A NEW MEMBER OF THE ZYGOPTERIDALES FROM THE LOWER UPPER DEVONIAN (FRASNIAN) OF ELLESMERE, N. W. T., ARCTIC CANADA

by

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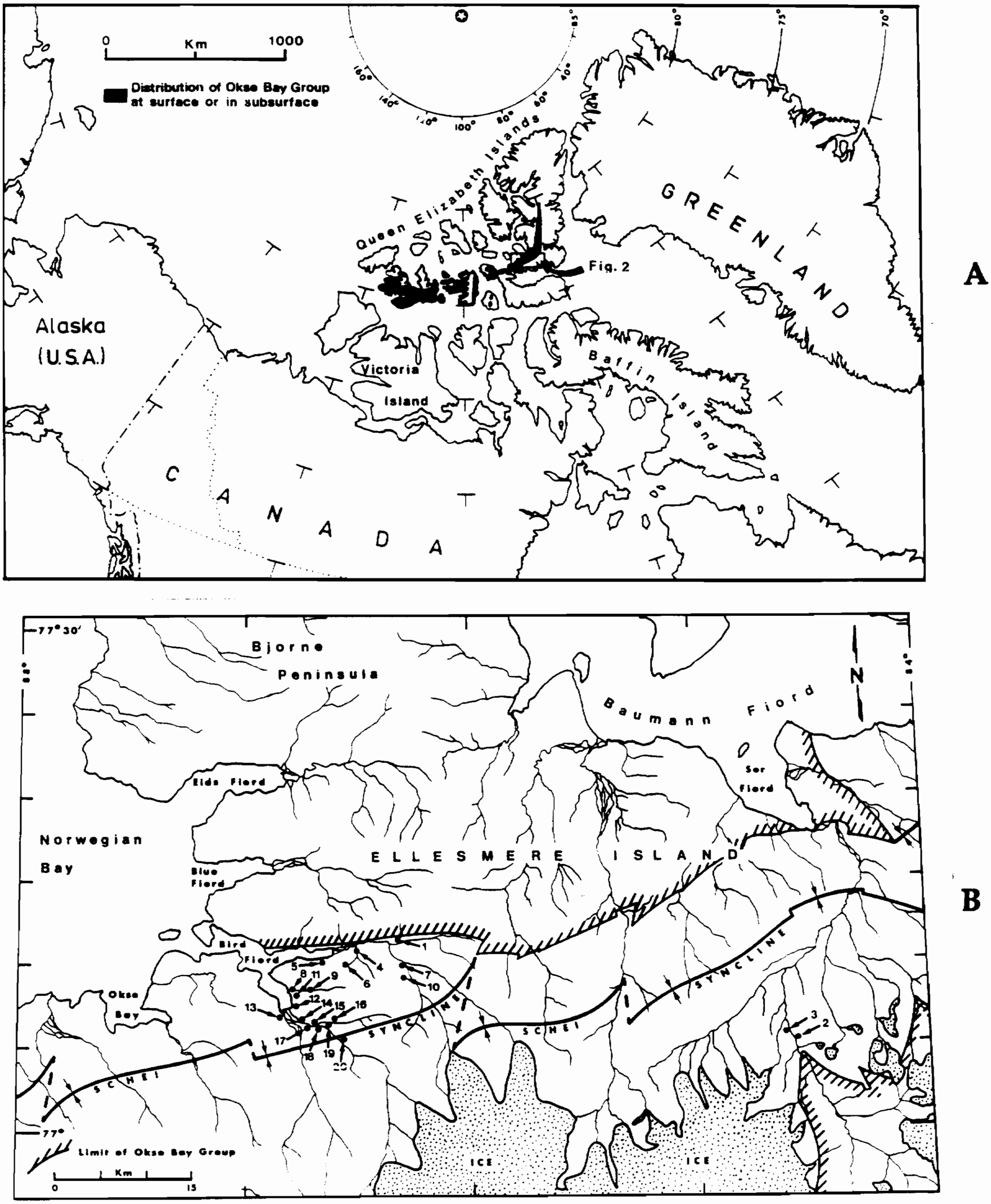
Chapter I

INTRODUCTION

In the summer of 1988, Dr. James F. Basinger and Dr. Stephen E. Scheckler initiated a survey of the fossil flora of the Okse Bay Group, a series of Middle to Upper Devonian rock formations found on Ellesmere Island, N.W.T., of arctic Canada (Text fig. 1). During the course of examining exposures of one of these formations, the Nordstrand Point Formation, at Bird Fiord in southern Ellesmere, Basinger and Scheckler discovered a number of new fossil plant taxa - including a fern-like plant with unique laminated ultimate appendages. It is the purpose of this thesis to name and describe this plant, and to interpret its evolutionary relationships and significance.

