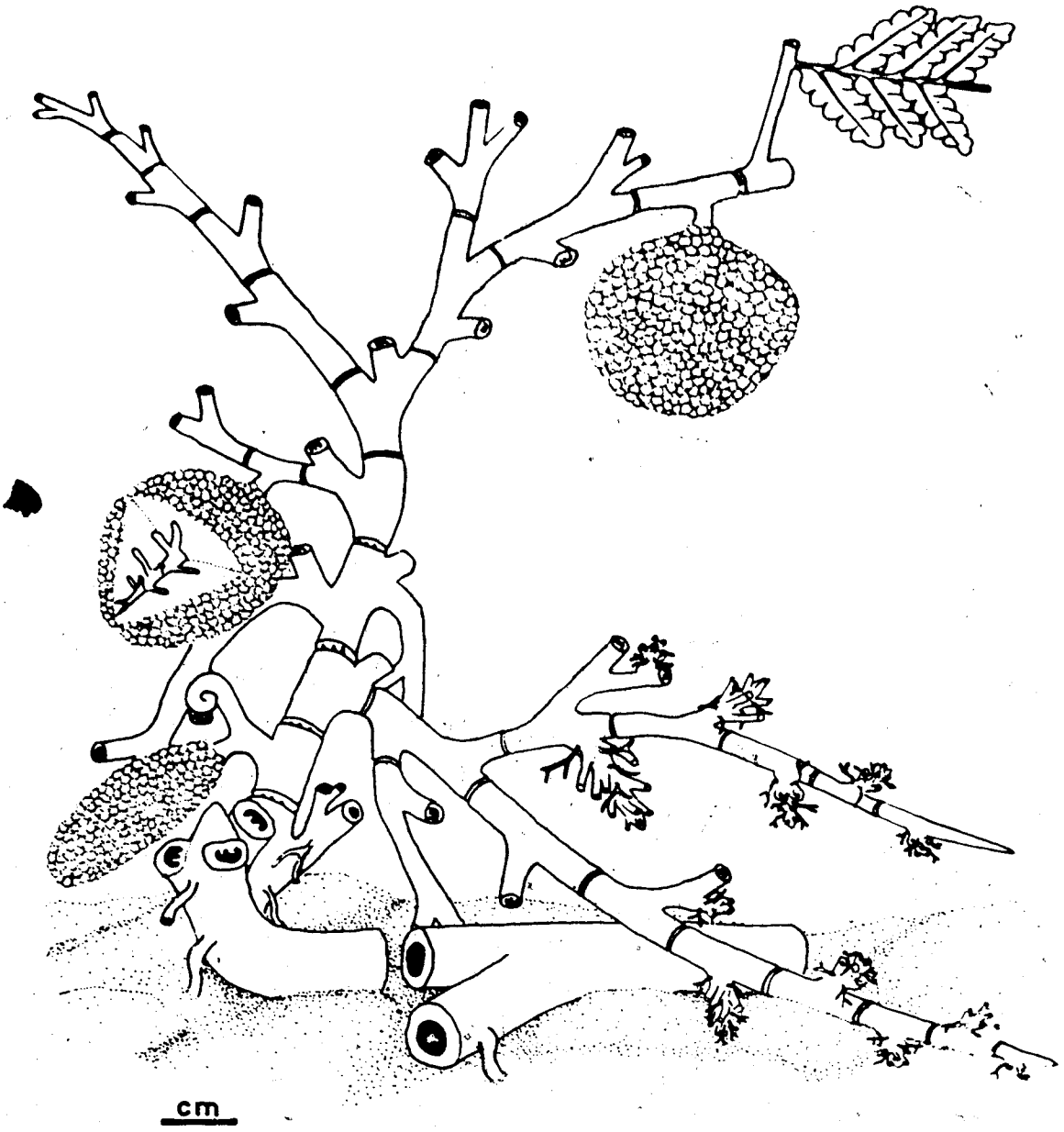
In a coal ball from the Berryville locality (late Pennsylvanian) containing a preponderance of *B. forensis*, Phillips (1961) was able to follow its rhizome for a length of 12 cm. The maximum diameter of the rhizome in this specimen is 1.0 cm, while the diameter of the largest petiole is 7.0 mm. Corsin (1937) figures a *B. forensis* with a diameter of 8.0 mm. From the descriptions provided by Phillips and others one can visualize *B. forensis* as an extremely bushy fern that may have attained a height up to 50 cm (see reconstruction, text figure 1).

The Rhizome. In his 1961 account of *B. forensis* Phillips gives a detailed account of the way in which stems and foliar members (petioles) branch. The best description of the internal structure is found in the work of Mamay and Andrews (1950). Starting at the surface of a rhizome they depict the epidermis as consisting of a single layer of thin-walled cells. These are nearly isodiametric and measure 35 µm to 50 µm. The epidermis possesses widely separated, unbranched, multicellular hairs. At their bases, the hairs have an average diameter of about 75 µm and arise from a group of several epidermal cells. They are truncated structures with an average length of 900 µm. Stomata were not observed among the epidermal cells.

The outer cortex consists of thin-walled cells which are elongated in the direction parallel to the stem axis. The cells are irregularly angular in cross section and range in diameter from 45 µm to 90 µm. The cells of the outer cortex are smaller toward the periphery of the stem, and toward the center. In longitudinal section, Mamay and Andrews describe the outer cortical cells as having oblique end walls and lengths from 200 µm to 300 µm.

The next zone to the inside is quite variable in structure and

Text Fig. 1. Reconstruction of *Botryopteris forensis* showing the creeping habit of the rhizome and the attachment of petioles, foliage, plantlets, roots and fructifications.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there is a corresponding lack of uniformity in its designation. Mamay and Andrews call it the "sclerotic-secretory tissue"; Phillips (1970) describes it as middle cortex. He reports the presence of a well-defined band of secretory-like cells in the middle cortex of the type specimen of *B. forensia*. This band as measured by Mamay and Andrews is 1.0 mm thick. Other specimens of *B. forensia* lack the secretory-like cells in any part of the cortex. When present these cells have diameters ranging from 50 µm to 70 µm and lengths up to 300 µm. They also contain dark contents and are of the same shape and orientation as those cells of the outer cortex. Because of variation in position of the cells in the cortex and because of their similarity in size and shape to cells of the outer cortex, I think it best to regard this sclerotic-secretory zone as part of the outer cortex.

Although they are somewhat smaller, the cells of the inner cortex are the same shape and have the same orientation as those of the outer cortex. Inner cortex cells have diameters of approximately 30 µm and lengths of 150 µm to 200 µm. Phillips describes the inner cortex as composed of small parenchyma cells and scattered cells containing dark materials.

According to Mamay and Andrews, tissues between the inner cortex and the xylem of the vascular strand are too poorly preserved to allow their description. When seen in cross-section the xylem of the rhizome has the appearance of a terete protostele. They were unable to distinguish protoxylem strands but concluded that *B. trisecta* was exarch. In another stem showing the initiation of petiole trace formation, Phillips (1961) was able to observe decurrent protoxylem

strands which are mesarch. The pitting on the metaxylem tracheids, according to Mamay and Andrews, varies with the diameters of the tracheids: large metaxylem tracheids have multiseriate-reticulate pitting and those with small diameters have annular thickenings.

The rhizome produces primary petioles in a 1/3 phyllotaxy. At the base of each primary petiole occur one or two lateral shoots, usually called plantlets, which served a probable function of vegetative reproduction (Phillips, 1974). Petiole trace formation from the main stem or rhizome occurs in the manner described by Phillips (1961):

> "Indications of foliar trace formation from primary cauline axes are the enlargement and elongation of xylem in the direction of emission and the simultaneous appearance of a pair of sub-marginal groups of protoxylem. The protoxylem subsequently occurs higher both outward toward each margin and inward toward the center. The foliar trace separates as a solid ellipsoid of xylem. The xylem segment supplied to the trace may be either larger or smaller than the remaining cauline xylem."

Leaves.

Foliar members (petioles) -- Phillips (1961) uses the term foliar member or structure for what Renault (1875) originally called a petiole. According to Phillips *B. forensis* foliar members have a bilaterally symmetrical xylem strand, omegoid in cross section, and do not bear adventitious roots. The term petiole will be used here mainly for convenience. Isolated petioles range in diameter from 2.1 mm (Phillips, 1961) to 8.0 mm (Corsin, 1937). As a result of the work of Delevoryas and Morgan (1954) and Phillips (1961) three orders of branching are known for petioles. The shape of the vascular bundle of the petiole ranges from trident-shaped to omega-shaped.

The first detailed histological descrption of a petiole was provided by Renault (1875). He recognized two zones in the cortex, a

fibrous outer zone consisting of cells with oblique end walls and an inner zone of cells with transverse end walls and sparsely scattered gum canals (Figs. 3, 5). Unfortunately, Renault did not name the tissue layer immediately to the inside of the cortex. If he had, it may have prevented later confusion in differentiating between a zoned cortex and two distinct cortical layers. The unnamed tissue (probably an inner cortex) layer is composed of small, thin-walled cells, in which gum canals occasionally occur. Located between the unnamed layer and the vascular bundle is a layer of elongated, fibrous cells. The omega-shaped vascular bundle (Fig. 1) contains metaxylem with pitted walls. Petiole metaxylem pitting has been described by Mamay and Andrews (1950) as multiseriate-reticulate and by Delevoryas and Morgan (1954) as multiseriate-curcular bordered (Figs. 4, 6). The latter also described the pitting of the protoxylem, which is located at the tip of the omega-shaped vascular strand, as annular, spiral and scalariform. In a later publication, Renault (1896) illustrated a petiole with an epidermis covered with "equisetiform hairs" which correspond to the uniseriate, multicellular hairs described by Corsin (1937), Mamay and Andrews (1950), Delevoryas and Morgan (1954), and Phillips (1961).

As observed by Phillips (1961), the manner in which the ellipsoid foliar xylem strand of the primary petiole becomes trident or omega-shaped is as follows:

> "Usually the tridentate configuration occurs after the first lateral emission and slightly before or during the second. Where only one lateral trace is formed, the foliar xylem may assume a tridentate shape before the lateral trace completely departs. The manner in which the foliar xylem strand becomes omegoid in shape is somewhat variable. In a specimen from Calhoun a non-tracheidal slit occurred within the xylem on the

> side from which the first lateral trace departed; the non-tracheidal slit subsequently opened adaxially forming a narrow lateral arm. The other lateral arm was formed by a similar slit opening in the xylem before the lateral trace completely separated. The xylem strand may also appear tridentate at first and become omegoid by the abaxial extension of non-tracheidal development. In summary, the tridentate to omegoid shape of the xylem strand occurs after lateral trace formation and slightly before or during trace emission."

As the primary petiole trace proceeds upwards into the petiole it increases in diameter and becomes more typically omega-shaped.

Two patterns of petiole to petiole trace formation occur in *B. forensis*. The first pattern described by Phillips (1961) involves the production of a single lateral trace, while in the second pattern, two closely spaced alternate traces arise. In the first type, Phillips explains that trace formation begins with a:

> "....simultaneous outward crooking of the adaxial portion of a lateral arm and the increase and lateral extension of protoxylem from the nearest protoxylem flange or the median arm. In early trace formation the crooked tip of the lateral arm comes in proximity to the protoxylem extended from the median arm; union of the two was not observed.
>
> The adaxial part of the lateral arm becomes progessively more C-shaped as the group of protoxylem extends abaxially and separates from the median arm. During the departure of the C-shaped trace the group of protoxylem derived from the median arm joins the shortened lateral arm which has slightly extended adaxially. Additional tracheids are formed along the lateral arm during and following departure of the trace.
>
> The xylem strand, therefore, regains almost immediately its characteristic omegoid shape with prominent protoxylem groups. The adaxial portion of the lateral arm involved in trace formation ranges from about one-half to only the tip."

The lateral trace is at first C-shaped, but it soon changes to a solid cylinder of tracheids, similar to the protostelic cauline structure or plantlet. The protoxylem groups are located on the adaxial face of the ellipsoid trace formed in this way. According to Phillips,

"nontracheidal islands" (nontracheary thin-walled tissue) develop inside the ellipsoid trace and extend adaxially to form the omegoid-shaped petiole bundle.

The second pattern of trace formation, one of the two lateral traces is markedly smaller than the other. As mentioned by Phillips, the structure supplied by the smaller trace may be no more than a vascularized bulge in the cortex of the parent petiole. The larger trace departs extramarginally (a pinna trace derived from adaxial portion of the leaf trace, but below the adaxial tips or margins of the leaf trace) instead of the typical marginal trace departure. Phillips (1961) further writes that:

> "....the curved tip assumes a more abaxial position along the lateral arm. The trace segment may or may not become indistinguishable from the rest of the lateral arm; in cases where the trace segment merges, the lateral arm becomes markedly enlarged. The main strand often regains its characteristic omegoid shape prior to trace departure, and the trace appears to have arisen from the side of the parent strand. The trace departs from the side of the lateral arm instead of the tip, i.e. extramarginal instead of marginal; nevertheless, the trace is marginal in formation. Foliar structures with extramarginal trace departure were supplied with traces of regular marginal origin. These two methods of trace emission are joined by a series of intermediate forms and are not essentially distinct."

The relationship of attached primary, secondary, and tertiary petioles was illustrated by Delevoryas and Morgan (1954) and Phillips (1961). The orientation of the secondary petiole with respect to the primary petiole is approximately 50 degrees. The tertiary petiole is oriented in the same plane as the secondary petiole; thus the branching reflects a transition from a three-dimensional pattern to a two-dimensional pattern. The penultimate pinna rachis (pinnule-bearing rachis) is arranged in one plane.

In his description of croziers, Phillips notes the presence of

straight hairs, extending from the surface, that may reach lengths of 1.8 mm.

Plantlets have terete protosteles composed of tracheids and bear adventitious roots (Phillips, 1961). Traces of plantlets from petioles may originate as a single trace or one of two alternate traces. Phillips (1961) interpreted those plantlets which were supplied by a solitary trace as being borne in distal positions on petioles, while those plantlets which were supplied by one or two alternate traces or by a single trace near the base of a petiole strand as being in proximal positions. Traces to basal plantlets from primary petioles attached to the rhizome may occur singly or alternately (Phillips, 1961). The distal plantlet trace originates from the petiole in the same manner as the foliar trace already described for the first pattern (see page 20). The difference lies in the fact that the solid ellipsoid trace of the plantlet remains closed, becomes more terete, and increases rapidly in diameter. It does not become omegoid-shaped.

In proximal trace formation the plantlet trace originates from a secondary petiole which itself originated from a petiole. It is then possible to see in a single cross-section the three different axes; that of the plantlet, the secondary petiole, and the primary petiole. Proximal plantlet trace formation of the single trace pattern proceeds in a manner described below by Phillips (1961):

> "The C-shaped foliar trace departs [the secondary foliar trace] from the parent foliar axis and closes to form a solid strand of tracheids. Two non-tracheidal islands develop in the solid strand to produce an omegoid shape. The island on the left occurred simultaneous with the adaxial opening of the xylem; the one on the right occurred first within the solid strand and then extended adaxially. As expansion of the adaxial portion of the lateral arm takes place, more than half of the arm separates as the cauline trace. The arm does not crook out

> or become a C-shaped trace. Reconstitution of the lateral arm takes place rapidly by the adaxial addition of tracheids and by the extension of protoxylem from the nearest median arm tip...."

Proximal plantlet or cauline trace formation of the alternate trace pattern is basically repeated as in the proximal, single trace pattern. The smaller of the two lateral traces may only supply a vascularized bulge on the parent petiole (Phillips, 1961). He further writes that:

> "The lateral arm nearest the main foliar axis [primary foliar member] becomes distinct and is perceptibly enlarged. In a stage of incipient separation the cauline trace is connected both to the lateral arm and the median arm. The cauline trace undergoes rapid expansion in diameter upon departure, and the contributing lateral arm is rapidly reconstituted."

Plantlets -- The first histological study of a *Botryopteris* plantlet was produced by Renault in 1875. He described a poorly preserved plantlet of *B. forensis* which lacks epidermis, roots and some internal tissues. The preserved portion of the outer cortex consists of slender fibrous cells, while the inner zone has elements which have the appearance of parenchyma cells. The stele is composed of large centrally located tracheids having reticulate thickenings and smaller peripheral tracheids showing scalariform pitting. His figures show the omega-shaped vascular traces of two petioles still attached to the stem by their corticies.

Mamay and Andrews (1950) described the branching sequences of several proximal secondary pinnae (basal plantlets). Specifically they write that:

> "....the proximal pinna appears as a separate entity, its cortex having been separated from that of the petiole; here the resemblance to a stem, except for a difference in size, is very striking. Its diameter is 5 mm., with a terete strand of 1 mm."

From the above statement, one can deduce that the histology of the basal plantlet is very similar to that of the main rhizome. The basal plantlet should then possess an epidermis, an outer cortex, a variable middle cortex, an inner cortex, an endodermis, a phloem zone, and a terete stem stele. From what one can determine after examining the figures prepared by Mamay and Andrews (1950) and Phillips (1960), this is indeed the case. The presence or absence of the middle cortex is recognized by Phillips (1970) as indicated by the following statement:

> "In *B. trisecta* the distinct middle cortical zone occurs for some distance in attached petioles, appears in the stems upon the petioles and also in some large isolated foliar members. It is completely lacking in some specimens of each of these organs."

A single specimen (557 G top) of a petiole plantlet was found and sectioned serially. The pattern of petiole to plantlet trace formation follows the manner described by Phillips (1961) for proximal, single trace plantlet origin. The diameter of the plantlet trace as it separates from the parent foliar strand is .8 mm x .51 mm (Fig. 7). Approximately 6.0 mm higher the diameter of the plantlet strand has increased to 1.14 mm (Fig. 8).

This plantlet (specimen 577 G top) is approximately 1.34 cm in length and with a maximum diameter of 5 x 4 mm. The plantlet produces one petiole and abundant diarch roots, which arise endogenously and are usually not associated with the petiole.

The cells of the epidermis of the stem are not distinct, from the cortical cells immediately below. Since the outer layer of cortex-like cells is invested with typical *Botryopteris* hairs, it is believed to be epidermal in nature. The size of the epidermal cells range from 25.6 µm to 57.6 µm (radial) wide and 44.8 µm to 70.4 µm (tangential) in

breadth.

The outer cortex which lacks distinct zonation has cortical cells with diameters ranging from 32 µm to 96 µm, and with the small and large cells that are randomly intermixed. The inner cortex is not well preserved, though its former position represented by a space can be seen in Fig. 8. Although a well-preserved endodermis is not present in the specimen, the remains of a layer of cells, one cell thick, appears in the position of an endodermis. Only the brownish colored outer tangential walls of these cells are preserved (Fig. 10). Part of the phloem is preserved adjacent to the xylem of the stem. Here it is composed of cells which in some places appear to be radially aligned (Fig. 9). The phloem zone ranges from 64 µm to 240 µm thick with individual cells having diameters from 7.04 µm to 32 µm.

The haplostele of the stem is entirely composed of tracheids with the largest tracheids in the center grading into smaller peripherally located tracheids (Fig. 9). The stem stele has the larger diameter tracheids in the central stelar region, while the smaller tracheids are located in the peripheral stelar region. Tracheid diameters range from 12.8 µm to 96 µm. No persistent protoxylem groups were observed.

The gross plantlet (proximal and distal) features were most completely clarified by Phillips (1961). He found plantlets attached to petioles ranging in diameter from 4.7 mm to 3.5 mm with stelar diameters ranging from 1.3 mm x 1.1 mm to 1.1 mm. The longest plantlet is 2.4 cm and bears five petioles in a 2/5 phyllotaxy. Foliar trace formation from the plantlet stele follows a sequence similar to foliar trace formation from the main rhizome. Phillips explains that:

"In proceeding up the cauline structure indications of foliar

> departure are the presence of two sub-marginal groups of decurrent protoxylem which coincide with the enlargement and elongation of the xylem in the direction of emission. On each side of the incipient trace is a group of protoxylem which subsequently appears outward toward each margin and inward toward the center."

The foliar trace assumes an omega shape upon separation from the plantlet stele and may give rise to one or two lateral terete traces (alternate or opposite).

Phillips (1961) has noted that basal plantlets produce petioles in a spiral with each subsequent petiole positioned 120 degrees from the preceeding petiole. This positioning of the petioles would suggest a phyllotaxy of either 2/5 or 1/3. The 2/5 phyllotaxy of the other plantlets described by Phillips would also suggest that the phyllotaxy of the basal plantlet is also 2/5. Phillips (1961) writes that:

> "The first foliar member borne on the secondary cauline [basal plantlet] axis typically bears one lateral appendage proximally; higher foliar members bear one or two lateral appendages. Subsequent divisions of lateral appendages have tridentate to terete xylem strands (the smallest); each order of division is oriented at a right angle to the preceding one where orientation can be determined. Although the secondary foliar structures are non-laminate, they are anatomically all foliar. The branching of secondary foliar structures is strongly three dimensional, and each lateral segment consists of a relatively short and densely branched cluster of cylindrical branchlets."

The position of the first petiole on the basal plantlet with respect to the main rhizome, as explained by Phillips (1970), is on the side of the plantlet stem away from the main rhizome. A lateral division of the petiole strand usually occurs just above the point of petiole trace departure from the plantlet stele.

It is known that three dimensional branching occurs in fertile pinnae and plantlets of *Botryopteris forensis* (Phillips, 1974) and that there is a change in branching patterns, in foliar units, from three-

dimensional to two-dimensional (Phillips, 1961). From these observations one can conclude that in a plant of *B. forensis* there would exist both three-dimensional and two-dimensional branching patterns. The three-dimensional branching is assumed to represent the primitive state.

The well-preserved plantlet specimen (577 G top) observed in this study shows a root trace arising from the margin of the stem stele (Figs. 14, 15). An indication that a root trace is arising here is the presence of tracheids with large diameters instead of those with small diameters, characteristic of the peripheral tracheids of a stem stele.

At a higher level, illustrated by Fig. 16, the root trace is detached completely from the stem stele and is surrounded by its own cortex. For additional details concerning *B. forensis* roots, see the next section.

The single petiole trace is initiated by an enlargement and elongation of a segment of the stem stele in the direction of emission (Fig. 11). Notice also that this lateral petiole trace segment has started to separate from the side of the stem stele.

The presence of two submarginal protoxylem groups, described by Phillips (1961) (see text page 26) was not observed in petiole trace formation in specimen 577 G top. The separation of the petiole trace proceeds from the exterior to the interior of the stem stele; as a result, the middle adaxial portion of the petiole trace is the last to detach from the stem stele (Fig. 12). At a higher level (Fig. 13) the petiole trace assumes a somewhat elliptical configuration and is completely detached from the stem stele. A "non-tracheidal island" (non-tracheary tissue) appears at one side of the trace. The low angle of trace departure and lack of preservation distally prevented further

study of the petiole trace in this specimen.

Roots -- Roots of *B. forensis* were observed by Mamay and Andrews (1950) to arise from the stem (main rhizome), at the base of the petiolar segment (primary petiole), and the proximal secondary pinna (plantlet). Renault (1875) was the first to illustrate plantlet roots, although he did not give anatomical details. Descriptive details are restricted to the work of Mamay and Andrews (1950) who describe the roots as having an:

> "....average about .9 mm in diameter and the cortical cells ranging up to 50 μ in diameter, lack intercellular spaces and have rather thick walls. The xylem is diarch, consisting of about 20 tracheids, the larger central ones presenting multiseriate-reticulate pitting.
>
> In one interesting sequence paired roots have been seen departing at three successive nodes, the pairs departing from petiolar segments shortly before or after the segment is separated from the stele. In all other cases, however, roots seem to depart at random, and in only one case has a root been noted to branch."

The adventitious roots attached to the plantlet (specimen 577 G top) range in diameter from 542 μm to 837 μm. They depart in a random pattern and are usually not associated with petioles. In one case, however, a root was observed at the base of a petiole. The root epidermis is usually not preserved. Where the epidermal cells are preserved, they are smaller in cross-section than the immediately interior cortical cells. No root hairs were observed. Roots show no sign of cortical zonation so apparent in the cortex of petioles and rhizomes. A brown colored layer, one cell thick tentatively identified as the endodermis, because of its position, occurs just interior to the inner edge of the cortex. It completely encircles the diarch vascular strand. A space, presumably once occupied by phloem surrounds the

xylem of the root. The diarch strand of xylem consists of approximately 14 to 25 tracheids. The tracheids have uniseriate scalariform to multiseriate-reticulate to multiseriate-scalariform to elliptical-bordered pitting and range in diameter from 6.4 μm to 83.2 μm. Roots lateral to the parent root arise endogenously. Where it can be determined, the orientation of the vascular strand of the lateral roots is perpendicular to that of the parent root strand.

Sterile foliage -- In 1896 Renault figured *Botryopteris forensis* pinnules, which were identified by their "equisetiform" hairs. Laminar pinnules attached to a penultimate pinna rachides having the anatomy of *B. forensis* were found by Delevoryas and Morgan (1954). A reconstruction of this portion of the plant appears in their paper, and is the first positive evidence that *Botryopteris* foliage had laminar, planted pinnules. *Sphenopteris burgkensis*, a Lower Permian compression fossil from Germany, was identified as *Botryopteris sp.* by Barthel (1970). In comparing petrified *B. forensis* pinnules (in paradermal section) with those *Botryopteris* pinnules of Barthel's, I find some close similarities. These similarities are the angle of divergence of the pinnules with respect to the penultimate pinna rachis, the pattern of the vascularization of pinnules, and the distance between the midveins of adjacent pinnules. Two species of *Botryopteris, B. forensis* and *B. renaulti*, are known to occur in Middle Stephanian sediments of France; therefore, the foliage described by Barthel may belong to either species, or to one not yet discovered.

In cross-section, the penultimate pinna rachis shows a distinct adaxial groove (Fig. 20). Its epidermal cells are smaller in cross-section than the cortical cells immediately to the inside. The outer

cortex may be either homogeneous or two-zoned. The homogeneous appearance was observed in the basal region of the penultimate pinna rachis (Fig. 19). Progressing distally from the point of attachment to the parent petiole, the cortex of the penultimate pinna rachis becomes distinctly two-zoned (Fig. 20). The cortical cells, in this area, ranged in diameter from 16 μm to 47.6 μm. The smaller cortical cells are are located towards the periphery of the outer cortex. The endodermis and phloem zone were not observed. The penultimate pinna rachis has an omega-shaped vascular strand (Fig. 20), which possesses metaxylem with scalariform to multiseriate-reticulate to elliptical bordered pitting and diameters ranging from 12.8 μm to 57.6 μm.

The terete trace supplying a pinnule is derived from the tipe of the lateral arm of the omega-shaped trace in the penultimate pinna rachis. As the pinnule trace departs from the lateral arm of the omega-shaped trace the protoxylem group of that arm becomes the protoxylem of the pinnule trace. This "lost" protoxylem group in the penultimate pinna rachis is replaced distally by a lateral extension of the median arm of the omega-shaped trace (Fig. 21). Trace formation from the parent petiole to the penultimate pinna rachis occurs in the same sequence as does distal foliar to foliar trace formation (see page 20). The parent petiole is approximately 2.0 mm and shows the typical features of a *B. forensis* petiole.

In cross-section the pinnules show structures identical to those described by Delevoryas and MOrgan (1954). The pinnule is arched over the prominant midrib (Fig. 23). Hairs were observed on the pinnule midrib, but not on the lamina. The epidermis is now well enough preserved to allow study of stomata placement and their relationship to one another.

In transverse and peradermal sections, the pinnules show their broad attachment to the adaxial region of the penultimate pinna rachis (see Figs. 23, 29). The pinnules are oriented at angles ranging from approximately 50 to 70 degrees to the penultimate pinna rachis (Figs. 27, 29). The pinnules reach lengths up to 1.4 cm or more. The maximum width is 6 mm. The distance between adjacent pinnule midribs is approximately 6 mm.

The identity of an entire pinnule is at times difficult to determine. This occurs when the individual lobes of a pinnule appear to constitute a separate, entire pinnule (Figs. 27, 28, 30, 31).

The lobed edges of the pinnule laminae recurve sharply downward making it difficult when observing paradermal sections to determine the true margin of the leaf. The pinnules show an open dichotomous venation pattern with alternate lateral veins arising from the midvein of the pinnule. Occasionally, a lateral vein may dichotomise once near the base of a short round pinnule lobe with repeated dichotomies occurring as the veins approach the margin of the lobe.

Most commonly, a lateral vein traverses the middle of a long or short, rounded pinnule lobe and can itself produce laterals in a pseudomonopodial branching pattern. These latterals then dichotomise toward the edges of the pinnule lobe (Figs. 27 - 30).

The epidermal cells, where preserved, appear to have straight walls (Figs. 24, 25). The range in length of the epidermal cells is 19.2 µm to 70.4 µm, while the range in widths is 19.2 µm to 32 µm. The long axis of the epidermal cell is oriented parallel to the veins.

The mesophyll cells have wavy walls and interconnect with one another to enclose intercellular spaces (Fig. 26).

Fertile foliage -- Fertile foliage of *Botryopteris* has received many different designations in the literature. Among these are fertile petiole, fructification, fertile pinna, and sporangial structure.

The fertile petiole of *B. forensis* has been known since the genus was erected by Renault (1875). He was of the opinion that *B. forensis* was heterosporous. The dimensions given by Renault for this fructification are 5 cm (length) x 3 cm x 3 to 4 cm. The pyriform fertile sporangia range in length from 1.5 to 2.0 mm and in width from .7 to 1.0 mm. Pyriform sterile sporangia, located at the periphery of the fructification, are 9 mm in length and .4 mm in width in their greatest cross-sectional diameter. Renault (1896) assigned a protective role to the surrounding sterile sporangia. The sporangia are clustered in groups of two to many. According to Renault the spores are of two forms; one, the multicellular "microspores" which measure 60 to 70 μm and give the appearance of being multicellular and polyhedral; the other form, the "macrospores" which measure 40 μm (Renault (1883) and are spherical with smooth walls.

Darrah (1939) distinguished *B. globosa* from *B. forensis* by the larger spore size (70 μ) of *B. forensis*. The spores of *B. globosa* are reported by Darrah to range from 0.05 mm to 0.65 mm. Other than differences in spore size, Darrah finds the two species to be similar in details such as the annulus, sporangial wall, sporangial attachment and spore number. He observed sporangia that vary in length from 1.5 to 1.7 mm and in diameter from 1.0 to 1.2 mm.

After studying the type material of *B. globosa* from Iowa and additional material from Kansas and Illinois, Murdy and Andrews (1957) concluded that all these specimens belong to the same species. They

also provided an amended description of *B. globosa* as follows:

> "A massive, globose aggregation of sporangia measuring approximately 5x5x6 cm.; attached to the plant on which it was borne by a botryopterid frond fragment measuring 7.5 by 4.5 mm. which contains a ω-shaped trace; the latter gives off two rows of appendages which divide profusely bearing several sporangia on each ultimate extremity; entire fructification consists of upwards of 50,000 closely crowded sporangia; sporangia are pyriform measuring about 1.5 mm. long and 1.0 mm. in diameter with a massive annulus occupying about three fourths of the area of the sporangium; the annulus is divided into two more or less equal parts by a longitudinal band of 2-3 rows of elongate thin-walled cells; sporangia around the periphery of the fructification characterized by greatly enlarged, radially elongate cells in the distal region; spores spherical, trilete, with a wortose to obervermiculate sculpturing and range in size from 40-55 μ.

Phillips and Rosso (1970), after reviewing previous work on fertile *Botryopteris*, concluded that there are two species of *Botryopteris* fructifications, *B. americana* and *B. globosa*. They state that the fertile pinna of *B. americana* and *B. globosa* are not separable on the basis of sporangial morphology or pinna anatomy. The two species are, however, separated by Phillips and Rosso (1970) by spore ornamentation. They describe *B. americana* spores as:

> "....verrucate to rugulate with verrucae fusing to a variable extent to form bars and convolute ridges;".

and *B. globosa* spores as:

> "....vermiculate or fossulate to densely rugulate with scattered verrucae."

Galtier (1971), after redescribing the type material of *B. forensis*, suggested that *B. americana* spores were identical to *B. forensis* spores.

Fertile Specimens Observed:

Table 1, page 37, provides a partial summary of information resulting from my study of six fructifications, obtained from West Mineral, Kansas coal balls.

TABLE 1. Data on fructifications, sporangia and spores of *Botryopteris forensis*.

	Diameter of parent petiole(s)	Diameter (basal of fertile frond	Approximate size of fructification	Addition number (length, width, breadth)	Number of main paired laterals	Sporangia (max. diameter) interior	Sporangia (max. diameter) peripheral	Sporangia (max. length) interior	Sporangia (max. length) peripheral	Spore size	Ornamentation of the spores
	5 mm x 5 mm	2 mm x 4 mm	3.3 cm (L) x 1.1 cm x	7.74		504.0 µm to 1102.5 µm	598.5 µm to 945.0 µm	787.5 µm to 1260.0 µm	661.5 µm to 1323.0 µm	26.84 48.8 µm	mostly psilate to verrucate-vermiculate
38-b		(oblique ks)	3.34 cm			748.44 µm aver.	729.162 µm aver.	1049.58 µm aver.	949.284 µm aver.	37.57 µm aver.	
	3 mm x 4 mm	3 mm x 3 mm	3.2 cm (L) x 2.3 cm x	9.95	13	630.0 µm to 1102.5 µm	535.5 µm to 1102.5 µm	787.5 µm to 1320.0 µm	787.5 µm to 1260.0 µm	24.4 µm to 51.24 µm	rarely psilate to verrucate-vermiculate
38-a			3.0 cm			841.995 µm aver.	784.98 µm aver.	1091.16 µm aver.	1001.70 µm aver.	38.47 µm aver.	
	3.5 mm x 3.0 mm	3.0 mm x 2.0 mm	2.62 cm (L) x 2.5 cm x	6.82	15	630.0 µm to 1008.0 µm	630.0 µm to 945.0 µm	845.0 µm to 1260.0 µm	787.5 µm to 1260.0 µm	26.84 µm to 51.24 µm	psilate to mostly verrucate-vermiculate
38-f			1.7 cm			776.16 µm aver.	740.25 µm aver.	1031.184 µm aver.	948.70 µm aver.	39.43 µm aver.	
	8 mm (1st order) 6.0 mm (2nd Order)	3.0 mm x 4.0 mm	3.5 cm (L) x 1.1 cm x	5.60		346.5 µm to 787.5 µm	472.5 µm to 787.5 µm	535.5 µm to 945.0 µm	472.5 µm to 1102.5 µm	24.4 µm to 48.8 µm (from peels)	psilate to verrucate
265			1.0 cm			558.495 µm aver.	608.90 µm aver.	785.38 µm aver.	848.925 µm aver.	38.552 µm aver.	
		3.5 mm x 4.0 mm	5.4 cm (L) x 4.0 cm x	11.9	16	630.0 µm to 850.5 µm	630.0 µm to 850.5 µm	787.5 µm to 1260.0 µm	787.5 µm to 1260.0 µm	21.96 µm to 51.24 µm	weakly verrucate to densely rugulate
537			2.5 cm			739.62 µm aver.	754.74 µm aver.	1081.08 µm aver.	999.18 µm aver.	34.98 µm aver.	
335	5.1 mm x 5.0 mm (1st order) 3.8 mm x 6.0 mm (2nd order)	4 mm x 4 mm	3.15 cm (L) x 1.5 cm x 3.0 cm	7.65	10						

The fertile pinnae complexes are usually borne at the base of a primary petiole member which immediately terminates in a crozier (Phillips, 1974). Occasionally, however, the attachment of the central axis of fertile pinnae to either a primary parent petiole or a secondary parent petiole has been noted (Phillips, 1970). Petioles with diameters between 5-7 mm are considered primary petioles (Phillips, 1961). Using this criterion I have found attachments of the central axis of fertile pinnae to secondary parent petioles, which in turn may be attached to primary parent petioles. Specimen 265 shows an attachment of the fertile axis to a primary petiole, which in turn is attached to a petiole with a diameter of approximately 8 mm. The largest reported diameter for a petiole of *B. forensis* is 8 mm (Corsin, 1937). In only one case, (specimen 265) was the primary parent petiole observed to terminate in a crozier, and this was poorly preserved.

Trace Formation

Specimen 38-a best illustrates trace formation from a parent petiole (secondary) to the axis of the fertile pinna. Trace formation begins with a lateral extension of tracheids from the median arm to a position which is approximately midway between the lateral arm tip and the base of the median arm. These tracheids will become part of the next lateral arm of a somewhat trident-shaped vascular strand (Figs. 33, 34). The old lateral arm can be seen still attached to the parent strand. Figure 35 shows the old lateral arm, i.e. the trace to the fertile axis, detached from the parent foliar strand. At this level the trace is somewhat elliptical with the smaller tracheids

confined to a portion of the adaxial (left half) and lateral faces of the trace. The trace lies in a plane perpendicular to the parent foliar strand. Distally, the trace is still somewhat elliptical and the smaller tracheary elements are confined to the right half of the adaxial face and to a position at the tip of the developing left arm (Fig. 36). The left arm develops by the formation of non-tracheary tissue (Phillips, 1961), which extends to the adaxial surface. In this case the adaxial opening developes simultaneously with the appearance of the non-tracheary cells. The orientation of the trace is slightly out of the plane of the parent petiole. One can detect at this level (Fig. 37) the left arm, a median bulge (the median arm) and a slight bulge to the right. Between the median arm and the right bulge is a slight concavity, which is the position into which the non-tracheary tissue island will extend.

Specimen 335 provides additional information about the initial changes in the trace to the fertile pinna axis. Figure 38 illustrates the fertile axis strand at a basal level just distal to the point of its attachment to the parent petiole. The trace has a well-developed right arm, a median arm, and a weakly-developed left arm. All three arms possess small tracheids (probably protoxylem) at their tips. Non-tracheary tissue is present and extends adaxially to delineate the right arm of tracheids of the trace. At this level the left arm of the xylem trace has not been differentiated. At a slightly higher level (Fig. 39) the non-tracheary tissue makes its appearance. It has not, however, become adaxially extended so as to delineate the left arm of the xylem trace. Figure 40 represents a slightly more distal level of the fertile pinna axis and shows the left non-tracheary tissue

extended and opened out to isolate the left arm.

Trace formation to the paired laterals differs depending on the level at which trace formation is initiated. The patterns explained below are from a reconstructed fructification, which is based on specimens numbered 355, 38-a, and 537. No one fructification has all the indicated patterns of trace formation. At the base of the reconstructed fructification, lateral trace formation from the somewhat trident-shaped parent strand begins with the lateral extension of tracheids from the median arm. At the same level a small bulge of tracheids can be seen in a position approximately midway between the lateral tip and the base of the median arm (Fig. 41). The lateral extension and the bulge join together to form the next lateral arm (Fig. 42). The lateral trace (the outermost lateral arm) may detach during or slightly after the separation of the new lateral arm from the median arm (Fig. 43). The detached trace appears as a slightly curved bar and is oriented perpendicularly to that of the parent foliar strand. Distal to the above position, trace formation may begin with the development of a protoxylem group in a position approximately midway between the median arm and the lateral arm. An extension from the median arm may or may not be produced. If it is produced, it appears before the newly developed protoxylem divides. The length of the developing arm may be accentuated by the formation of a non-tracheary tissue (Fig. 45). The protoxylem is then itself divided by the intercalation of non-tracheary tissue; the result is a somewhat c-shaped trace, which is still attached to the parent strand (Fig. 46). When the c-shaped trace becomes detached it is oriented in a plane perpendicular to that of the parent foliar strand. In the most distal

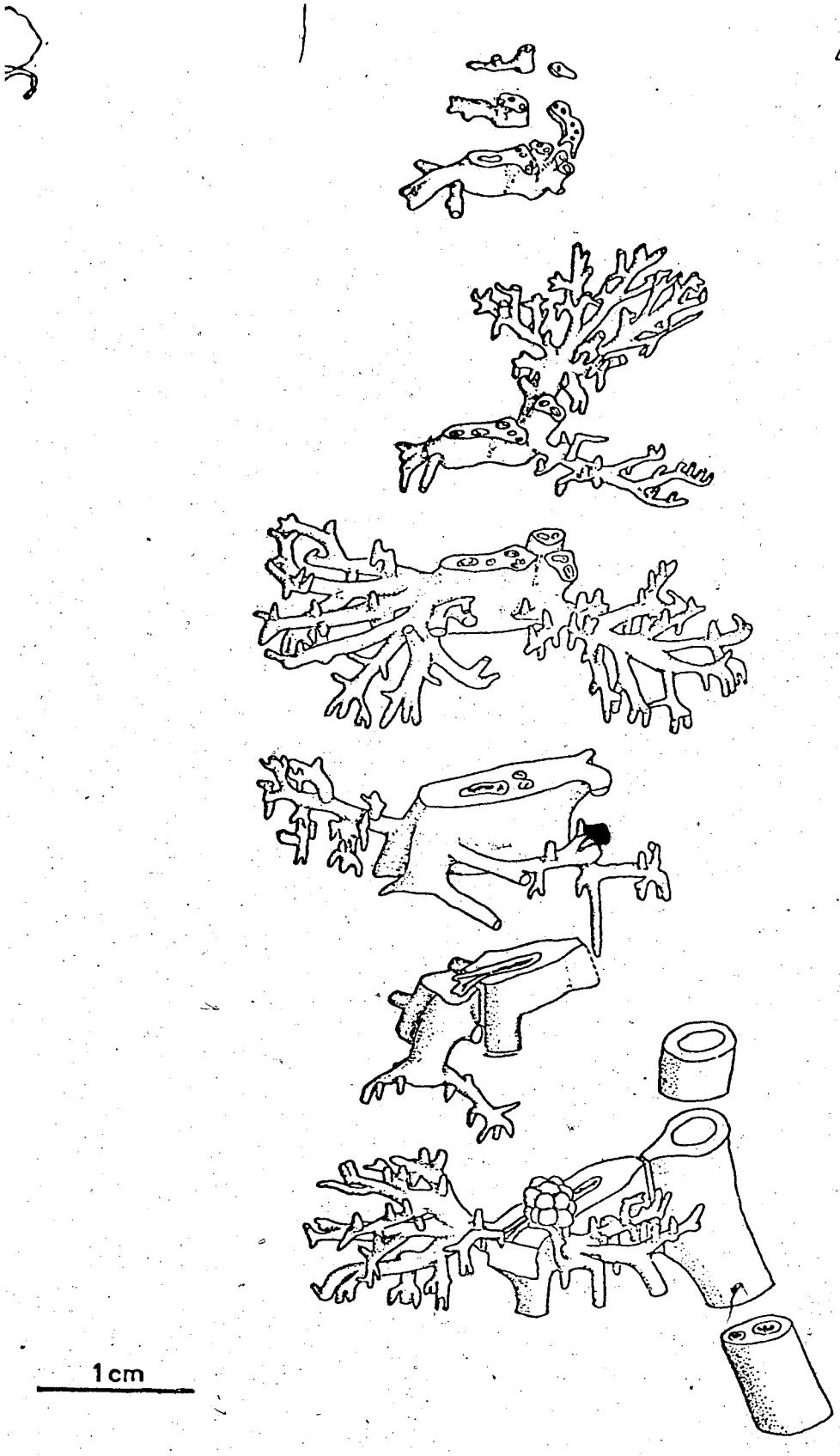
regions of the fructification, trace formation begins with the formation of tracheids with small diameters which extend from the tip of the median arm downward along its lateral face.