The Basinger/Scheckler team represents only the third group of paleobotanists to have sampled the fossil flora of what is now called the Okse Bay Group. A. G. Nathorst was the first paleobotanist to describe plant fossil remains from this group of five formations on Ellesmere. Nathorst's material (collected by Per Schei as a member of the Sverdrup Expedition from 1898 to 1902) derived solely from the early to mid Frasnian age Fram formation at Goose Fiord on the southern coast of Ellesmere, and included specimens of *Archaeopteris fissilis, A. obtusa, Lyginodendron sverdrupii,*



Text figure 1: Map of Collection Locality of Fossil Material from Bird Fiord Region of Ellesmere, N.W.T., Canada
A = Ellesmere Island (arrow labeled Fig. 2)
B = Close up view of collection area (14 = holotype locality)

and a possible pinnule of *Sphenopteridium keilhauii/Cephalopteris mirabilis* (Nathorst 1904). The *Sphenopteridium*-like pinnule, however, may have been a contaminant from Nathorst's Bear Island collection. In 1962, H. N. Andrews, T. L. Phillips, and N. W. Radforth again sampled the Fram formation at Goose Fiord, but discovered no new fossil taxa other than a petrified root that they assigned to *Callixylon* sp. (Andrews, Phillips, and Radforth, 1965). This group also visited the Bird Fiord area, but did not report any fossil plant finds. Thus, the Basinger/Scheckler team (which included the author during the 1989 field season) represents the first group of paleobotanists to have sampled the mid to late Frasnian age Nordstrand Point Formation flora. Furthermore, this is the first such group to have thoroughly examined all the Okse Bay Group formations on Ellesmere. The findings of this team have significantly expanded our knowledge of the paleobotanical content of the Okse Bay Group, increasing the number of known taxa from the three (or maybe four) reported by Nathorst to at least thirteen.

In addition to its importance as a previously unsampled geologic sequence, the Nordstrand Point Formation (as well as the rest of the Okse Bay Group) affords a rare look at Late Devonian plant life from a non-equatorial paloeolatitude . The vast majority of current information concerning Late Devonian plants has come from regions of North America and Europe that were probably near-equatorial in setting during this time period. Now, knowledge of the probably subtropic ($\pm 30^0$ paleolatitude) floras of the Nordstrand Point and other Okse Bay Group formations provides further evidence for ancient terrestrial ecosystems during the Late Devonian.

The plant upon which this thesis is based is the first new taxon to be formally described from the University of Saskatchewan and V.P.I. and S.U.'s joint study of the Devonian strata of present day arctic North America. Twenty-six rock specimens - consisting of compression/ impression fossils and one pyrite/limonite petrified axis - were recovered during the 1988 field season. An additional season of collection yielded no new specimens of this plant. All exposed outcrops of the Nordstrand Point Formation at Bird Fiord have now been thoroughly sampled. However, the occurrence of permafrost has limited access to the outer surface (approximately 15-20 cm) of these outcrops. Thus, weathering of the Bird Fiord rock exposures may in the future yield additional specimens of this plant. This could prove to be a lengthy process, as the rate of erosion in this region seems relatively slow (based upon our observations of minimal changes in the same outcrop from one year to the next).