The lateral tracheary arm is then formed by the adaxial expansion in the lateral portion of the strand, of non-tracheary tissue (Figs. 47, 48).

Paired lateral traces are borne on the main axis of the fructification in a quadriseriate (4-rowed), alternate pattern. The higher more distal orders of branching may be either biseriate (2-rowed) or quadraseriate. The actual orientation of the lateral pairs varies. In general, the lower (basal) lateral pairs tend to be oriented towards the base of the fructification and are pendulous, while the upper more distal pairs tend to be oriented towards the apex of the fertile axis. The orientation of the paired laterals in specimen 38-a differs somewhat from the general plan, in that the paired laterals on the one side are pendulous, while the laterals on the other side are directed towards the apex of the fertile axis (see reconstruction, text fig. 2). It is possible that the final spacing of paired laterals may be due to available space. In any one pair of laterals, the ultimate divisions of each member tend to be located at the periphery of the fructification; thus, the most peripheral clusters of sporangia are (as seen in a cross-section of the fructification) located on the ultimate divisions of a particular pair member.

The distance between nodes of alternate pairs of laterals is very short. In fact, at times trace formation to alternate pairs of laterals appears to be opposite, though the final orientation is indeed alternate.

Text Fig. 2. Reconstruction of the fructification of *Botryopteris forensis* showing branching patterns. (See text for full explanation.)


1cm

Higher order branching patterns are clearly illustrated by specimen 38-a. The shape of the vascular traces in orders of branching distal to the main fertile axis ranges from bar to c to terete in shape. Well-defined protoxylem is often difficult to observe. In some specimens small tracheids appear scattered along the adaxial face of the trace. These may be interpreted as more or less isolated protoxylem cells. It is my experience that the best way to describe divisions of a trace is to relate the division to the development of the intercalating non-tracheary tissue. This is contrary to the usual method of description which relates the division of the trace to the divisions of protoxylem stands.

The non-tracheid forming areas may at first develop opposite one another, on the adaxial and abaxial faces of the trace. Distally each area of non-tracheary tissue develops inwardly (towards each other), producing a trace, which may be of the same or smaller size than the other member of that division. Non-tracheary areas were also observed developing on the abaxial side of the trace and progressing towards the adaxial face, thus dividing the strand.

The slightly curved, bar-shaped trace (the trace to the paired laterals), which develops from the axial strand of the fertile axis, does not close as is the case with trace development in a distal vegetative petiole. Distal to its point of attachment, the trace becomes more c-shaped and oriented in a plane perpendicular to that of the parent strand. Shortly after the lateral trace has become c-shaped, it divides into two (Fig. 49). One of the resulting traces may be smaller than the other. Each of these traces is the incipient trace for a member of the lateral branch pair. While still in cortical

attachment with each other and the parent axis, each strand divides to produce a lateral trace which will lead to an appendage at the base of each lateral pair member (Fig. 50). The basal appendage traces occur with a high degree of regularity, however, in some cases they are lacking. The lateral appendages branch to form a biseriate pattern (Fig. 51). Slightly above the level of attachment of the lateral appendages, the lateral pair members are separated from each other and the parent axis (Fig. 52). The lateral member to the right (Fig. 52) will be discussed and illustrated in order to bring out details of its branching. Three traces and one parent strand can be seen in cross-section of the axis of this member pair. The two traces to the left originated as a single trace from the parent strand, which is the strand located at the center of the axis (Fig. 53). The trace which divides to produce the two traces above mentioned is at the point of initiation in the same plane as the parent strand that it is derived from. As the trace proceeded outward it became oriented at right angles to the trace of the parent strand. The trace then divides and the two members of that division become oriented at an angle of approximately 90 degress with respect to each other. One can also observe at this level that the parent strand has also produced a trace to the right which is at right angles to the trace of the parent strand. Figure 54, distal to that shown in Fig. 53, shows that each of the traces to the left and described above, has divided into two. The two traces to the right originally described as a single trace, have become oriented perpendicular to the parent strand. Each of the two sets of lateral traces supply a left and right pair of laterals having a quadraseriate arrangement. The left pair of quadraseriate laterals (Figs. 55,56)

differs somewhat from the right pair, in that, one member of that left pair divides near the base of the other member and appears as a quadraseriate pair borne by the other member.

The right pair of laterals (Figs. 55, 56) of which each member is developed equally and biseriately branched, is the common type of quadraseriate pair occurring on higher orders of branching in the fructification.

A variation of branching, a pattern somewhat intermediate between the quadraseriate and biseriate pattern also occurs in this fructification. Figure 57 illustrates an axis with four strands (two traces to the right and one to the left of the parent strand). We will be concerned only with the two traces to the right. They originated from the parent strand as a single trace, which later divides to form the two traces. One trace supplies a lateral appendage, which branches biseriately (Fig. 59); the other trace at this level does not supply a lateral appendage as would normally be the case. Rather, it remains within the parental cortex and divides into two (Fig. 61). The destination of these traces was not determined due to the position of the saw kerf.

Paired laterals, which are borne on the main axis of the fructification ultimately divide by a two, three, or four-parted division.

In summary, the branching of the fructification ranges from quadraseriate to biseriate. At times one member of a quadraseriate pair is smaller in diameter then the other member. One member of a quadraseriate pair may also divide very early, i.e., at the base of the joined pair and thus give the appearance of being borne by the other member (Fig. 55). In my opinion, the quadraseriate branching pattern

represents the primitive branching condition (at least in the fructification) and the biseriate pattern is derived either by suppression or subordination of one member of the quadraseriate pair.

Sporangia and Spores

Reconstruction of *B. forensis* sporangia has been accomplished by Murdy and Andrews (1957), Phillips and Andrews (1965), and Galtier (1971). The latter redescribed the type material of *B. forensis* and provided additional information on the sporangia and spores.

Sporangia -- According to Galtier (1971), the sporangia are attached to a lateral protuberance of parenchymatous tissue, which is fortified by scalariform tracheids. These tracheids can be followed to the base of each sporangium. The sporangia are grouped in clusters of 2 or 3 or many and the annulus of each is oriented towards the interior of the group or cluster.

The fertile, pyriform sporangia measure 1.5 mm to 2.0 mm in length and 0.7 mm to 1.0 mm in width. The sporangial wall usually appears as a single layer of cells, though occasionally an inner layer was observed. The sporangia are bilaterally symmetrical, possessing an annulus that occupies 2/3 of the proximal face. The annulus extends from the pedicel to a position somewhat below the apical region of the sporangium and to a degree along the lateral faces. The annular cells are large, hexagonal, and elongated parallel to the sporangial axis. These cells near the distal apex of the sporangium are isodiametric. The pedicel of the sporangium is formed of small cells with relatively thick walls.

Dehiscence is longitudinal and is effected by a band of elongated cells (3-4 cells wide), which extend from the distal region of the sporangium to the pedicel opposite the annulus. The rest of the sporangial wall consists of large cells either polygonal or slightly sineous in shape.

Galtier (1971) describes the peripheral sterile sporangia as being 0.9 mm in length to 1.3 mm in length and containing an internal tissue of polygonal cells. The cells of the wall in the distal region are very elongated in the radial direction and terminated by a rounded point. He states that these cells appear to be modified non-annular cells.

Immature sporangia, located in the central region of the fructification, have a sporangial wall composed of cells that appear matured. The interior of the sporangia, however, consists of slightly altered spores and a tissue of polyhedral cells 50 - 60 μm to 75 - 90 μm in size. Some spores are grouped in tetrads, while others show a trilete mark and possess a distinct ornamentation. These polyhedral cells may be the "multicellular microspores" described by Renault (1896).

Sporangia observed in this study came from the West Mineral locality and compare closely with sporangia described by Galtier (1971) from the type material; therefore, morphological and anatomical details need not be repeated.

Figures 73, 74 show fertile and sterile sporangium with distal, radially-elongated cells.

Sterile sporangia are either empty or filled with a parenchymatous tissue. If they occur, the sterile sporangia, if present, generally are restricted to the periphery of the fructification where they are

borne on the distal, ultimate appendages. These sporangia may form an irregular layer surrounding the fructification. The peripheral layer of sterile sporangia is often discontinous with the gaps in the layer being filled by fertile sporangia. In some fructifications (Fig. 63) the covering layer of sterile sporangia may be absent. In this case, most of the peripheral sporangia are fertile. The variability in the number of sterile sporangia between fructification specimens (which were sectioned transversely or longitudinally) can be seen in Table 2.

There is a general trend (exceptions specimen 265 and in part specimen 537) for the lengths and widths of sporangia to be less in the peripheral zone than in the internal zone. The smallest sporangium measured was 346.78 µm in its greatest diameter (specimen 265), while the largest measured was 1102.5 µm (specimens 38-a, 38-b). The shortest sporangium length measured was 472.5 µm (specimen 265) while the longest measured was 1320.0 µm (specimen 38-a). Histograms of measured diameters and lengths of sporangia for each fructification specimen can be seen in Table 3.

Spores -- The spores redescribed by Galtier (1971) are of two forms. They are essentially of the same dimensions and can be found within the same sporangium. One form is subspherical, trilete, and provided with a distinct ornamentation. The other form has a polyhedral shape and is apparently multicellular.

The ornamented spores have equatorial diameters ranging from 42 to 62 µm. The rays of the trilete mark are straight and range from 12 to 24 µm in length. The exine is ornamented with variable densities

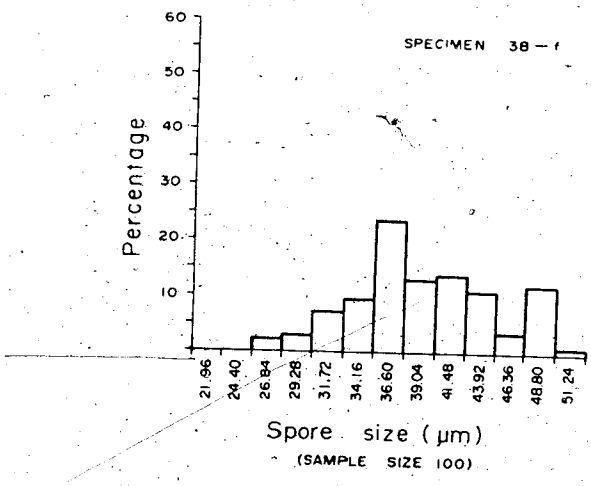
Table 2. Data comparing the percentages of sterile sporangia from internal and peripheral regions of *Botryopteris forensis* fructifications.

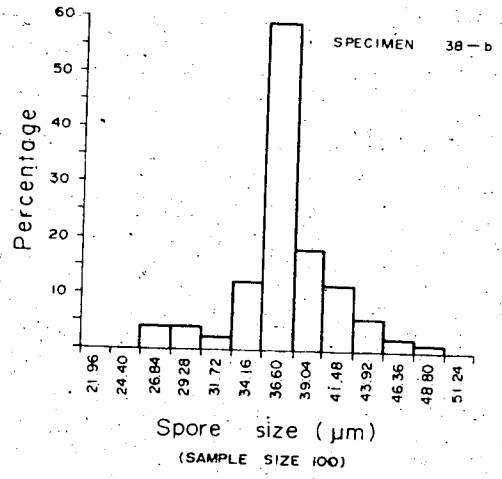
Specimen	No. of sterile sporangia measured (internal)	Total no. of sporangia measured	% sterile	No. of sterile sporangia measured (peripheral)*	Total no. of sporangia measured	% sterile
(XS) 537 Numbers based on slides H-bot #74, 105 and I-top #37	2	50	4	10	50	20
(XS) 38-a Numbers based on slides H-top #45, and 64	0	51	0	4	50	8
(LS) 38-b Numbers based on slides H-bot #107, 117, and 121	2	50	4	11	52	25.6
(XS) 38-f Numbers based on slides F-bot #62 and G-bot #3	1	44	2.27	12	43	28
(XS) 265 Numbers based on slides G-bot #12, 36, and 70	18	41	43.9	66	67	95.5

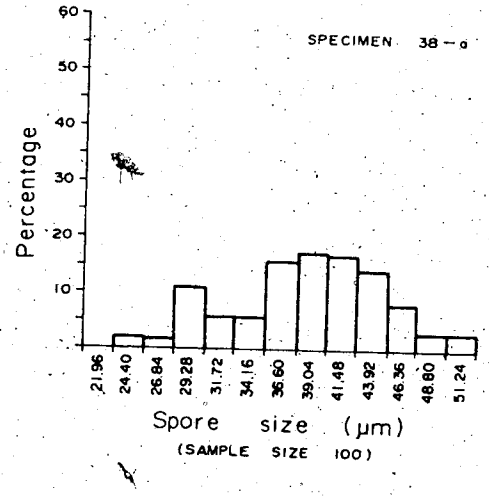
*A sporangium is considered peripheral if it falls within a zone which extends no farther inward from the outer edge of the fructification than five sporangia widths.

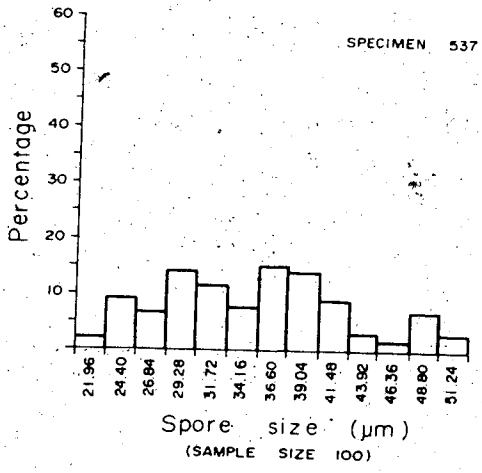
Table 3. Histograms showing the distribution of spore sizes from *Botryopteris forensis* fructifications.

HISTOGRAMS OF SPORE SIZES









of verrucae and rugulae. These elements can be circular or elongated to create irregular sinuses. The elements seldom exceed 1.0 µm in width or height. There is no observable difference in ornamentation between distal and proximal spore faces.

The polyhedral spores are of the same dimensions or slightly smaller (40 to 55 µm) than the other spore form. They possess a trilete mark and an ornamentation comparable to the spores described above. Galtier attributed the appearance of these polyhedral spores to the process of fossilization. He found little evidence to indicate heterospory as suggested by Renault.

Botryopteris forensis spores in this study range in diameter from 21.96 m to 51.24 m. The exine ornamentation varies from being psilate to densely rugulate (see Table 3 and spore histograms). Based on the observation of peels showing spores within sporangia, it appears that there is a wide range in the sizes of spores within any one fertile sporangium. A similar conclusion, based on deeply etched sections of sporangia, was made by Phillips (1970). Specimens 537, 38-a, 38-f, and 265 (based on peels only) showed no significant differences in spore size or ornamentation that could be related to the level in the fructification from which the spores were macerated. The fructification specimens listed above, lack observable spore tetrads. the majority of spores possess some degree of ornamentation. Psilate spores do occur, but they are rare.

Fructification 38-b (interpreted as being the least mature) possesses mostly psilate spores (some of which were still in tetrads) (Fig. 82). Occasionally, spores with a verrucate-vermiculate ornamentation were observed (Figs. 84, 86). Many of the sporangial walls are

completely broken down; as a result, there is a large number of dispersed spores within the matrix, outside of the boundaries of the fructification.

Generally speaking, the proximal and distal spore faces do not differ significantly. When differences do occur, however, they are not related to the size of spore (compare Figs. 91, 92). Notice that the interradial areas of the proximal face of the one spore (Fig. 91) lack ornamentation, while a spore of comparable size possesses a well-ornamented proximal face.

Spores of specimen 537 show the greatest degree of fusion of verrucae and they proved to be useful in illustrating the range of exine ornamentation patterns one can observe in spores of *B. forensis*. Figures 93 to 97 represent a possible sequence, showing the stages of the development or elaboration of exine ornamentation. Figure 93 shows a spore with ornamentation elements which are not as densely spaced or as prominent as are the elements on the spore illustrated by Fig. 94. In Fig. 94, which represents the next stage of exine development, notice that the verrucae show a range of diameters and irregular distances between verrucae. Certain verruca are slightly attached to each other by thin rods of depositional material, while others are attached by more substantial connections forming short rods or vermiculae. When these short bars or somewhat longer vermiculae become more numerous among the scattered verrucae but do not anastomose extensively with each other, then the next stage of exine elaboration is reached (Fig. 95). Figure 96 illustrates a more advanced developmental stage in which the short bars or vermiculae are fused with each other to form an anastomosing pattern. Notice that the verrucae which make up the fused

elements can be roughly deliminted by observing the positions of constrictions within a short bar or vermicula. This last ornamentation pattern I would call rugulate, while the previous patterns would be called verrucate, verrucate-vermiculate, or vermiculate depending on the degree of fusion between verrucae. The final developmental stage, represented by Fig. 97, shows the short bars or vermiculae fused to each other forming a densely rugulate pattern. The individual verrucae of the fused elements cannot be delimited. Gradations between the developmental stages occur.

Fructifications 38-a, 38-f, and 265 (based on peels) possess spores with exine ornamentation ranging from psilate to verrucate to vermiculate (see Figs. 64 - 71). The spores of these fructifications do not show the degree of fusion among fused elements as do spores of specimen 537. This fact may indicate that specimen 537 was more mature (based on spore ornamentation) or produced more sporopollenin.

Botryopteris tridentata

Botryopteris tridentata, first described in 1886 by Felix as *Rachiopteris tridentata*, is known from the U.S.S.R, West Germany, and the U.S.A. It has a stratigraphic range extending from the Westphalian A-B boundary of West Germany (Katherina horizon) to North American sediments (Bevier coal), which are equivalent in age to the basal Westphalian D (Phillips, 1970, 1974; Kosanke *et al.*, 1960; Kosanke, 1969).

The main rhizome and fertile organs are not known, while petioles, plantlets, and laminar pinnules have been described.

B. tridentata has been extensively studied by Phillips (1961, 1970, 1974) and Snigrevskaya (1961); as a result, the materials studied here will serve to illustrate anatomical and morphological details brought to light by the former authors as well as to provide new information concerning the species.

Leaves (petioles)

Petioles vary in diameter from 0.25 mm (Snigrevskaya, 1961) to 6.0 mm (Phillips, 1961). The smallest petiole (non-laminar) observed in this study is a penultimate pinna rachis which is approximately 1.0 mm in diameter. Three successive and connected orders of petioles are known from the work of Snigrevskaya in 1961 and the work here. Phillips (1970) provided an emended diagnosis of *B. tridentata* and stated that a petiole possesses a:

> "....bilateral symmetry, flattened to slightly convex adaxial face with rounded abaxial face and sides,...."

Figure 104, illustrates a typical petiole

Phillips (1970) described the epidermal cells as being up to 75 µm thick, square to rectangular, and larger than the underlying cortical cells (Figs. 106, 107). Multicellular uniseriate hairs are up to 2.0 mm in length (Phillips, 1961) and borne on multicellular hair bases, the largest of which are found on *B. ramosa* and *B. tridentata* (Phillips, 1970).

The outer cortex is most commonly composed of uniformly, thick-walled cells. Cells in the outer region of the outer cortex often have dark contents. This gives these cells a thick-walled appearance and the outer cortex as a whole a two-zoned appearance (Fig. 106). In other

specimens of petioles the outer cortex does not show this two-zoned appearance even though the cells of which it is composed are thick-walled (Fig. 104). The innermost "outer" cortical cells are smaller in diameter than the other outer cortical cells and often tangentially flattened (Phillips, 1970). Proceeding outward from these innermost cortical cells, cells of the cortex attain diameters up to 85 µm and then diminish in diameter towards the epidermis (Phillips, 1970). In longitudinal section, the outer cortex can be divided into an inner zone of cells with transverse end walls and an outer zone of cells with oblique end walls. The cells with transverse end walls range in length from 62 µm to 1007.5 µm, while in width from 31 µm to 77.5 µm (from a petiole 7 mm x 3 mm). The lengths of the cells with oblique end walls range from 139.5 µm to 1007.5 µm in length, while widths range from 23.25 µm to 46.5 µm.

An inner cortex may or may not occur in a petiole. Usually the region between the vascular bundle and the outer cortex is not preserved. Phillips (1970) observed a petiole 2.8 mm x 2.2 mm thick with parenchyma between the xylem and outer cortex, which was differentiated into two zones. He suggested that the outer zone may be an inner cortex. Inner cortical zones are known to occur in petioles of *B. forensis*. Specimen 552, a petiole of *Botryopteris tridentata*, possesses a zone of parenchymatous tissue between the vascular bundle and the outer cortex. In longitudinal section, one can observe both typical thin-walled parenchyma cells and also cells, probably glandular or secretory cells, filled with a brownish substance that appears reticulate or frothy (Fig. 137). Phloem cells were not distinguished.

In cross-section the vascular bundle is trident-shaped. Phillips

(1970) described the xylem strand as broadly elliptical in cross-section with a flattened to concave abaxial face and with three adaxial ridges, each with a protoxylem group (Fig. 106). Snigrevskaya (1961) described the pitting on metaxylem as multiseriate-scalariform or multiseriate-reticulate and gave metaxylem diameters which range from 30 μm to 160 μm. Elliptical to circular bordered pits do occur on well-preserved metaxylem (Fig. 105). Protoxylem ranges in diameter from 10 to 20 μm and possesses spiral and scalariform thickenings (Snigrevskaya, 1961). The latter described parenchyma-like tissue associated with the xylem strand. The distribution and dimensions of this tissue vary but are usually best developed on the adaxial side of the branch. Cells of the tissue have very thin walls. Phillips (1970) wrote that Snigrevskaya (1971) regarded parts of this tissue, the larger cells, as adaxial and abaxial phloem zones.

Pinna trace formation begins with the separation of xylem (the adaxial portion of the lateral arm) from the parent strand. The protoxylem is replaced or restored by a diagonal extension from the median arm across the adaxial face of the parent strand to the lateral ridge area (Phillips, 1971) (Figs. 110, 111).

Specimen 311 contains a petiole 5.0 mm x 4.0 mm in diameter, which produces alternately a plantlet and a lateral pinna. The lateral pinna (3.0 mm x 1.1 mm) in turn gives rise to another lateral pinna 1.0 mm in diameter, which is the penultimate pinna rachis. Attached to the penultimate pinna rachis in an alternate fashion, are two-rows of laminar pinnules.

The orientation of the first order lateral pinna strand is at first perpendicular to that of the parent foliar strand. It has a monarch

arrangement of its xylem. Distally, the lateral pinna strand becomes oriented just out of the plane of the parent foliar strand and is triarch. Details of trace formation to the penultimate pinna rachis from the first order lateral pinna were not available due to the lack of preservation.

The penultimate pinna rachis is pendulous on the lateral pinna and produces three alternate distichous pinnule traces. In transverse section, one of the pinnules can be seen in Fig. 109. The penultimate pinna rachis is approximately 1.0 mm in diameter near its point of attachment with the lateral pinna, while approximately 8.0 mm distal to that position the rachis is .70 mm in diameter.

B. tridentata differs significantly from all other species of *Botryopteris* by its possession of a siphonostelic (medullated protostele) plantlet. A further distinction, which *B. tridentata* shares with *B. ramosa*, is that cauline and pinna trace formation are quite different from each other (Phillips, 1970). *B. tridentata* is evolutionarily significant because it represents the earliest occurence of a siphonostele (medullated protostele) in the genus (Phillips, 1970).

Phillips (1971) described trace formation from a parent petiole to a plantlet as beginning with:

> "....a marked increase in size of the lateral portion of the foliar xylem strand [fig. 112]. This lateral xylem segment subsequently develops a distinct additional lateral lobe [fig 112]; at this stage, tracheids may join the lateral arm to the tip of the median arm. The additional lobe or incipient xylem trace becomes progressively more hook-shaped [fig. 114], and finally the hook recurves to form an incipient xylem trace which is siphonostelic [fig. 116]. As the cauline trace departs, numerous adventitious roots radiate about the siphonostele; the portion of the lateral arm which gave rise to the cauline trace is typically enlarged at this stage and subsequently resumes a size comparable to the other lateral arm."

Five plantlet specimens were serially sectioned for this study, three of which were transversely sectioned, while the other two were obliquely sectioned (see Table 4).

Plantlets

The epidermis is not well defined, as is the case with *B. forensis* plantlets, and differs very little from the underlying cortical cells. The outermost layer of cells is usually covered with multicellular, uniseriate hairs which usually are attached to a multicellular hair base. Phillips (1961) reported hairs up to 2.0 mm in length for this species. The maximum hair length observed in this study for this species is approximately 1.1 mm.

The outer cortex (in cross-section) is uniformly thick-walled and dark brown in color (Fig. 113). The cells show a slight gradation in diameter from the innermost cells with the smaller diameters to the outer cells with the larger diameters. Cells of the outer cortex often contain a dark brown substance, which at times completely fills the cell lumen. The outer cortical cells ranged in diameter from 19.2 µm to 78.6 µm (specimen 380).

The inner cortex is composed of thin-walled cells, that typically do not contain the brown substance; as a result, these cells appear much lighter in color. The diameters (radial) of the inner cortical cells, on the average are smaller than those of the outer cortical cells, ranging from 12.8 µm to 32 µm. The inner cortical cells also are tangentially flattened, though in the contact region between the inner and outer cortices the inner cortical cells are more polygonal. The color difference between the two cortices is quite distinct, with the inner cortex

Table 4. Data on plantlets of *Botryopteris tridentata*.

Specimen	Diameter of parent foliar member	Maximum plantlet diameter	Length of plantlet	Maximum diameter of stele	Number of petioles	Phyllotaxy
311	5.0 mm x 4.0 mm	5.0 mm x 5.0 mm	1.58 cm	1.1 mm	7 leaf gaps 1,4,5, and 6	2/5
380	2.1 mm x 3.0 mm	4.0 mm x 5.0 mm	2.44 cm	1.5 mm x 1.0 mm	12 leaf gaps petiole 1	2/5
240	1.0 mm x 1.1 mm	2.6 mm	1.59 cm	1.0 mm	10 leaf gaps 1,3,4,5,6, and 7	1/3
577	4.0 mm x 3.0 mm	4.0 mm	2.1 cm	1.0 mm	----	--
303	3.0 mm x 2.9 mm	3.0 mm	1.1 cm	.9 mm	----	--

lighter in appearance than the outer cortex (Fig. 113).

Internal to the inner cortex is occasionally found a brown colored, single-celled thick layer of cells, which were interpreted as the endodermis (Fig. 118). These cells have widths (radial) of 12.8 µm and breadths (tangental) of 32 µm to 44.8 µm.

The phloem zone is not well enough preserved for histological study but ranges in thickness from 96 µm to 160 µm. The stelar xylem consists of larger metaxylem cells at the interior and smaller metaxylem at the exterior (Fig. 118). The center of the protostele is parenchymatous with occasional scattered tracheids, which ranged in diameter from 12.8 µm to 96. x 64 µm.

Protoxylem becomes evident at the onset of petiole trace formation on the inner face of the medullated protostele, between the parenchyma and the metaxylem (Fig. 118). The decurrent protoxylem gives the first indication of incipient petiole trace formation. The pitting of the metaxylem cells ranges from scalariform to multiseriate-scalariform to multiseriate-reticulate with occasional bordered pitting (Fig. 117). Tracheids of the cauline xylem, as reported by Phillips (1961), have annular to scalariform thickenings along the outer periphery and multiseriate-reticulate bordered pits toward the center.

In longitudinal section (Fig. 115), the inner cortical cells are, on the average, shorter than the outer ones; both tissue layers possess cells with oblique or transverse end walls. The lengths of the outer cortical cells range from 64 µm to 544 µm, while the lengths of the inner cortical cells range from 51.2 µm to 256 µm.

Plantlet petioles possessed an epidermis and hairs typical of petioles of the species. The petiole cortex appears either uniformly

thick-walled and dark brown or distinctly zoned with a lighter inner zone of thick or thin-walled cells and an outer zone with thick-walled cells only.

Figures 125 to 127 show basal, median, and distal sections respectively of a petiole attached to a plantlet (specimen 577). Fig. 125 shows a light-colored inner cortex which consists of thin-walled cells. As the inner cortex continues into the petiole it becomes darker colored, and diminishes in volume. The cells of the inner cortex also become thick-walled (Fig. 126). Finally, distal to the previous position, the zone of contact between the inner and outer cortices remains dark in color, while the rest of the cortical tissue becomes lighter in color (Fig. 127).

A petiole (Figs. 123, 124) attached to the plantlet specimen #311 has a zoned outer cortex with an inner zone of larger diameter, thin-walled cells of large diameters and an outer zone of thick-walled cells with smaller diameters. The latter cells are also darker in color because of the deposition of the brown substance (Fig. 124). The inner cortex consists of cells with small diameters which are tangentially flattened (Fig. 124).

Plantlet phyllotaxy, where determined, is either 2/5 or 1/3. The largest number of petioles borne by a plantlet is twelve (specimen #380) in a 2/5 phyllotaxy. The longest plantlet is 2.44 cm (specimen #380), while the shortest is 1.1 cm (specimen #303).

As mentioned earlier, the first indication of incipient petiole formation begins with the occurrence of a decurrent group of protoxylem on the inner face of a segment of the stem xylem (Fig. 118). When followed distally (Figs. 119, 120), the segment of the stem stele

destined to become a petiole trace, progresses outward until it becomes completely separated from the stem stele. The petiole xylem segment becomes detached simultaneously from both sides of the stem xylem. The petiole trace initially is either C- or D-shaped. If C-shaped, it becomes D-shaped in its more distal parts. The protoxylem group is at first confined to a region on the adaxial face of the petiole trace (Fig. 121). Distally, the protoxylem cells become distributed across the adaxial face of the trace. Finally, three arms with their respective protoxylem groups become differentiated (Fig. 122).

Roots

The initiation of root traces occurs in a fashion similar to root initiation in *B. forensis*. Roots of *B. tridentata* were reported by Phillips (1961) to be less than .8 mm in diameter. *B. tridentata* roots observed in this study range in diameter from 240 µm to 600 x 696 µm. The outermost layer of cells is interpreted as the root epidermis, which lack observable root hairs.

The underlying cortical cells commonly have thickened, brown colored walls (Fig. 129), although, as illustrated by Figs. 130, 134, one can observe a range in color and thickness of the cortical cell walls. The innermost zone of cortical cells (Fig. 130), which ranges from a single to a few cell layers thick, consists of tangentially flattened cells with radial diameters of 6.4 µm to 12.8 µm and tangential diameters of 25.6 µm to 32 µm. External to this zone the cells are more polygonal and range in diameter from 19.2 µm to 44.8 µm.

The zone between the diarch root strand and the cortex is not preserved. The root strand consists of at least ten tracheid elements

ranging from 12.8 µm to 51.2 µm in diameter. The protoxylem groups are located opposite one another in the diarch strand. Metaxylem pitting is biseriate to multiseriate scalariform-reticulate to occasionally elliptical bordered (Figs. 135, 136).

Lateral roots branch from the parent root pseudomonopodially (Fig. 132) or endogenously (Fig. 131). A root which arises pseudomonopodially shows a cortex which is continuous (homogeneous) with the cortex of the parent root. This reflects an unequal division of the parent root apex. The smaller member of that division would become the lateral root apex. Lateral root branching was observed to occur after the parent root emerged from the stem. Phillips (1970) reported roots of *B. hirsuta* branching within the outer cortex or immediately upon their exit from the stem. The diarch vascular bundle of lateral roots is oriented perpendicular to that of the parent root. Figure 133 shows a root with a triarch bundle, which gives an indication of incipient lateral root trace development.

Sterile foliage

The penultimate pinna rachis is D-shaped in cross section and approximately 1.0 mm in diameter. In contrast to the well-developed adaxial ridges on the penultimate pinna rachis of *B. forensis*, the ridges on the penultimate pinna rachis of *B. tridentata* are not well-developed (compare Figs. 20, 140).

The epidermis consists of cells having the typical appearance of *B. tridentata* epidermal cells. These are rectangular to square-shaped and larger than the immediately underlying cortical cells. The diameters of the epidermal cells range from 25.6 µm to 32 µm (radial)

to 32 µm to 38.4 µm (tangential) (Fig. 141).

The outer cortex presents a rather homogeneous appearance in contrast to the usually distinctly zoned outer cortex of the penultimate pinna rachis of *B. forensis*. The outer cortical cells of the former vary from thin-walled to thick-walled. The innermost cortical cells of the "outer cortex" which may be, in reality, inner cortical cells, are most often tangentially flattened. External to these cells are polygonal cells, which show a gradation of diameters from large to small, from the inside to the outside of the penultimate pinna rachis (Fig. 141).

The vascular strand is trident-shaped with the arms of the strand facing the adaxial surface (Fig. 141). The protoxylem is located at the tips of the arms. The metaxylem cells have diameters which range from 19.2 µm to 57.6 x 83.2 µm. Metaxylem pitting is uniseriate- to multiseriate-elliptical to circular-bordered. Often the borders are not well preserved thus giving a different appearance to the wall pitting of the metaxylem cells.

Pinnule trace formation occurs in an alternate, distichous pattern and begins with the appearance of a slight elongation of the lateral arm of the penultimate pinna rachis strand. The trace then departs and enters the base of a pinnule. Before the lateral arm departs as a trace, an additional lobe of tracheids with a group of protoxylem develops near the apex of the median arm and distally diagonally crosses the adaxial face of the pinna strand (Fig. 141). The tracheids of this lobe replace the tracheids emitted as the trace and become the new lateral arm.

Tracheid connections between groups of protoxylem, which occur at various positions on the adaxial face of the pinna strand, vary in

number in respect to other protoxylem groups with which they are connected (Figs. 139, 141, 142).

In cross section, the pinnule blade or lamina does not significantly arch over the pinnule midrib, as do the pinnule blades of *Botryopteris forensis* (Fig. 138). Hairs (uniseriate and multicellular) are on the abaxial sides of pinnule veins and in one case on the blade margin. The margins of the pinnule blade recurve slightly downwards (Fig. 138).

The pinnule blade or lamina of *B. tridentata* differs from the pinnule lamina of *B. forensis*. The former appears thin and compressed, while the latter appears thick and shows little compression. The epidermis is not preserved on the pinnules of *B. forensis*, while it is on those of *B. tridentata*. It is suggested that *B. forensis* pinnules were fleshy, while those of *B. tridentata* were more leathery (compare Figs. 20, 147).

Details of *B. tridentata* pinnule histology are usually unavailable because most pinnules are compressed. As a result of this the lamina (in cross section) appears with the exception of the uncompressed pinnule veins as a thin, brown layer. In a rare case, the lamina was not compressed, though still considerably thinner than the lamina of pinnules of *B. forensis* (Fig. 147) and histological details were available. The mesophyll tissue is not differentiated into a palisade and spongy layer, but consists of thin-walled cells with large intercellular spaces (Fig. 147). Stomata are present only on the lower surface (abaxial) and occur above substomatal chambers (Fig. 148).

In paradermal sections the pinnules are seen as deeply lobed and broadly attached to the adaxial side of the penultimate pinna rachis. Like the pinnules of *B. forensis*, the pinnules of *B. tridentata* show a

range in size and shape; therefore, the term pinnule will be used for the laminar structures that are attached to the penultimate pinna rachis.

Lengths and widths of pinnules ranged from 8.0 mm to 11 mm or more and from 4.0 mm to 6.0 mm respectively. Venation of the pinnules is open, dichotomous with alternately produced lateral veins arising from the midvein. The lobes of the pinnules are separated by sinuses, some of which are rather deep. Because of this, a particular lobe separated by deep sinuses ma look like an individual pinnule (Figs. 143, 145).

A lateral vein from the pinnule midvein may dichotomize near the base of a rounded pinnule lobe. As one traces the resulting veins towards the margin of the pinnule lobe the veins may dichotomize once or twice. A lateral vein may also transverse the middle of a long pinnule lobe or a short rounded pinnule lobe and produce laterals in a pseudo-monopodial branching pattern. These laterals also dichotomize towards the edge of the pinnule lobe (Figs. 143, 145). The epidermal cells have wavy walls and are 76.8 to 96.0 μm in length and 38.4 to 44.8 μm in width. The long axes of the cells are oriented parallel to the veins. Stomata (44.8 μm to 41.2 μm in length) are also oriented with their axes parallel to the veins and lack subtending subsidary cells (type 1) (Fig. 144). Mesophyll cells are usually poorly preserved and appear as illustrated in Fig. 146.

DISCUSSION

Comparison: *Botryopteris forensis* and *Botryopteris tridentata*

Vegetative features

Upon examining the reconstruction of *B. forensis* (text fig. 1), the reader will observe that the pinnules are lobed and broadly attached to the penultimate pinna rachis. The pinnules of *B. tridentata* are also lobed and broadly attached.

As characterized by Arnold (1947), the pinnules assigned to the form genus *Sphenopteris* are lobed, contracted at their base, and often attached by a short stalk. He also characterized pinnules assigned to the form species *Mariopteris* as being coriaceous, lobed or unlobed, and broadly attached or slightly constricted at their bases. The basal pinnules of the latter are distinctly larger than the others and are two-lobed.

After comparing Arnold's characterizations of the two form genera, *Sphenopteris* and *Mariopteris*, two obvious differences can be noted. 1) *Sphenopteris* pinnules are contracted at their bases, while *Mariopteris* pinnules are broadly attached or slightly constricted at their bases. 2) The basal pinnules of *Mariopteris* are distinctly two-lobed. It is because the pinnules of *B. forensis* and *B. tridentata* do not show the basal lobing, characteristic of the basal pinnules of *Mariopteris*, that I assign both of the above to the form genus *Sphenopteris*.

One of the major results of this study is a better understanding of the detailed vegetative structure of *B. forensis* and *B. tridentata*. The

following are lists of the characteristics of the two species based on information gained from this study and other sources, where noted.

Botryopteris forensis	*Botryopteris tridentata*
Foliar members	
1. Diameters ranging from 1.0 mm to 8.0 mm	1. Diameters ranging from 0.25 mm to 6.0 mm
2. Shape; typically with an adaxial groove and a rounded abaxial face	2. D-shaped
3. Orders of attached petioles; three	3. Orders of attached petioles; three
4. Epidermal cells; 35 to 50 µm along one side (Mamay and Andrews, 1950)	4. Epidermal cells; up to 75 µm wide (Phillips, 1961)
5. Outer cortex; typically zoned	5. Outer cortex; homogenous
6. Vascular bundle; typically omega-shaped, though somewhat trident-shaped in the base of the rhizome attached petiole	6. Vascular bundle; trident-shaped
7. Metaxylem pitting; multiseriate reticulate to elliptical to circular bordered pitting	7. Metaxylem pitting; multiseriate reticulate to circular bordered pitting
8. Pinna and plantlet trace; similar to each other	8. Pinna and plantlet trace; different from each other
9. Replacement of tracheids emitted as a trace by an extension from the median arm	9. Replacement of tracheids emitted as a trace by an extension from the median (penultimate pinna rachis) as well as by a diagonal extension of tracheids across the adaxial face of the parent strand
10. Position of the plantlet with respect to the parent foliar member; lateral	10. Position of the plantlet with respect to the parent foliar member; lateral

Botryopteris forensis	*Botryopteris tridentata*
Plantlets	
1. Stem diameters ranging from 3.5 mm to 4.7 mm (Phillips, 1961)	1. Stem diameters ranging from from 2.6 mm to 5.0 mm
2. Stem length; up to 6.4 cm (Phillips, 1961)	2. Stem length; ranging from 1.1 cm to 2.44 cm
3. Stem stele diameter; ranging from 1.1 mm to 1.5 mm (Phillips, 1961)	3. Stem stele diameter; ranging from 1.0 mm to 1.5 mm x 1.0 mm
4. Stem stele histology; solid protostele and mesarch with metaxylem pitting of multiseriate reticulate	4. Steme stele histology; medullated protostele and mesarch with metaxylem pitting of multiseriate scalariform to reticulate
5. Epidermis of stem; differs little from the underlying cortical cells	5. Epidermis of stem; differs little from the underlying cortical cells
6. Hairs; multicellular and uniseriate though attached to multicellular hair bases	6. Hairs; multicellular and and uniseriate though attached to multicellular hair bases
7. Number of decurrent groups of protoxylem associated with incipient petiole trace formation; two	7. Number of decurrent groups of protoxylem associated with incipient petiole trace formation; one
8. Phyllotaxy; 2/5	8. Phyllotaxy; 1/3 to 2/5
Roots	
1. Diameters up to .9 mm (Mamay and Andrews, 1950)	1. Diameters up to .8 mm (Phillips, 1961)
2. Origin from stem; endogenous	2. Origin from stem; endogenous
3. Lateral root branching; endogenously	3. Lateral root branching; pseudomonopodially or endogenously
4. Orientation of the lateral root strand with respect to the parent root strand; perpendicular	4. Orientation of the lateral root strand with respect to the parent root strand; perpendicular

Botryopteris forensis	*Botryopteris tridentata*
Roots (continued)	
5. Root stele; diarch	5. Root stele; diarch
6. Metaxylem pitting; multiseriate reticulate to elliptical bordered	6. Metaxylem pitting; multiseriate reticulate to elliptical bordered
7. Outer cortex; thin-walled	7. Outer cortex; thin or thick-walled
8. Root hairs; none observed	8. Root hairs; none observed

When making comparisons between the two species of *Botryopteris*, characteristics of the petiole, such as the shape of the petiole (xs), the shape of the petiole strand, histology of the cortex, size of the epidermal cells with respect to the immediately underlying cortical cells, and details of lateral trace formation (plantlet and pinna) have proven to be most useful. In conjunction with the former characteristics, plantlet characteristics, origin and development of the plantlet trace, plantlet orientation on the parent petiole, and the type of stem stele also seem to be distinctive. When all of their characteristics are taken into consideration, one can see that they differ for the two species to such a degree as to leave no doubt that *B. forensis* and *B. tridentata* are distinctive phylogenetic entities and not ontogenetic variants. This conclusion is fortified by the fact that the species characteristics are constant for many specimens.

Fertile Material of *Botryopteris forensis*

The structure of the fertile material (sporangia) is known for *B. antiqua*. Most recently, Galtier (1967) redescribed the French

material of *B. antiqua* and concluded that their sporangia appeared more specialized (less primitive) than those of *B. globosa*.

The two fructification species of *Botryopteris*, *B. forensis* and *B. globosa*, differ in spore ornamentation, though not in sporangial morphology or pinna anatomy (Phillips and Rosso, 1970). *B. globosa* has so far been found only at Iowa localities, while *B. forensis* is known in North America from Kansas and Illinois localities (Phillips, 1970). Phillips and Rosso also noted that the Kansas specimens exhibit the greatest variation in spore exine morphology. Fructification specimens used in this study (Kansas specimens) possess spores (some of which were still in tetrads) which are predominately psilate (specimen 38-b) to scabrate, verrucate-vermiculate to occasionally rugulate (specimens 38-a, 38-f) and verrucate-vermiculate to densely rugulate (specimen 537). Differences in the predominate ornamentation of spores of each fructification may reflect a stage of maturity. Psilate spores are interpreted here as being the least mature because they lack ornamentation and occur occasionally in tetrads (specimen 38-b). On the other hand, densely rugulate spores are considered to be the most mature. Spores of specimens 38-a, 38-f are somewhat intermediate in the degree and kind of ornamentation.

In light of the fact that spores of fructification specimens from the West Mineral, Kansas locality, show such a great diversity in spore ornamentation, it is suggested here that *B. globosa* (a species based on the single character of spore ornamentation) should be placed into synonymy. The name applied to the fructifications should be *Botryopteris forensis*.