Chapter II

BACKGROUND

A brief synopsis of the current state of our understanding of plant evolution, as it relates to this study, seems appropriate as part of an introduction to the remaining chapters of the thesis. Plant life on land is now believed to have originated much earlier than was previously recognized - probably by the Middle Ordivician, if not earlier. By the Late Precambrian, a cyanobacterial crust had begun to stabilize near shore terrestrial sediments, establishing the primary successional foundation for future plant communities (DiMichele and Hook 1992). Plants of an apparent non-vascular, bryophytic grade gradually took advantage of this moist, stable, relatively nutrient-rich substrate, and initiated the process of adaptation to the stressful existence of terrestrial life. Plants of this early type, of which there may have been a number of independent lines, eventually gave rise to a cluster of simple, rhizomatous plants, which branched dichotomously (or anisotomously in some) and bore sporangia terminally. Plants of this group are collectively referred to as rhyniophytes (*sensu lato*). Initially non-vascular, this line eventually evolved vascular tissue, concentrated in a centrarch haplostele (as in *Cooksonia*). Plants of the zosterophyll line of evolution (including modern lycopods) presumably diverged from a rhyniophyte-like ancestral stock early within the Devonian (or perhaps in the Late Silurian - Stewart, 1983).

By the middle Lower Devonian (Pragian), rhyniophytes had given rise to a more complicated, fairly diverse assemblage of plants known as trimerophytes (Stewart, 1983). Improving upon the primarily dichotomizing design of their forebears, trimerophytes evolved the capacity for pseudomonopodial branching (by which at each successive branch node, one of a pair of laterals became overtopped by its sister branch). This branching system resulted in the development of a main axis that bore lateral branches. A construction of this style generated increased height (improving access to the sun's rays) and resulted in the development of lateral appendages that were better adapted for harvesting sunlight. As a result of such design innovations, these plants quickly became dominant elements of the world flora, towering over their competitors. Early trimerophytes demonstrated much the same internal anatomical plan as did the rhyniophytes (centrarch haplostele). However, later trimerophytes (such as *Pertica*) with more complicated branching patterns derived more complex protostele architectures, with multiple lobes, multiple protoxylem poles, and mesarch maturation (Gensel, 1989). Tracheids of these plants were characterized exclusively by scalariform bordered pits.

By the Frasnian, trimerophytes were virtually extinct, having successfully generated numerous lineages that pioneered a wide range of architectural and ecological innovations. The few remaining trimerophytes seem to have begun to adopt new lifestyles as well. In one specific example, an as yet undescribed trimerophyte, from the lower Frasnian Yahatinda Formation of Alberta, Canada, appears to have become adapted to an understory habit in a shady *Archaeopteris* forest (Scheckler 1977a, 1977b). This plant, which was of significantly reduced stature in comparison to earlier trimerophytes, displayed new patterns of anatomy and morphology. In particular, this plant possessed an elliptical-shaped, bipolar, mesarch main axis stele, related to the bilateral arrangement of its lateral branches. Specifically, branches were arranged on the main axis in distichous pairs. Also, in addition to the scalariform pitting seen in earlier trimeropytes, tracheid cell walls of this plant demonstrated a transformation towards circular pitting at the ends of cells. As will become apparent during the course of the thesis, these anatomical and morphological features seem to anticipate basic characteristics of some later Devonian and Carboniferous fern-like groups.

The diversity of trimerophytes paved the way for a wide range of descendant plant groups. Trimerophytes were perhaps the direct progenitors of such groups as the progymnosperms (some of which were perhaps ancestors of seed plants), sphenophytes (horsetails and their relatives), iridopterids, cladoxylalean ferns, and zygopterid ferns (a sister group of modern ferns). Selection pressure (due to the increasingly crowded nature of terrestrial environments) drove each of these descendant lines to resculpt their lateral branch systems for improved photosynthetic display. In each case, a naked, three-dimensionally arrayed branch system became planated and webbed (i.e., interconnected by photosynthetic tissue) - resulting in the development of a multi-veined lamina. In this manner, all the known descendant lines of trimerophytes independently attained the capacity to produce megaphyllous leaves.

Not surprisingly, the megaphyllous leaves of these different lines demonstrated a variety of architectural styles, related to ecologic adaptation and independent innovation. However, it should also not be surprising that in some cases similar foliar strategies, which offered effective solutions to common ecologic circumstances, were employed. Thus, several descendant lines from trimerophytes, including archaeopterid progymnosperms, pteridosperms, and many early fern groups convergently developed branch systems or compound megaphyllous leaves organized into frond-like units.