Development of the Fructification

While investigating the structure of the six fructifications for this study, it became evident that certain developmental stages were present. In this regard specimen 265 is unique in that the basal main laterals are two-ranked, expanded and possess attached sporangia (both sterile and fertile) (Figs. 98, 99), while the apical (distal) laterals that surround the axis of the fructification, are compact (not expanded) and possess no sporangia (Figs. 100, 101). Trace formation to main laterals from the parent axis is distichous and quadraseriate.

A possible explanation for the unusual morphology of this specimen is that expansion of laterals and the main axis was under the influence of the sporangia; where no sporangia develop the laterals and main axis does not expand.

Peterson and Cutter (1969) explained that the peduncle subtending the sporangial area of *Ophioglossum petiolatum* elongated considerably, which brought the sporangial area above the sterile segment. Removal of the sterile segment of the frond had no effect on peduncle elongation, nor did removal of the sterile tip or any portion of the sporangial area, as long as a few sporangia were left. When auxins are applied to excised sporangial areas the peduncle is induced to elongate. The auxin stimulated peduncle cells to elongate without maintaining the mitotic activity of the intercalary meristem. Aborted spikes lacked sporangia and an intercalary meristem and failed to elongate.

Based on observations of the kind presented above it seems possible that the fructification of *B. forensis* could have been influenced by a similar sporangia-produced auxin. Subsequent development

(expansion) of the branches could have been dependent on sporangial auxin being produced. Such a final stage is exhibited by specimen 335, which is fully expanded, has no sporangia (abscised) and developed vascular strands which extend into the parenchymatous sporangia attachment area (Figs. 102, 103).

Another interesting puzzle derives from the sterile and fertile sporangia. It is assumed that initiation of sporangia (both types) was identical and only later in development did distinction between the two types become evident. The sterile sporangia (if they occur) are restricted to the periphery of the fructifications and on the most distal branches. Steeves and Sussex (1972) working with sporelings of *Todea* report that they were able to grow them in culture containing very high concentrations of sucrose. When this was done, the sporelings developed adult-type leaves and in many cases initiated sporangia, which produced viable spores. If excised leaves were exposed to the same concentration of sugar, they also initiated sporangia, but the development of the sporogenous tissue was arrested at the spore-mother cell stage.

From the above experiments, it was suggested that the development of spores or division of spore-mother cells was under the influence of hormone(s) produced outside the leaf and transported to the spore-mother cells initiating their division.

The presence of such hormonal gradients in *Botryopteris forensis* could explain the development of both sterile and fertile sporangia in its fructification. One can speculate that in order for a sporangium in a fructification to develop spores, the spore-mother cells had to undergo division. They did so only after a threshold in the concentration of the hormone was reached. If the concentration level was not reached the

spore-mother cells would remain as undivided parenchyma cells, which often occur in sterile sporangia of *B. forensis*. If such a threshold occurred in *Botryopteris* fructifications, it could account for the distinct delimitation between sterile and fertile sporangia. The division of spore-mother cells and the possible influence of sporangia on the expansion of the fertile frond are regarded as two separate phenomena; thus, sterile sporangia as well as fertile sporangia could cause frond expansion.

Relationships of *Botryopteris* to Extant Ferns

Relationship between the genus *Botryopteris* and the Ophioglossales has been suggested by Renault (1875), Scott (1908, 1920) and with the Osmundaceae by Scott (1908, 1910, 1920), Pelourde (1910), Galtier (1967) and Phillips (1965). I believe that the relationship of the Botryopteridaceae with the Ophioglossales is the most logical choice. Scalariform lateral pitting is the most common type in the ferns (Bancroft, 1911; Deurden, 1940; Eames, 1936; After White, 1963). Bordered circular pits do occur in the Ophioglossales (Eames, 1936) and the Marattiaceae (Bierhorst, 1960). Based on differences in pitting and sporangial morphology close relationship of the genus *Botryopteris* with the leptosporangiate ferns (excluding the Osmundaceae) is very unlikely.

Fossil evidence for the Osmundaceae extends back unquestionably to the upper Permian (Miller, 1971). The latter writes:

> "Thus, neither of the two species of *Grammatopteris* [from the lower Permian of France and West Germany] can be considered the direct ancestor of the Osmundaceae. However, these ferns are closer to the early members of the Osmundaceae than any other ancient fern."

and that:

> *Catenopteris* [Upper Pennsylvanian of Illinois] must be considered in the same category as *Grammatopteris*; rather than being the actual progenitor, it probably represents a larger group from which the Osmundaceae might have evolved."

Based on the above statements by Miller, it is probable that the Osmundaceae is related to coenopterid ferns other than the Botryopteridaceae.

The Marattiales also have a well documented fossil record, which extends back to the Middle Carboniferous. Members of this order have eusporangia grouped into elongate sori or synangia on the adaxial surface of the frond, large simple pinnate to tripinnate fronds, and stems with complex dictyostelic vascular cylinders. Based on the above characters the extant members of the Marattiales can be related to the Paleozoic members and not to the Botryopteridaceae.

Stems of *Catenopteris* and *Grammatopteris*, as well as members of the Osmundaceae show consistently a compact spiral phyllotaxy. The phyllotaxy of Botryopteridaceae is either 1/3 or 2/5 and is not in a compact spiral; thus, there is an additional difference in phyllotaxy between these two groups.

By the process of elimination, relationships of *Botryopteris* with the leptosporangiate ferns, the Osmundaceae, and the Marattiaceae seem to be excluded. This leaves the extant Ophioglossales, which has undisputable fossil representation extending back to the Paleocene (Chandrasekharam, 1972). The following is a list of comparisons between the Botryopteridaceae and the Ophioglossales.

Botryopteris	*Ophioglossales*
Stems (rhizome)	
1. Habit; horizontal with an erect apex (Phillips, 1974)	1. Commonly short and erect (*Botrychium* and *Ophioglossum*) or creeping (*Helminthostachys*)
2. Stele; solid protostele (mesarch) (Rhizomes known in *B. antiqua, B. mucilaginosa* and *B. forensis*)	2. Ectophoic siphonostele (endarch and mesarch) Young sporeling protostelic and showing a transition stele with a mixed pith leading to a siphonostele (Lang, 1913)
3. Metaxylem; multiseriate reticulate to circular bordered pitted	3. Metaxylem; Subgenus *Eubotrychium* and *Ophioglossum*-reticulate to occasionally circular bordered *Helminthostachys*-tracheids with circular bordered pits
4. Secondary wood; none	4. Secondary wood; genus *Botrychium* (variable)
5. Branching; dichotomous (*B. mucilaginosa*) and unknown for *B. antiqua* and *B. forensis*	5. Branching dichotomous in some species of *Ophioglossum* (Petry, 1915); Lateral apices occur on rhizomes of *Helminthostachys* and *Botrychium* (Petry, 1915; Lang Lang, 1915; Gwynne-Vaughan, 1902; after Bierhorst, 1971).
Petioles (foliar members)	
1. Shape of trace (upper Carboniferous) elliptical *B. hirsuta, B. ramosa, B. mucilaginosa* C-shaped, D-shaped or (typically) trident-shaped *B. tridentata*	1. Shape of trace, single (most commonly) and C-shaped (basal region of the petiole) - *Botrychium, Helminthostachys* Subgenus *Euophioglossum*; double in Subgenus *Ophioderma* (Gerwirtz and Fahn, 1960)

Botryopteris	*Ophioglossales*
Petioles (foliar members) continued	
2. Metaxylem; elliptical, bordered pits predominate	2. Metaxylem; intermediate protoxylem of all three genera circular bordered. Last formed metaxylem uniformly circular bordered in *Botrychium* and *Helminthostachys*, but scalariformly bordered in *Ophioglossum* (Bierhorst, 1971)
3. Circinate vernation; hairy young tips	3. Vernation reported by Davenport (1878) in *Botrychium*; naked and hairy
4. Origin of lateral (pinna) trace from the petiole; marginal	4. Extramarginal to marginal (Nozu, 1954)
5. Phloem zones; adaxial and abaxial in *B. hirsuta, B. ramosa, B. tridentata* (Phillips, 1970)	5. Phloem zones; ectophloic (outer) (Ogura, 1972); Internal phloem observed by Chrysler (1910) in *Botrychium virginianum*
6. Shape of petiole; D-shaped *B. ramosa, B. tridentata* Grooved adaxial face and rounded abaxial face *B. hirsuta, B. forensis*	Shape of petiole; circular (Ogura, 1972)
7. Petiole-borne fertile spike	7. Fertile spike
8. Fertile spike (frond) branching; biseriate to quadraseriate	8. Fertile spike branching; biseriate
9. Sclerenchyma; fibers occur within stele of foliar members of *B. hirsuta* and *B. forensis*	9. Lack of sclerenchyma in plant body (Foster and Gifford, 1974)
Plantlets	
1. Occurrence; Lateral *B. hirsuta* *B. ramosa* *B. tridentata* *B. forensis*	1. Occurrence; In axils at bases of petioles of *B. lunaria*((Lang, 1913) and *Helminthostachys* (Gwynne-Vaughan, 1902)

Botryopteris	*Ophioglossales*
Plantlets (continued)	
2. Adaxial *B. renaulti*	2. From roots *Botrychium virginianum* and *Ophioglossum* (McVeigh, 1937)
3. Stele; solid protostele to a medullated protostele	3. Stele; medullated protostele (*Ophioglossum aitchison*) Vasisht (1928)
4. Metaxylem; see #3-Rhizome	4. Metaxylem; see #3-Rhizome
5. Plantlet borne on petioles; monophyllous or polyphyllous 2/5 or 1/3 phyllotaxy	5. Plantlet borne on petioles; monophyllous or polyphyllous loose spiral (Vasisht, 1928)
Roots	
1. Stele; diarch	1. Stele; monarch to octarch (Ogura, 1971)
2. Origin from stem; Endogenously, occasionally associated with petioles, but usually not and arising all around the stem. Often a profusion of roots at base of the plantlet	2. Origin from stem; endogenously, usually one root attached to stem near each leaf (Foster and Gifford, 1974). Often a profusion of roots at base of stem of *B. lunaria* (Lang, 1913)
3. Root branching; endogenously	3. Root branching; pseudomonopodially, if at all (Foster and Gifford, 1974)
4. Roots hairless	4. Roots hairless
Foliage	
1. *Sphenopteris* type Fleshy - *B. forensis* Thin - *B. tridentata*	1. *Botrychium*, Subgenus *Sceptridium*, large, ternately decompound and fleshy. Subgenus *Eubotychium*, sterile blade pinnate or palmate, glabrous and fleshy Subgenus *Osmundopteris*, sterile blade large, deltoid, much divided, usually thin in texture, and sometimes hairy, *Helminthostachys*, palmately pinnate

Botryopteris

Foliage (continued)

2. Venation; open dichotomous

3. Epidermal cell walls
   straight - *B. forensis*
   wavy- *B. tridentata*

4. Stomatal placement
   B. forensis (Renault, 1896), upper surface
   B. tridentata, lower surface

5. Type of stomata
   Type-1, which also occur in the Marattiaceae, Osmundaceae and the genera, *Thyrsopteris*, *Culcita* (Dicksoniaceae) (Thurston, 1967, 1970)

Sporangia - *B. forensis*

1. Size, up to 1.1 mm in diameter and 2.0 mm length

2. Vascular bundle extending to the base of the sporangia

3. Well developed annuli

4. Sporangia spore count
   Iowa specimen - 1,680
   Illinois specimen - 1,457-2,110 (Phillips, 1970)

5. Dehiscence
   Longitudinal

Ophioglossales

1. *Ophioglossum*, subgenus *Ophioderma*, strap-shaped
   Subgenus *Euophioglossum*, simple (Nozu, 1954)

2. Venation; open dichotomous or reticulate

3. Epidermal cell walls wavy, *O. vulgatum*

4. Stomatal placement on the adaxial and abaxial or just abaxial.

5. Type of stomata
   Type-1 (the simplest [illegible] or type, which is the result of a single division of a stoma mother cell) (Thurston, 1967, 19[illegible])

1. Size, diameters of 0.5 mm to 1.5 mm (*Botrychium* sp.) (Chandrasekharam, 1972)

2. Vascular bundle extending to the base of the sporangia

3. In *Botrychium* the sporangial wall at maturity is composed of 4 to 7 inner layers and an outer layer of cells with thickened inner and anticlinal walls (Bierhorst, 1971)

4. Sporangia spore count
   Botrychium 1,500 - 2,000 (Christensen, 1967)

5. Dehiscence
   Helminthostachys - vertical
   Botrychium - transverse
   (Christensen, 1967)

Botryopteris	*Ophioglossales*
Sporangia - *B. forensis* continued	
6. Spore ornamentation *B. forensis*, psilate to densely rugulate (21.96 µm to 51.24 µm) Specimen 537	6. Spore ornamentation Pitted, pocked or tuberculate, i.e., verrucose, 20 µm to 50 µm (McVeigh, 1935)
7. Tapetum-plasmodial type originating from potentially sporogenous cells (Galtier, 1971)	7. Tapetum-plasmodial type Tapetal organization of *Botrychium ternatum* similar to *Botryopteris forensis* (Galtier, 1971). In some cases (*Ophioglossum fibrosum*) the transition between the tapetum and the outer layer of sporogenous cells is so complete that it is difficult to delimit one from the other (Maheshwari and Singh, 1934)
Distribution	
1. *Botryopteris* is known from localities in England, France, Germany, U.S.S.R., and North America	*Helminthostachys*, Asia-Polynesia *Botrychium*, Arctic and Northern temperate zones, a few in the tropics and Antarctic *Ophioglossum*, world wide, except at the poles (after Christensen, 1967; Clausen, 1938)

Pitting (circular-bordered), branching and development of the fertile frond, and sporangial anatomy are regarded here as being the significant characters of similarity between the Botryopteridaceae and the Ophioglossales.

Wagner and Wagner (1976) report that approximately 20% of living fern genera show more or less extreme dimorphism between the sporophyll and the trophophyll. Thus, the character of frond dimorphism alone is probably of little phylogenetic value, but when combined with details

of branching and development of the frond, it may be significant. In regards to sporangial anatomy, the plasmodial type of tapetum occurs in the Psilotales, Ophioglossales and in Equisetum (Foster and Gifford, 1974); thus, among the extant ferns this type of tapetal organization appears to be restricted to the Ophioglossales. The plasmodial type of tapetum was suggested to occur in sporangia of *Botryopteris forensis* by Galtier (1971). Scott (1920) reported that sporangial pedicels which are traversed up to the base of the capsule by a vascular bundle are rare among recent ferns, though approached in *Helminthostachys* and *Botrychium*. A vascular bundle in the base of *Botryopteris forensis* sporangia was also reported by Galtier (1971). In combination the three above mentioned characteristics, pitting, development and branching of the fertile frond, and sporangial anatomy, appear to be unique among the Ophioglossales, though being characters in common between the Botryopteridaceae and Ophioglossales.

The branching of the fertile frond and the shape of the vascular strand of the petiole of *Botryopteris* present the most serious objections to accepting the hypothesis of a phylogenetic relationship between *Botryopteris* and the Ophioglossales.

This objection seems less important when one remembers that c-shaped strands *do* occur in the bases of the main laterals and in the more distal division of the laterals of the fertile frond of *Botryopteris*. One might suggest that the trend for the production of c-shaped traces has made its appearance in the Botryopteridaceae by Pennsylvanian times.

Quadraseriate and biserate branching, a conspicuous feature of *Botryopteris* is also reflected in certain instances in the Ophioglossales. Nishida (1957) explained the divisions of the strand in the petiole of

most Ophioglossales as representing the result of two ancient dichotomies, which were oriented perpendicular to each other. He illustrated a series of sections from a petiole, *Sceptridium ternatum*, in which the trace is initially c-shaped then divides to form two c-shaped traces, which face each other and each of which subsequently supplies a separate division of the normally single, undivided sterile frond. The uniqueness of this specimen is that it shows a pattern of fertile frond strand-division identical to that at the base of the main laterals of the fertile frond of *Botryopteris forensis*.

Another objection to accepting the proposed hypothesis is that the fertile spike of the Ophioglossales is commonly oriented adaxially on the parent petiole. Chrysler (1925) described a specimen of *Botrychium lanuginosum* Wall., which had a fertile spike in a position comparable to a sterile pinna (not in an adaxial position, but in a lateral position). He also described (1926) and diagrammed five methods of insertion of fertile spikes in abnormal specimens of *Botrychium obliquum*. In the first method of insertion, the fertile spike forked equally part way up its stalk. In the second, a pair of spikes, of equal development arose right and left at the same level. The third, a pair of spikes as in the preceeding group, but an additional spike arises further up. The fourth method occurs when there is a normal spike with a smaller additional one inserted higher up; finally the fifth type, with a normal spike, and a pair of smaller ones inserted further up. Chrysler reported that the fourth type occurred more frequently than the others and probably includes two classes, cases where the upper (smaller) spike represented one pinna and where it represented two fused pinna, as shown by the single or double vascular supply. He further comments

that the strand supplying such a spike may arise from one edge of the c-shaped leaf trace, which is the method of trace formation in *Botryopteris*, or a strand may arise from each edge of the trace.

The occurrence of sporangia on ordinarily sterile pinnae is known among species of *Botrychium* (Chrysler, 1926; Bower, 1923). From the above information, it can be stated that the fertile spike and the sterile frond are homologous structures. I believe that the fertile spike and the sterile frond, which occur in the Ophioglossales represent as a whole the equivalent of a quadriseriate pair of laterals, which occur on the fertile axis of *Botryopteris forensis*.

Based on any one similarity between *Botryopteris* and the Ophioglossales one can not make phylogenetic conclusions. Based on the total number of similarities, however, I suggest that *Botryopteris* is the Paleozoic representative of an ophioglossalian line. This conclusion is, at best, tentative and can only be substantiated by further revelations from the fossil record.

Figs. 1 - 6

Fig. 1 Transverse section of two petioles showing the left petiole with the typical zoned cortex of *B. forensis* and the right petiole with a more atypical "homogeneous" (non-zoned) cortex. Note the omega-shaped vascular strands. C.B. 552 J top #3. Bar/3.2 mm.

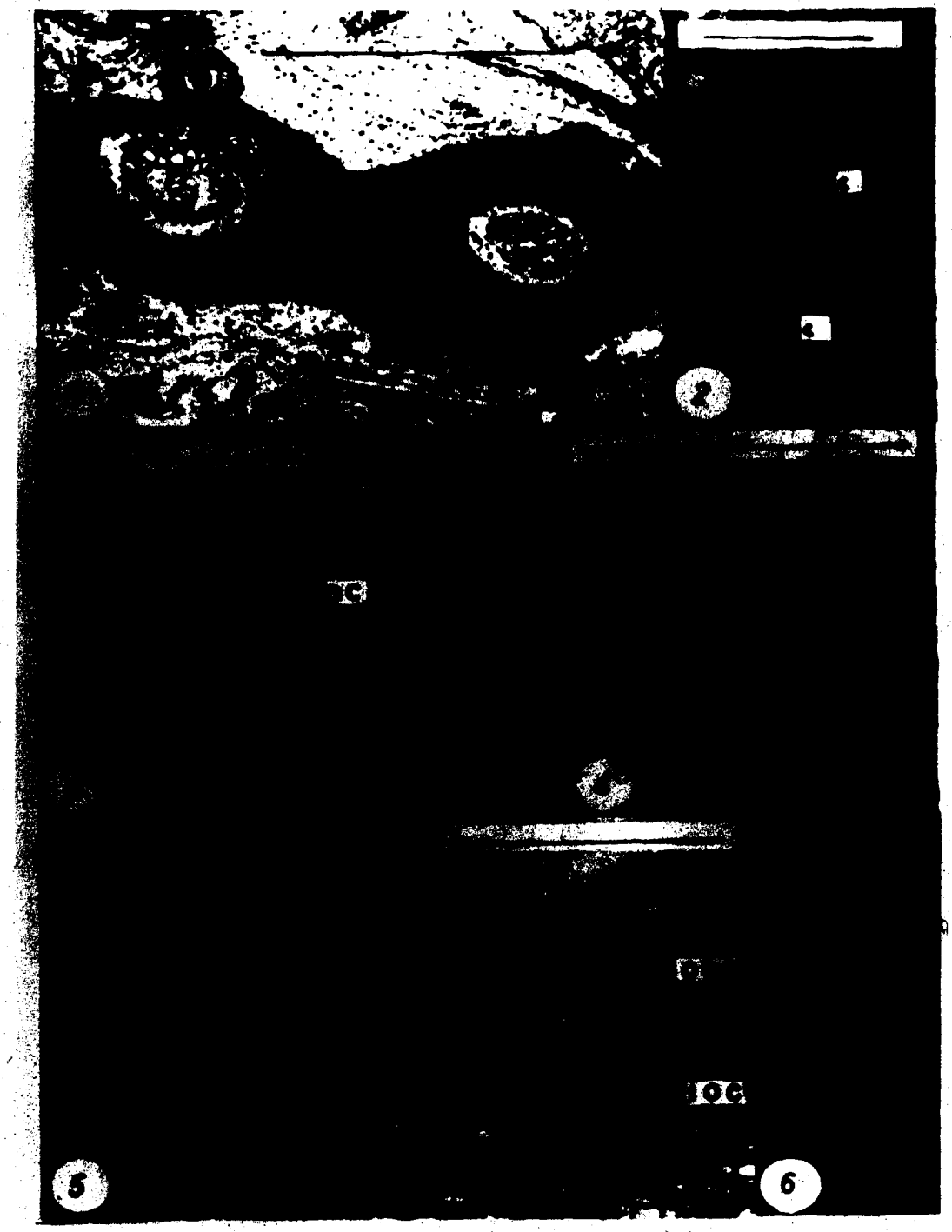
Fig. 2. "Equisetiform hairs", Renault (1896). Note the convoluted suture of the indicated cells. C.B. 265 G bottom #60. Bar/192 µm.

Fig. 3. Transverse section of a petiole of *B. forensis* showing the zonation of the outer cortex (ioc/inner outer cortex, ooc/outer outer cortex). C.B. belonging to slide #2700. Department of Botany, University of Alberta, Edmonton, Alberta, Canada.

Fig. 4. Metaxylem of a petiole of *B. forensis* showing elliptical to circular bordered pits. C.B. 461 H top. Bar/147.2 µm.

Fig. 5. Longitudinal section of petiole of *B. forensis* showing the zonation of the outer cortex (ioc/inner outer cortex, ooc/outer outer cortex). C.B. 552 C bottom #2. Bar/1188 µm.

Fig. 6. Same as Fig. 4.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Figs. 7 - 12. *Botryopteris forensis.*

Fig. 7. Transverse section of a petiole producing a plantlet trace. (Pt/plantlet trace). C.B. 577 F bottom #26. Bar 840 µm.

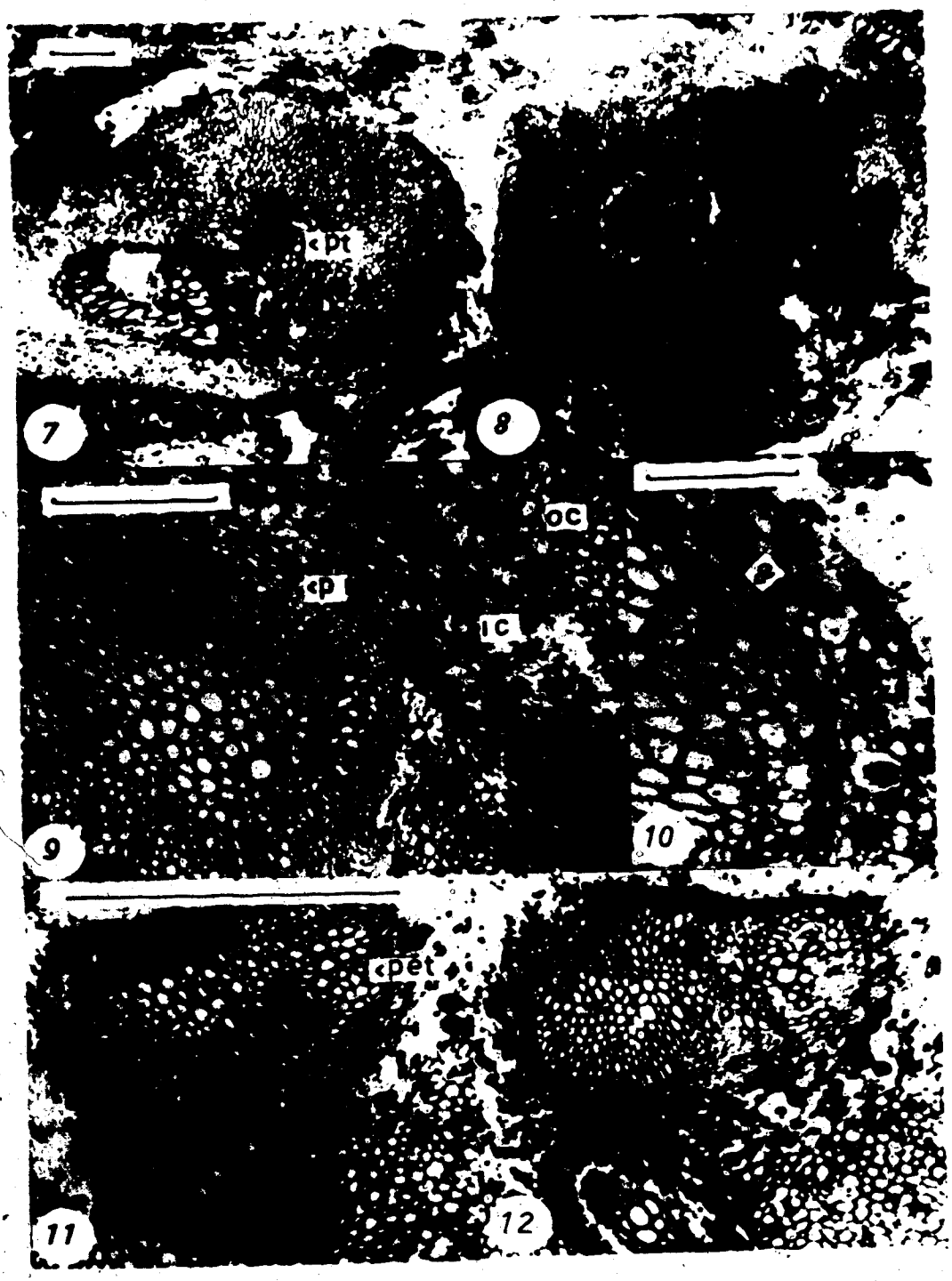
Fig. 8. Transverse section of a plantlet (distal to Fig. 7). Note the change in the diameter of the plantlet stele (compare with Fig. 7). C.B. 577 G top #2. Bar/same as Fig. 7.

Fig. 9. Transverse section of plantlet showing histology. (p/phloem, ic/inner cortex, oc/outer cortex). C.B. 577 G top #7. Bar/352 µm.

Fig. 10. Transverse section of plantlet showing histology. (e/endodermis). C.B. 577 G top #13. Bar/160 µm.

Fig. 11. Transverse section of plantlet showing petiole trace formation. Initial stage of trace formation showing elongation of xylem segment. C.B. 577 G top #28. Bar/1080 µm.

Fig. 12. Transverse section of plantlet showing petiole trace formation (distal to Fig. 11). Petiole trace of this level is attached to the stem xylem at its middle adaxial region. C.B. 577 G top #31. Bar/same as Fig. 11.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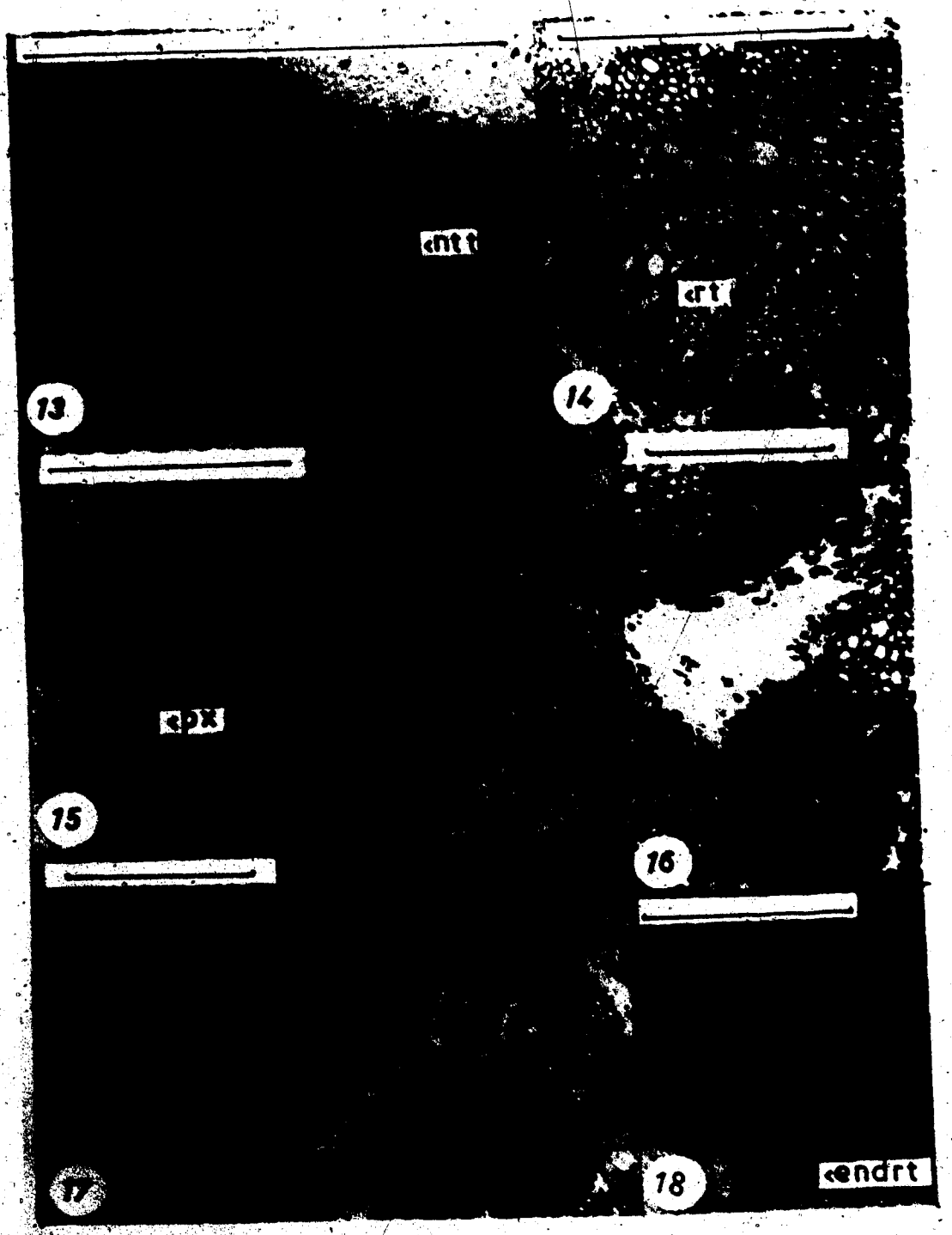
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Figs. 13 - 18. *Botryopteris forensis.*

Fig. 13. Transverse section of plantlet showing petiole trace formation. The petiole trace is free from stem xylem and has developed non-tracheary tissue. (ntt/non-tracheary tissue). C.B. 577 G top #33. Bar/1320 µm.

Fig. 14. Transverse section of plantlet showing root trace formation (distal to Fig. 13). Note that the root trace is partially detached from the stem xylem. (rt/root trace). C.B. 577 G top #14. Bar/768 µm.

Fig. 15. Transverse section of plantlet showing a root trace with a single protoxylem group (px/protoxylem). C.B. 577 G top #14. Bar/153.6 µm.

Fig. 16. Transverse section of plantlet (distal to Figs 14, 15) showing a diarch root trace detached from the stem xylem and surrounded by its own distinct cortex. C.B. 577 G top #24. Bar/672.0 µm.

Fig. 17. Transverse section of typical *B. forensis* Diarch roots. C.B. 577 G top #13. Bar/768 µm.

Fig. 18. Longitudinal section of parent root and a transverse section of an attached endogenous lateral root. (endrt/endogenous root). C.B. 577 G top #16. Bar/600 µm.

Figs. 19 - 26. *Botryopteris forensis.*

Fig. 19. Transverse section of parent petiole and penultimate pinna rachis. Note the homogeneous appearance in the cortex of the latter. C.B. 328 G top #83. Bar/1824 µm.

Fig. 20. Transverse section of the penultimate pinna rachis showing the typical two-zoned cortex. Note the prominent adaxial ridge. (ppr/penultimate pinna rachis, adr/adaxial ridge). C.B. 328 G top #10. Bar/1440 µm.

Fig. 21. Transverse section of the penultimate pinna strand showing a stage in the formation of a pinnate trace. (pt/pinnate trace, la/left arm, ma/middle arm, ra/right arm). C.B. 328 E top #2. Bar 326.4 µm.

Fig. 22. Transverse section of pinnule showing the pinnule blade. Note the lack of a distinct palisade layer. (pb/pinnule blade). C.B. 328 G top #1. Bar/232.5 µm.

Fig. 23. Transverse section of a pinnule near its base showing the pinnule blade arched over the midvein and the attachment of the pinnule to the penultimate pinna rachis. (p/pinnule, ppr/penultimate pinna rachis). C.B. 273 F top #44. Bar/1680 µm.

Fig. 24 - 25. Paradermal sections of pinnules showing epidermal cells with straight walls. (ec/epidermal cells). C.B. 328 D #22. Bar/82.45 µm (Fig. 24), Bar/315.25 µm (Fig. 25).

Fig. 26. Paradermal section of pinnule showing mesophyll tissue. (mc/mesophyll cells). C.B. 328 D #17. Bar/51.4 µm.


PPr
26

Figs. 27 - 32. *Botryopteris forensis.*

Fig. 27. Paradermal section of a portion of a frond showing pinnules and the penultimate pinna rachis. Note the short round pinnule lobes and the long pinnule lobes. Note, also, the venation of the long pinnule lobe. (p/pinnule, ppr/penultimate pinna rachis). C.B. 328 #26. Bar/2184 µm.

Fig. 28. Paradermal section of a pinnule. Note venation pattern of the pinnule lobes. C.B. 328 D #17. Bar/960 µm.

Fig. 29. Paradermal section of an attached pinnule to the penultimate pinna rachis. Note the short, rounded pinnule lobe and its venation. (pl/pinnule lobe, p/pinnule, ppr/penultimate pinna rachis). C.B. 328 H #60. Bar/3240 µm.

Figs. 30 - 31. Paradermal sections of a pinnule showing the shape and venation of the pinnule lobes. (p/pinnule). C.B. 328 D #22 and 24. Bar/1968 µm (Fig. 30), Bar/1728 µm (Fig. 31).

Fig. 32. Paradermal section of pinnule blade showing epidermal cells. (ec/epidermal cells). C.B. 328 D #22. Bar/same as Fig. 24.


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Figs. 33 - 42. *Botryopteris forensis.*

Fig. 33. Transverse section of a parent petiole strand showing an early stage of trace formation to the fertile axis. Note the lateral extension of tracheids from the middle arm. (le/lateral extension). C.B. 38-a G bottom #65. Bar/1080 μm.

Fig. 34. Transverse section of a parent petiole strand (distal to Fig. 33) showing trace formation. Note the further extension of tracheids from the middle arm. C.B. 38-a G bottom #[illegible]. Bar/ same as Fig. 33.

Fig. 35. Transverse section of a parent petiole strand (distal to Fig. 34) showing trace formation. Note the fertile axis trace departed from the parent strand and the position of the smaller diameter trachedis. (ft/fertile axis trace, st/small diameter tracheids). C.B. 38-a G bottom #46. Bar/same as Fig. 33.

Fig. 36. Transverse section of a parent petiole strand (distal to Fig. 35) showing trace formation. Note the position of the smaller diameter tracheids. (st/smaller tracheids). C.B. 38-a G bottom #29. Bar/same as Fig. 33.

Fig. 37. Transverse section of the fertile axis strand (distal to Fig. 36). Note the left arm developed due to the formation of an adaxial extension of the non-tracheary tissue. (nnt/non-tracheary tissue). C.B. 38-a G bottom #1. Bar/same as Fig. 33.

Fig. 38. Transverse section of a fertile axis strand at a basal level, near its attachment point with a parent petiole. (fas/fertile axis strand). C.B. 335 E bottom #55½. Bar/same as Fig. 33.

Fig. 39. Transverse section of a fertile axis strand (distal to Fig. 38). Note the development of the non-tracheary tissue. (nnt/non-tracheary tissue). C.B. 335 E bottom #60. Bar/600 μm.

Fig. 40. Transverse section of a fertile axis strand (distal to Fig. 39). Note the non-tracheary tissue adaxially extended to form the left arm. C.B. 335 #63. Bar/same as Fig. 39.

Fig. 41. Transverse section of a fertile axis strand. Note the tracheid extension from the indicated positions. (le/lateral extension). C.B. 335 E top #51. Bar/768 μm.

Fig. 42. Transverse section of a fertile axis strand (distal to Fig. 41). Note the tracheid extensions. (t/trace). C.B. 335 E top #48. Bar/same as Fig. 41.


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Figs. 43 - 50. *Botryopteris forensis.*

Fig. 43. Transverse section of a fertile axis strand (distal to Fig. 42). Note the new lateral arms are detached from the median arm and the lateral traces just beginning to separate from the parent strand. C.B. 335 E top #40. Bar/840 µm.

Fig. 44. Transverse section of a fertile axis strand (distal to Fig. 43). Note the new lateral arms and the detached lateral c-shaped traces. C.B. 335 E top #26. Bar/same as Fig. 43.

Fig. 45. Transverse section of a fertile axis strand. Note the attached trace and the newly developed lateral arm. (t/trace, la/lateral arm). C.B. 537 H top #83. Bar/same as Fig. 43.

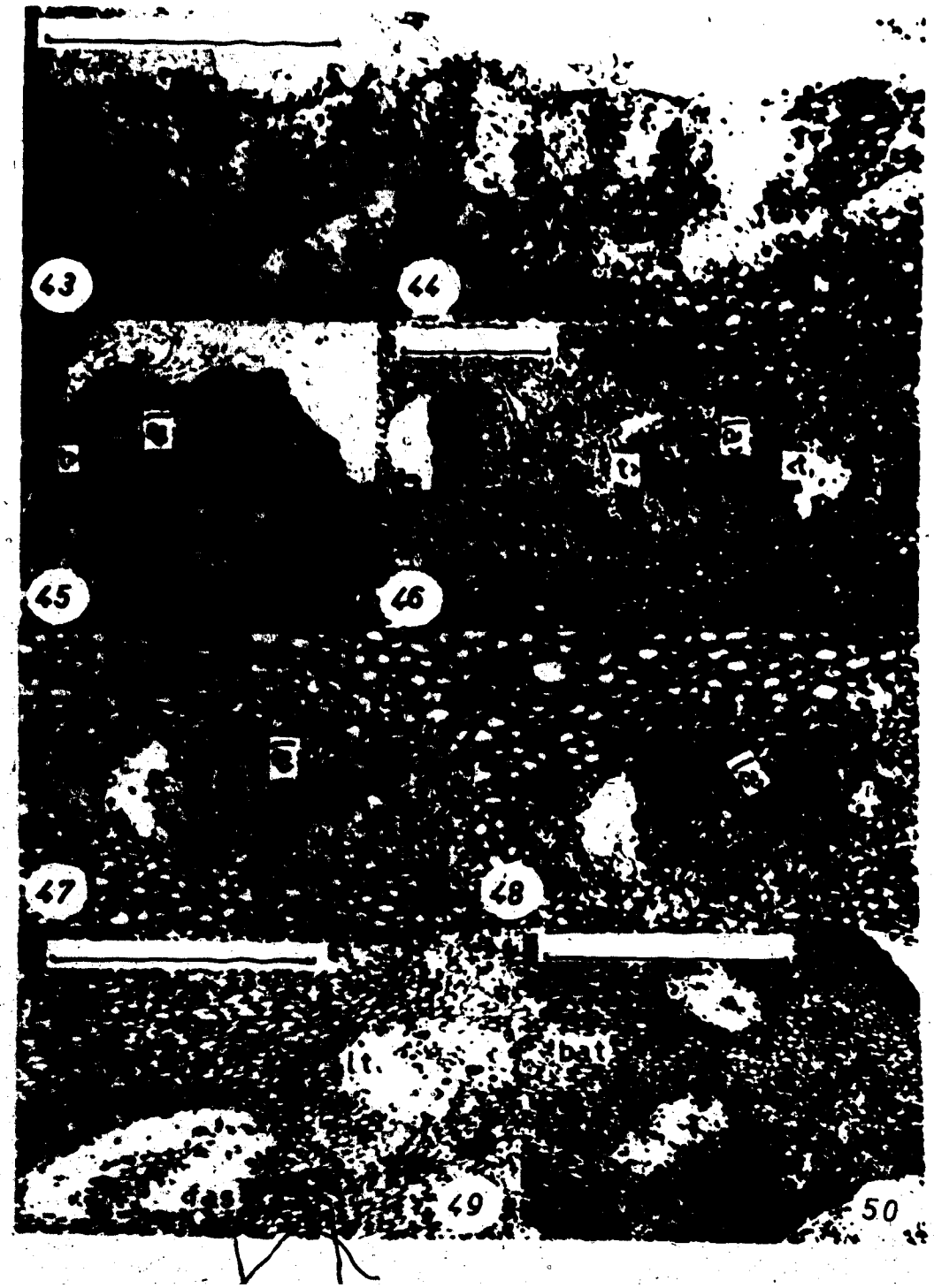
Fig. 46. Transverse section of a fertile axis strand. Note the attached c-shaped traces and the new lateral arm. (la/lateral arm, t/trace). C.B. 537 H bottom #74. Bar/648 µm.

Fig. 47. Transverse section of a fertile axis strand. Note the incipient lateral arm. (la/lateral arm). C.B. 537 H bottom #31. Bar/same as Fig. 46.

Fig. 48. Transverse section of a fertile axis strand (distal to Fig. 47). Note the small lateral arm. (la/lateral arm). C.B. 537 H bottom #25. Bar/same as Fig. 46.

Fig. 49. Transverse section of a fertile axis. Note the fertile axis strand and the two lateral traces, each of which will supply a member of the quadraseriate pair. (fas/fertile axis strand, lt/lateral trace). C.B. 38-a H top #70. Bar/1140 µm.

Fig. 50. Transverse section of a fertile axis (distal to Fig. 49) showing the traces to the basal appendages. (bat/basal appendage trace). C.B. 38-a H top #87. Bar/1824 µm.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Figs. 51 - 56. *Botryopteris forensis.*

Fig. 51. Transverse section of the fertile axis showing the attached basal appendages which branch in a biseriate manner. Note the quadraseriate pair of laterals is still in common cortical attachment with each other and the parent fertile axis. (ba/basal appendage). C.B. 38-a #93. Bar/1 cm.

Fig. 52. Transverse section of the fertile axis and the quadraseriate pair of laterals (distal to Fig. 51). Note each member of the pair is separate from each other and the parent axis. The member on the right will be used to illustrate details of its branching. (fa/fertile axis, rlm/right lateral member). C.B. 38-a H top #100. Bar/3 mm.

Fig. 53. Transverse section of the right lateral member (distal to Fig. 52). The parent strand has given rise to a trace to the left which has divided into two and a trace to the right. Each trace to the right and left will supply a quadraseriate pair of laterals. (lt/left trace, ps/parent strand, rt/right trace). C.B. 38-a #100. Bar/1344 µm.

Fig. 54. Transverse section of the right lateral member (distal to Fig. 53) showing the parent strand and the traces to the left, each of which has divided into two. C.B. 38-a H top #10[illegible]. Bar/1728 µm.

Fig. 55. Transverse section of the right lateral member (parent axis) and the left quadraseriate pair (distal to Fig. 54). Note that one member of the left pair (lpm-2) is divided into two and appears to be borne by the other member (lpm-1). The right pair of quadraseriate laterals is still attached to the parent axis. (lpm-1/left pair member-1, lpm-2/left pair member-2, ps/parent strand, rpmt/right pair member traces). C.B. 38-a H top #119. Bar/2.8 mm.

Fig. 56. Transverse section of the right lateral pair and the left quadraseriate pair of laterals. Oblique longitudinal section of the right quadraseriate pair (distal to Fig. 55). Note lpm-2 is separate from lpm-1 and also that both rpm-1 and rpm-2 branch in a biseriate manner. (ps/parent strand, rpm-1/right pair member-1, rpm-2/right pair member-2). C.B. 38-a H bottom #117. Bar/3.5 mm.


52
51
53
54
55
56
rpm
psr

Figs. 57 - 62. *Botryopteris forensis.*

Fig. 57. Transverse section of an axis (a member of a quadraseriate pair) showing four strands (two traces to the right, one trace to the left and the parent strand). (lt/left trace, ps/parent strand, rt/right trace). C.B. 38-a H top #35. Bar/864 µm.

Fig. 58. Longitudinal section of fertile sporangia from fructification 38-a. Note sporangia are attached to a vascularized parenchymatous base. (va/vascular tissue). C.B. 38-a H top #45. Bar/950 µm.

Fig. 59. Transverse section of an axis (distal to Fig. 57) showing one of the right traces supplying a biseriately branched lateral appendage. C.B. 38-a top #21. Bar/same as Fig. 57.

Fig. 60. Transverse section of sterile sporangia. Note that the sterile sporangia have radially elongated wall cells and lack spores. (ssp/sterile sporangia). C.B. 38-a H top #55. Bar/same as Fig. 58.

Fig. 61. Transverse section of an axis (distal to Fig. 59). Note that the remaining right trace has divided into two and still within the cortex of parental axis. C.B. 38-a H top #10. Bar/same as Fig. 57.

Fig. 62. Oblique transverse section of fertile sporangia from fructification 38-a. Note the vascularized parenchymatous sporangial base and the longitudinal line of dehiscence of the indicated sporangia. (va/vascular tissue, d/dehiscence zone). C.B. 38-a H top #45. Bar/same as Fig. 58.


lt
ps
rt
va
57
58
var
ssp
59
60
61
va
62

Figs. 63 - 71. *Botryopteris forensis.*

Fig. 63. Transverse section of fructification 38-a. Note the lack of a sterile sporangial zone in the peripheral regions of the fructification. (pp/parent petiole, fa/fertile axis). C.B. 38-a H top #45. Bar/2.8 cm.

Figs. 64 - 71. SEM photographs of spores macerated from fructification 38-a. Note the variability of spore exine ornamentation.


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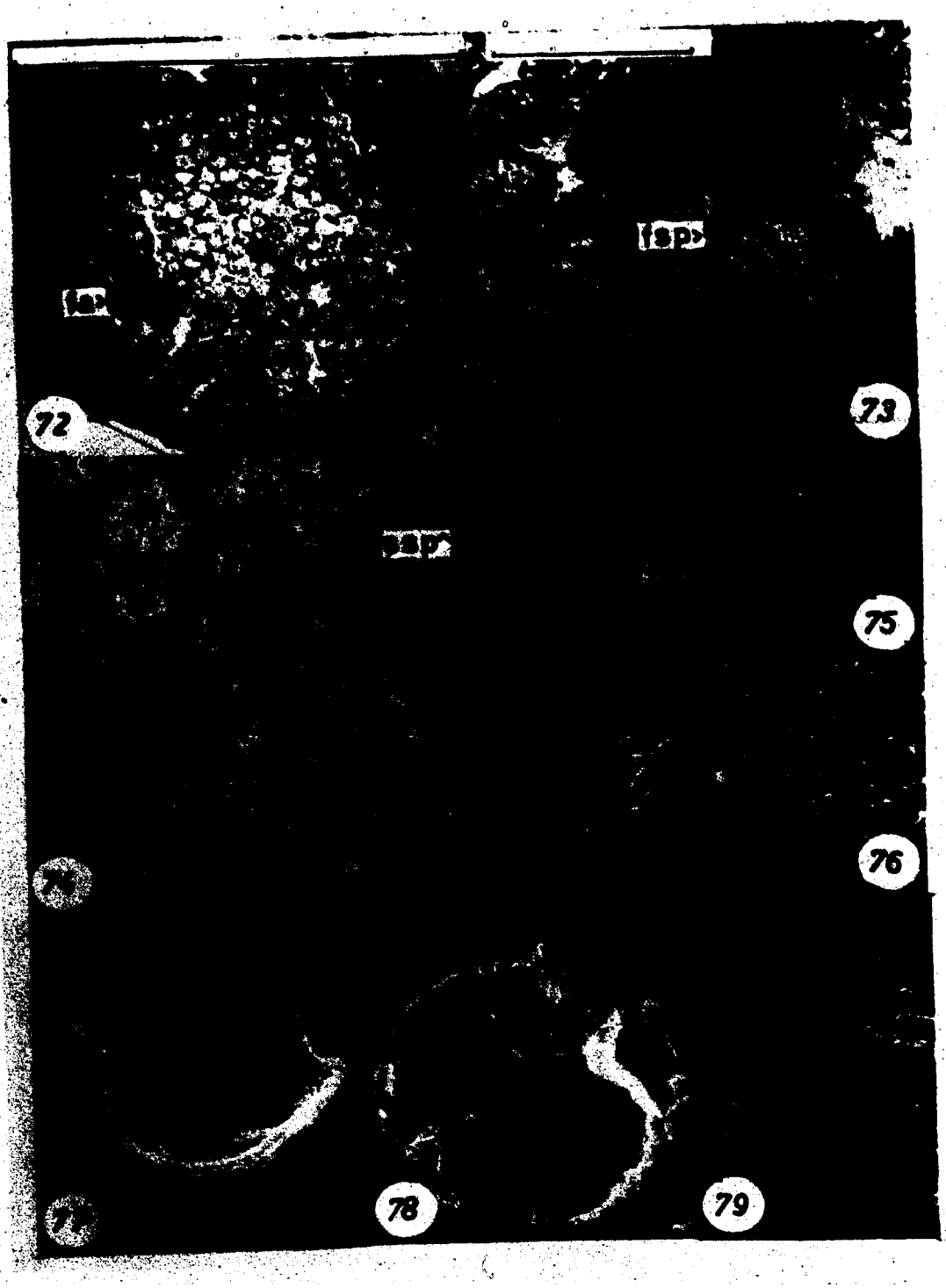
Figs. 72 - 79. *Botryopteris forensis.*

Fig. 72. Transverse section of fructification 38 F-G. (fa/fertile axis). C.B. 38 G top #3. Bar/1.4 cm.

Fig. 73. Transverse section of a fertile sporangia with radially elongated wall cells. (fsp/fertile sporangia). C.B. 38 F bottom #62. Bar/1080 µm.

Fig. 74. Transverse section of sterile sporangia with radially elongated wall cells. (ssp/sterile sporangia). C.B. 38 G top #3. Bar/same as Fig. 73.

Figs. 75 - 79. SEM photographs of spores macerated from the fructification 38 F-G. Note the variability of the spore exine ornamentation. (see text for full explanation).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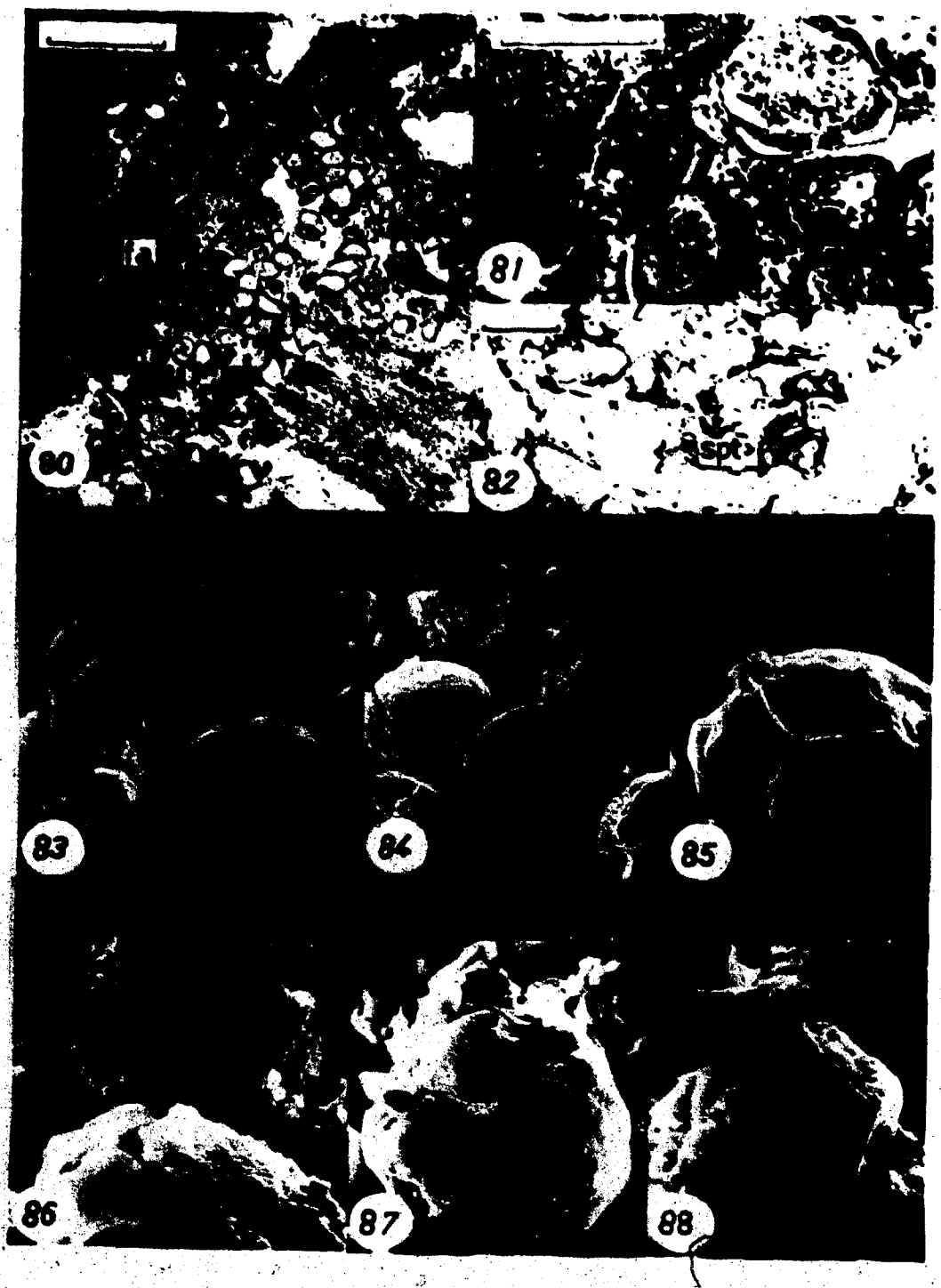
Figs. 80 - 88. *Botryopteris forensis.*

Fig. 80. Oblique longitudinal section of fructification 38-b. (fa/fertile axis). C.B. 38-b H top #109. Bar/3.0 mm.

Fig. 81. Transverse section of fertile sporangia from fructification 38-b. C.B. 38-B H top #93. Bar/888 µm.

Fig. 82. Spore tetrad. (spt/spore tetrad). C.B. 38 H bottom #115. Bar/53.35 µm.

Figs. 83 - 88. SEM photographs of spores macerated from fructification 38-B. Note the predominance of psilate spores.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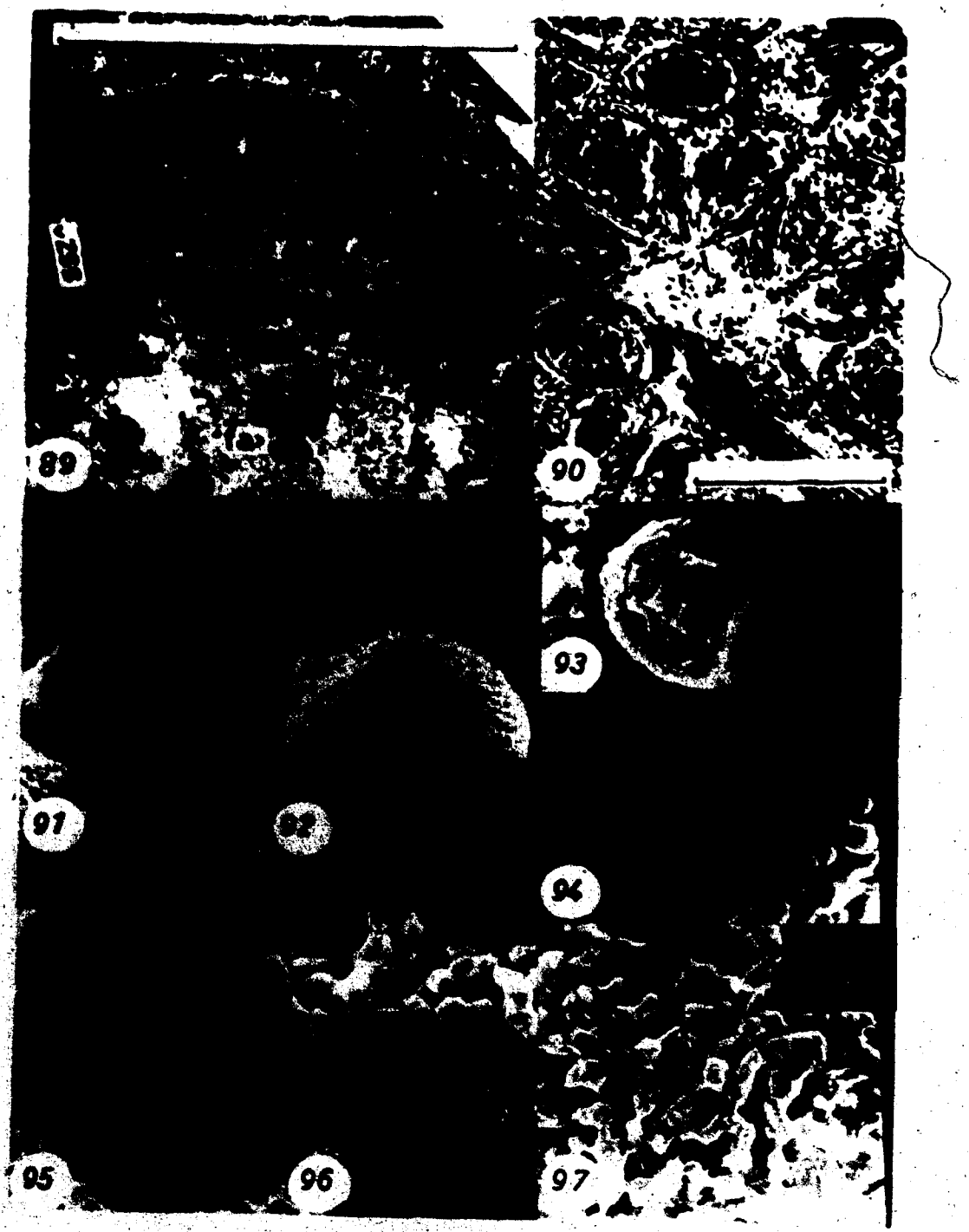
Figs. 89 - 97. *Botryopteris forensis.*

Fig. 89. Transverse section of fructification 537. (fa/fertile axis, ssz/sterile sporangial zone). C.B. 537 H bottom #29. Bar/2.2 cm.

Fig. 90. Transverse and longitudinal sections of sporangia of fructification 537. C.B. 537 H bottom #104. Bar/1127 μm.

Figs. 91 - 97. SEM photographs of macerated spores from fructification 537. (see text pages 54-55 for details).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Figs. 98 - 103. *Botryopteris forensis.*

Fig. 98. Transverse section of fructification 265. Note the sporangia, most of which are sterile. The region of the fructification with sporangia is more expanded (less compact) than regions which lack sporangia. Note also the quadraseriate trace formation pattern. (fa/fertile axis, t/trace). C.B. 265 G bottom #23. Bar/1.05 cm.

Fig. 99. Transverse section of sterile sporangia from fructification 265.

Fig. 100. Transverse section of the fertile axis (distal to Fig. 98). Note the compactness and size of the laterals attached to the fertile axis. Also note the lack of sporangia. (fa/fertile axis, la/lateral appendage). C.B. 265 H top #10. Bar/9 mm.

Fig. 101. Lateral appendage of Fig. 100. C.B. 265 H top #10. Bar/1128 µm.

Fig. 102. Transverse section of fructification 335. Note the expanded condition of laterals and the lack of sporangia. (fa/fertile axis). C.B. 335 E top #48. Bar/3.0 mm.

Fig. 103. Sectioned axis from fructification 335 showing a vascularized parenchymatous sporangial base. Fructification 335 is interpreted to have shed its sporangia some time after the fructification was in its expanded condition. (v/vascular tissue, pb/parenchymatous base). C.B. 335 E top #51. Bar/900 µm.


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Figs. 104 - 111. *Botryopteris tridentata.*

Fig. 104. Transverse section of *Botryopteris* petioles, *B. tridentata* on the left and *B. forensis* on the right. Note the homogenous outer cortex of the *B. tridentata* petiole and the zoned outer cortex of the *B. forensis* petiole. Also note the difference in the shape of the two species petiole strands. C.B. 552 G_2 top #3. Bar/2280 µm.

Fig. 105. Metaxylem of a petiole of *B. tridentata* showing elliptical to circular bordered pits. C.B. 328 E_1 bottom. Bar/117.6 µm.

Fig. 106. Transverse section of a petiole showing a two zoned outer cortex. C.B. 328 E top. Bar/2964 µm.

Fig. 107. Longitudinal section of the outer cortex of a petiole showing an inner zone of cells with transverse end walls and an outer zone of cells with oblique end walls. (ic/inner cortical zone, oc/outer cortical zone, ep/epidermis). C.B. 328 E_1 bottom. Bar/1080 µm.

Fig. 108. Transverse section of a parent petiole, a lateral pinna and the penultimate pinna rachis. (ppr/penultimate pinna rachis). C.B. 311 D bottom #59. Bar/5.5 mm.

Fig. 109. Transverse section of a pinnule (distal to Fig. 108) which was attached to the penultimate pinna rachis of Fig. 108. C.B. 311 D bottom #114. Bar/1536 µm.

Fig. 110. Transverse section of a petiole strand showing a stage in the development of a lateral pinna trace. The tracheid lobe will replace the tracheids "lost" to the incipient lateral trace (lateral arm). (la/lateral arm, tl/tracheid lobe, ma/median arm). C.B. 311 D bottom #26. Bar/360 µm.

Fig. 111. Transverse section of a petiole strand (distal to Fig. 110) showing the lateral detached from the parent strand. At this stage the lateral trace has developed only two arms, a lateral arm and a median arm. Note the tracheid lobe just in the position of a new lateral arm. (pt/pinna trace, tl/tracheid lobe). C.B. 311 D bottom #41. Bar/576 µm.


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Figs. 112 - 117. *Botryopteris tridentata.*

Fig. 112. Transverse section of a petiole strand showing a stage in the development of a plantlet trace. Note the enlarged lateral xylem segment and the additional lobe. (al/additional lobe, lxs/lateral xylem segment). C.B. 311 D bottom #26. Bar/1080 µm.

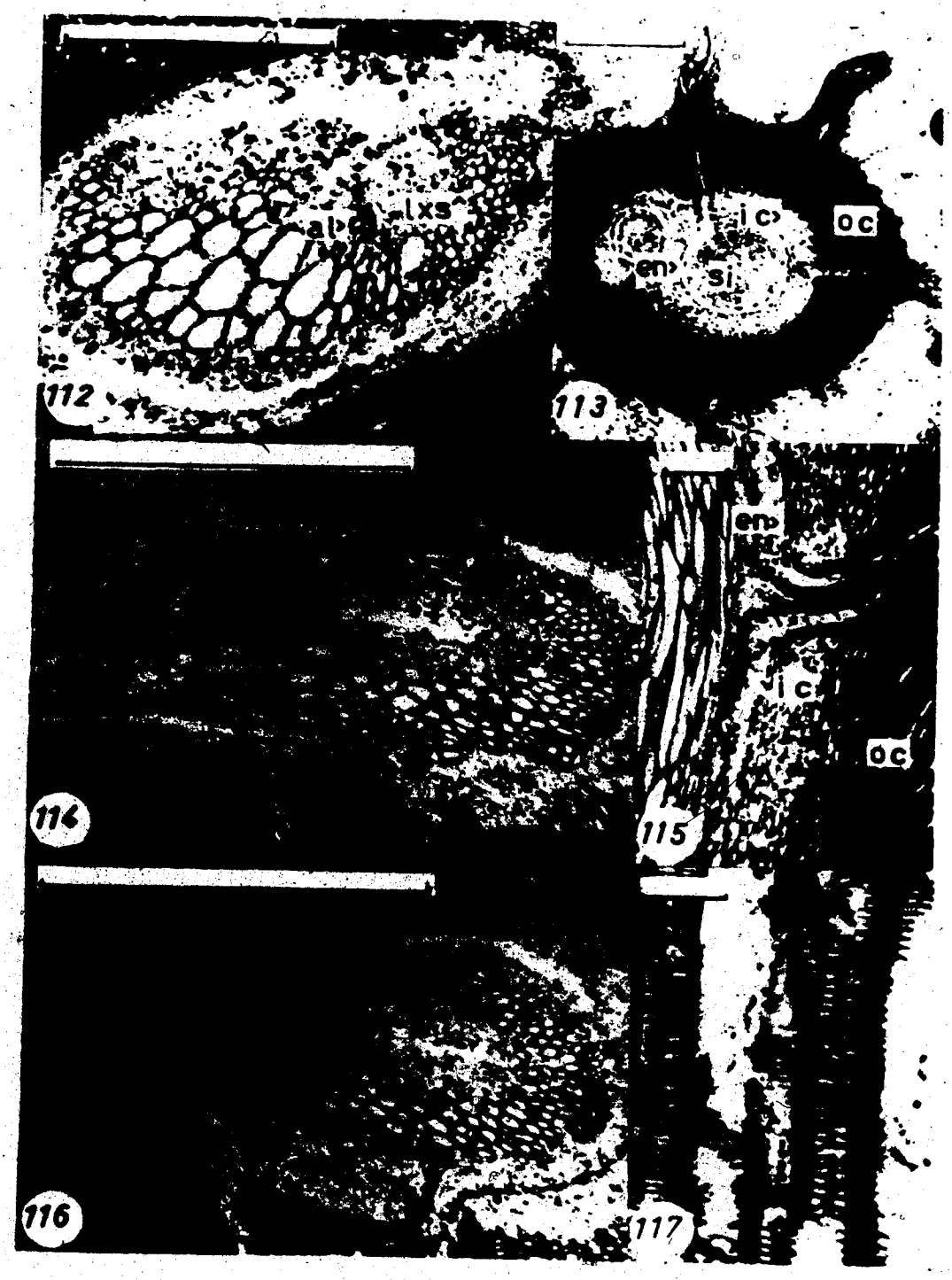
Fig. 113. Transverse section of a plantlet showing histology. (en/endodermis, si/siphonostele, ic/inner cortex, oc/outer cortex). C.B. 380 Q top #24. Bar/1272 µm.

Fig. 114. Transverse section of a petiole strand showing a stage in the development of a plantlet trace (distal to Fig. 112). Note the more hook-shaped lateral xylem segment. C.B. 311 D bottom #21. Bar/1560 µm.

Fig. 115. Longitudinal section of a plantlet showing the cortical zonation. Note the endogenous root. (en/endodermis, ic/inner cortex, oc/outer cortex). C.B. 577 D bottom # 49. Bar/2.88 µm.

Fig. 116. Transverse section of a plantlet siphonostele which is still attached to the parent petiole strand (distal to Fig. 114). C.B. 311 D bottom # 19. Bar/1680 µm.

Fig. 117. Metaxylem of a plantlet showing reticulate to multiseriate-reticulate pitting. C.B. 577 D bottom # 31. Bar/59 µm.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Figs. 118 - 123. *Botryopteris tridentata.*

Fig. 118. Transverse section of a plantlet showing a stage in the development of a petiole trace. Note the single decurrent protoxylem group associated with the incipient petiole trace. (dpxg/decurrent protoxylem group, st/scattered tracheids). C.B. 380 Q bottom #25. Bar/900 µm.

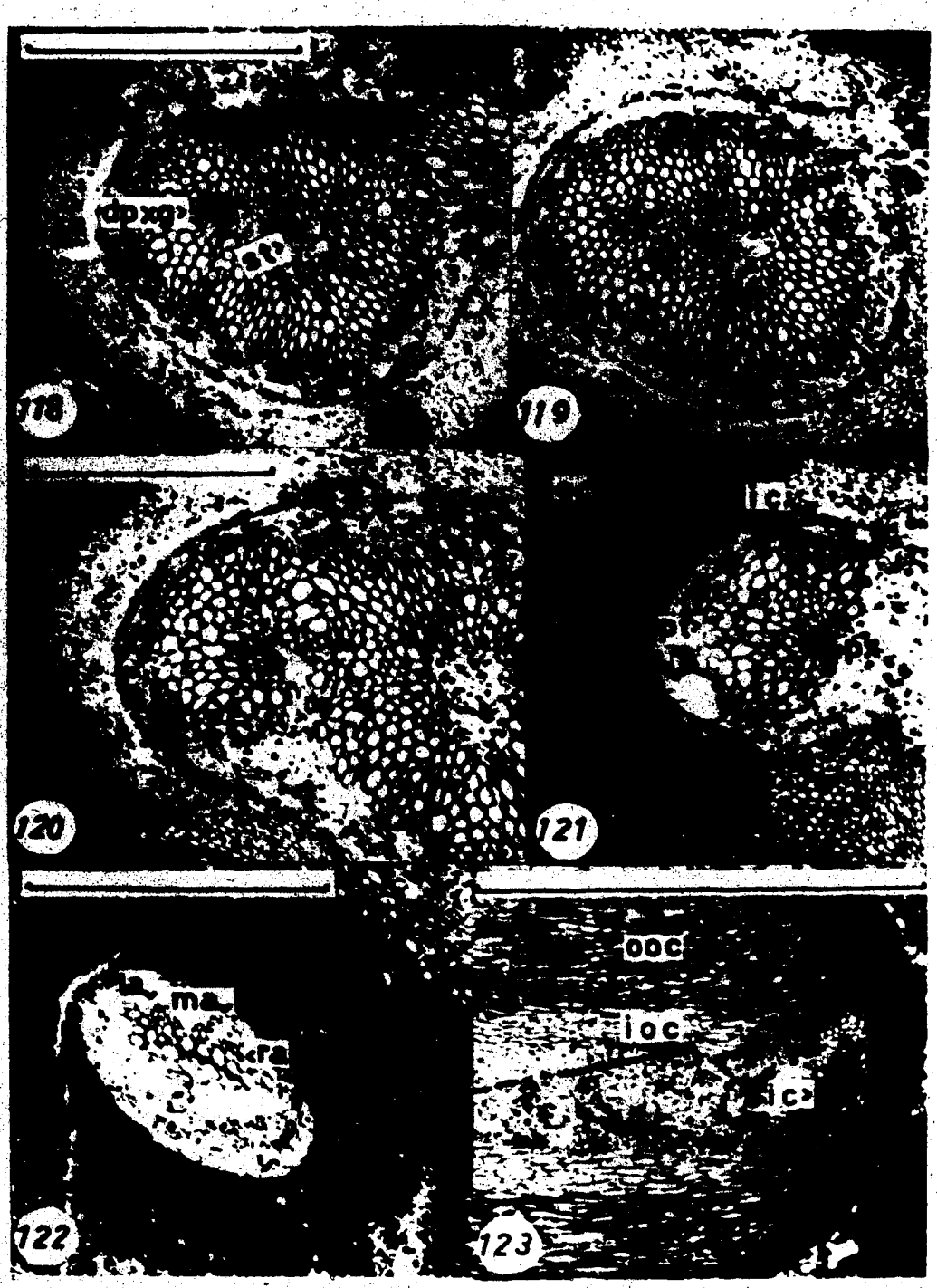
Fig. 119. Transverse section of a plantlet showing the next stage in the development of a petiole trace (distal to Fig. 118). The petiole xylem segment has elongated in the direction of emission. Note the lack of a leaf gap. C.B. 380 Q bottom #26. Bar/same as Fig. 118.

Fig. 120. Transverse section of a plantlet showing the petiole trace partially detached from the parent xylem strand (distal to Fig. 119). C.B. 380 Q bottom #28. Bar/768 µm.

Fig. 121. Transverse section of the detached elliptical petiole trace (distal to Fig. 120). The protoxylem is located in the indicated region. Distal to this position, the protoxylem will become distributed across the adaxial face of the petiole trace. Note that some inner cortical cell walls have become distinctly dark colored. (oc/outer cortex, ic/inner cortex, pt/petiole trace, px/protoxylem group). C.B. 380 Q bottom #30. Bar/same as Fig. 120.

Fig. 122. Transverse section of a petiole showing the strand with the characteristic three arms of a *Botryopteris* petiole (distal to Fig. 121). (la/left arm, ma/middle arm, ra/right arm). C.B. 380 Q bottom # 36. Bar/984 µm.

Fig. 123. Longitudinal section of a plantlet petiole showing the cortical zones. (ooc/outer outer cortex, ic/inner cortex). C.B. 311 E top 1-a. Bar/1896 µm.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Figs. 124 - 129. *Botryopteris tridentata.*

Fig. 124. Transverse section of a plantlet petiole showing cortical zonation. (ooc/outer outer cortex, ioc/inner outer cortex, ic/inner cortex). C.B. 311 E top #10. Bar/960 µm.

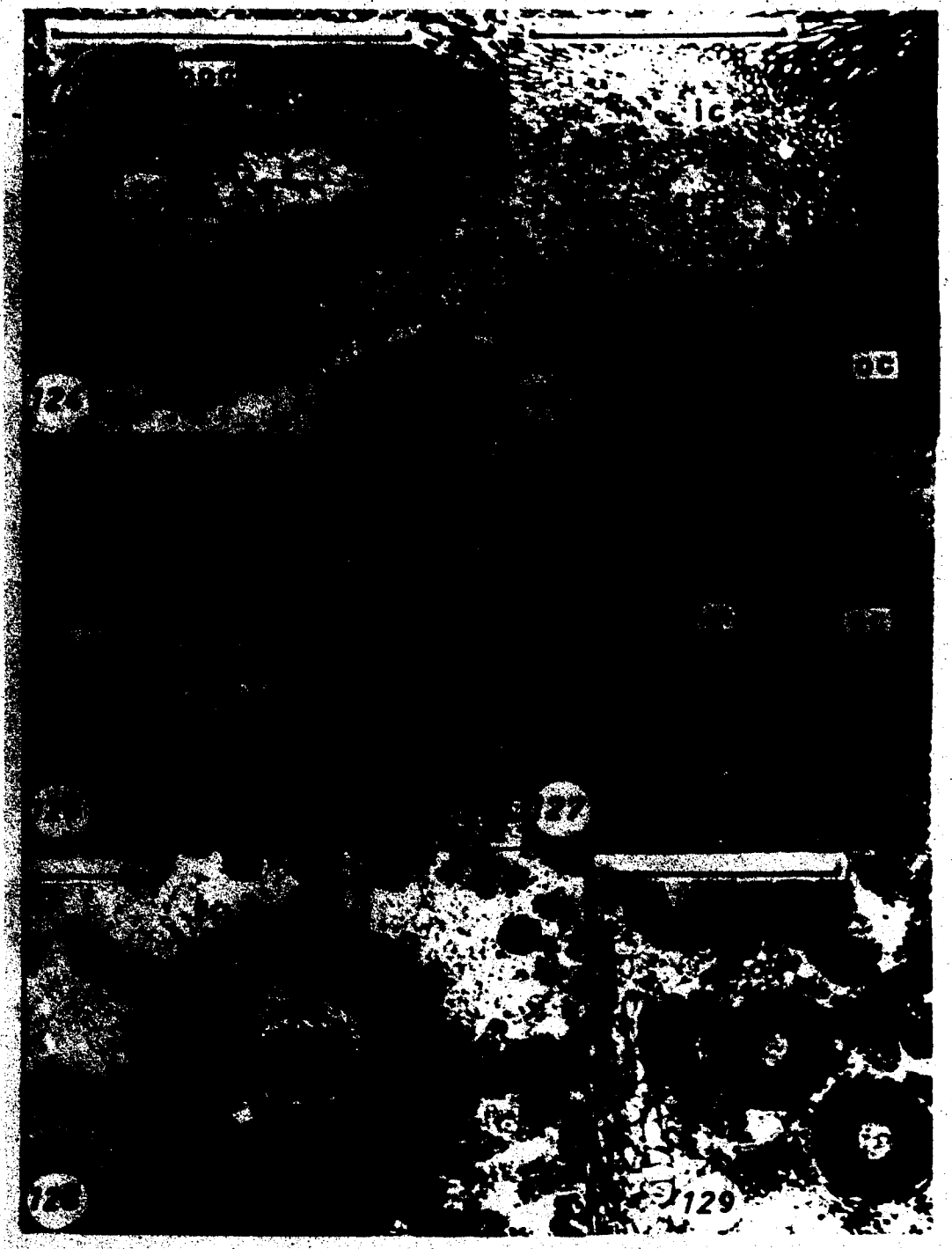
Fig. 125. Transverse section of a petiole near its attachment point to the plantlet showing the inner cortex and outer cortex. The inner cortical cells are either thin-walled and light colored or thicker-walled and dark colored. Note the small diameter of the inner cortical cells compared to the larger diameters of the outer cortical cells. (ic/inner cortex, oc/outer cortex). C.B. 577 D bottom #41. Bar/1032 µm.

Fig. 126. Transverse section of a plantlet petiole (distal to Fig. 125) showing the inner cortex and outer cortex. Note that most of the inner cortical cells are of a dark color similar to the outer cortical cells. The volume of the inner cortex has decreased at this level (compare with Fig. 125). (ic/ inner cortex, oc/outer cortex). C.B. 577 D bottom #49. Bar/same as Fig. 125.

Fig. 127. Transverse section of a plantlet petiole (distal to Fig. 126) showing the inner cortex, the zone of contact and the outer cortex. (cz/contact zone, ic/inner cortex, oc/outer cortex). C.B. 577 D bottom #56. Bar/same as Fig. 125.

Fig. 128. Transverse section of a plantlet showing endogenous roots. (enr/endogenous root). C.B. 380 Q top #24. Bar/1272 µm.

Fig. 129. Transverse section of typical *B. tridentata* roots. C.B. 311 D bottom # 12. Bar/1026 µm.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Figs. 130 - 136. *Botryopteris tridentata.*

Fig. 130. Transverse section of root showing the diarch strand and the root cortex. Note the tangentially flattened cells in the inner region of the root cortex and the more polygonal cells which make up the rest of the root cortex. C.B. 311 D bottom #12. Bar/210 µm.

Fig. 131. Section of root showing the endogenous origin of a lateral root from a parent root. Note that the cortex of the lateral root disrupts the cortex of the parent root. (enr/endogenous root). C.B. 311 E top #13. Bar/1826 µm.

Fig. 132. Longitudinal section of two roots showing the pseudomonopodial origin of a lateral root. The cortex of the lateral root does not disrupt the cortex of the parent root. The cortices of both roots appear homogeneous, continuous, and undisrupted. This suggests that the apex of the parent root divided unequally (pseudomonopodially) and the smaller member of that division became the apex of the lateral root. (pr/pseudomonopodial root). C.B. 311 D bottom # 126. Bar/1140 µm.

Fig. 133. Transverse section of a root showing the triarch strand. This condition of the normally diarch strand indicates incipient lateral root origin. (p/xylem pole). C.B. 575 H bottom #22. Bar/232.5 µm.

Fig. 134. Transverse section of roots showing the variation in the appearance of root cortices. C.B. 577 D bottom #50. Bar/480 µm.

Figs. 135 - 136. Metaxylem of a root showing reticulate to multiseriate-reticulate pitting. C.B. 240 A_3 bottom #46. Bar/32 µm.


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Figs. 137 - 142. *Botryopteris tridentata.*

Fig. 137. Longitudinal section of the parenchymatous tissue surrounding the vascular strand of a petiole. Note the thin-walled parenchyma cells and the glandular cells, which contain a frothy appearing brownish substance. (gc/glandular cell, pc/parenchyma cell). C.B. 552 C bottom #2. Bar/546 µm.

Fig. 138. Transverse section of the penultimate pinna rachis and pinnule lobes. Note the compressed appearance to the pinnule blade. (ppr/penultimate pinna rachis, pl/pinnule lobe). C.B. 265 E bottom #45. Bar/239 µm.

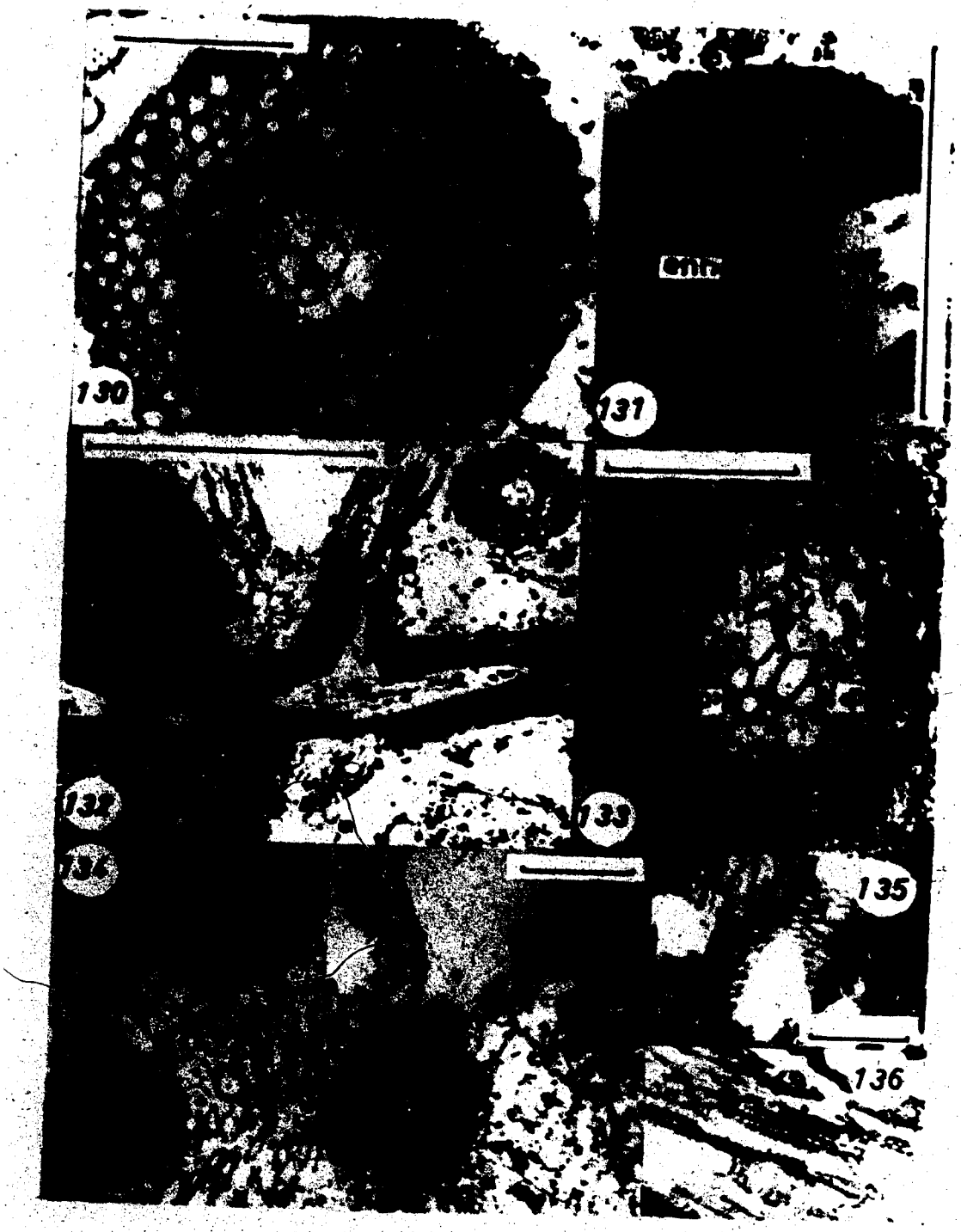
Figs. 139 - 142. Transverse section of penultimate pinna rachis illustrating general features and the variability in number and position of protoxylem connections, which occur during stages of pinnule trace formation. (ppr/penultimate pinna rachis, oxc/protoxylem connections, ep/epidermis, tc/tracheid lobe).

Fig. 139. Note the three protoxylem connections to the left lateral arm. C.B. 265 A bottom #86. Bar/1216 µm.

Fig. 140. Transverse section of the penultimate pinna rachis seen in Fig. 138. Note the hair base. C.B. 265 E bottom #45. Bar/same as Fig. 139.

Fig. 141. Note the two protoxylem connections, one to each of the lateral arms and the tracheid lobe which will replace the tracheids "lost" to the pinnule trace. C.B. 265 F bottom #82. Bar/same as Fig. 139.

Fig. 142. Note the two protoxylem connections, both to the one lateral arm. C.B. 265 E bottom #4. Bar/same as Fig. 139.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Figs. 143 - 148. *Botryopteris tridentata.*

Fig. 143. Paradermal section of a pinnule attached to the penultimate pinna rachis. Note the pinnule lobing. (ppr/penultimate pinna rachis, pl/pinnule lobe). C.B. 265 D #87. Bar/3.0 mm.

Fig. 144. Paradermal section of a pinnule showing stomata and wavy-walled epidermal cells. (ep/epidermal cells, s/stomata). C.B. 265 C #54. Bar/325 µm.

Fig. 145. Paradermal section of a portion of a frond showing the penultimate pinna rachis and two attached pinnules. Note the lobing of the left pinnule. (ppr/penultimate pinna rachis, p/pinnule). C.B. 265 C #51. Bar/4.0 mm.

Fig. 146. Paradermal section of a pinnule showing mesophyll cells. (m/mesophyll cells). C.B. 265 D #43. Bar/760 µm.

Fig. 147. Transverse section of a penultimate pinna rachis and the blade of an attached pinnule. Note the lack of compression. (ppr/penultimate pinna rachis, pb/pinnule blade). C.B. 265 A bottom # 4. Bar/600 µm.

Fig. 148. Transverse section of the pinnule blade seen in Fig. 147 showing a substomatal chamber below a stomate. (sc/substomatal chamber, s/stomate). C.B. 265 A bottom #16. Bar/134.4 µm.

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