A particularly remarkable example of such foliar convergence is seen in early pteridosperms and zygopterid ferns. As paleobotanists have long recognized (e.g., Seward 1898-1919; Scott 1923; Bower 1923, 1935; Darrah 1941; Taylor 1981; Galtier 1981; Galtier and Scott 1985), these two groups of plants independently derived a type of "fern" foliage often referred to as sphenopteroid. With respect to this type of foliage, perhaps the most clearly evident result of convergence in these groups is their shared expression of broadly lobed pinnules with dichotomizing veins, generally resembling those of the form genus *Sphenopteris* (but also assignable to other form genera such as *Pecopteris, Neuropteris,* and *Alloiopteris*). Yet, in addition, both groups adopted a general foliar strategy based upon forking frond units, with bilaterally symmetrical internal anatomy (the term "frond unit" here refers to the whole frond of gymnosperms, but only the primary pinna portion of zygopterid fronds).

The common fragmentation of plants with deposition and fossilization obscures or destroys whole frond architecture, and thus causes such superficial similarities to be even more apparent. Not surprisingly, this artifact of preservation greatly adds to the difficulty of evolutionary interpretation of individual fossil specimens. Yet, despite these general similarities, several key distinctions allow the distinguishment of early gymnosperm sphenopteroid foliage from that of zygopterid ferns:

1) spatial arrangement (i.e., organotaxis) of "frond units" on main axis (helical in most pteridosperms, except for *Schopfiastrum, Tetrastichia,* and *Quaestora*; quadriseriate arrangement -i.e., alternating pairs of laterals -

in zygopterids - Taylor 1981; Stewart 1983).

2) position of bifurcation (distally delayed in pteridosperms; immediate in zygopterids - Phillips 1974; Taylor 1981; Stewart 1983).

3) occurrence of a dichotomizing aphlebia at the point of frond bifurcation (although pteridosperms sometimes possess pinnules referred to as aphlebiae along the petiole, they do not display a dichotomous, scale-like aphlebia at the point of frond bifurcation - whereas zygopterids do exhibit such an appendage, at the base of each primary pinna - Gensel 1973; Taylor 1981).

4) anatomy of main axis which bears dichotomizing "frond units" (stem stele of early pteridosperms is three- to five-ribbed, with multiple protoxylem poles; phyllophore stele of zygopterids is bilobed and bipolar - Phillips 1974; Galtier 1988).

5) anatomy of traces departing from main axis, and entering "frond units" (*Lyginorachis* or *Kalymma*-type traces in pteridosperms; bilobed or C-shape traces in zygopterids - Stewart 1983).

6) general lamina form (Late Devonian to Early Carboniferous gymnospermous pinnules are generally deeply divided, with a somewhat rigid, sclerenchymatous texture; compared with Late Devonian to Pennsylvanian zygopterid pinnules which are not so deeply divided, or sclerenchymatous - Stockmans 1948; Long 1964; Boureau and Doubinger 1975;

Ramis, et al. 1979; Rothwell and Scheckler 1988).

7) occurrence of radially aligned, anastomosing bands of fibrous cells in the outer cortex of main axis that bears "frond units" (present in pteridosperms, and referred to as a sparganum/dictyoxylon-type cortex; absent in zygopterid ferns - Taylor 1981).

These points of differentiation, with regard to the frond architecture of the megaphylls of early pteridosperms and zygopterid ferns, will prove crucial in the comparison and discussion sections for evaluating the evolutionary affinities of this new plant from the Nordstrand Point Formation.

Chapter III

MATERIALS AND METHODS

The morphology of the plant has been investigated primarily by means of the uncovering technique of Leclercq (1951). Using this technique, sediment surrounding a specimen is slowly and carefully removed with needles (in this case composed of tungsten) - either by the force of a tack hammer, or by manual pressure-flaking. In this way, morphological features previously hidden from view by overlying sediment are revealed. This work was completed with the aid of a Nikon dissecting microscope under reflected light. Glyptal (an acetone-based glue), diluted with water, was often applied to stabilize areas of fragile organic material. A continuous photographic record, using a Canon A1 camera system, was compiled for all specimens to document each stage of preparation. Prior to being photographed, specimens were generally submerged in water, which greatly increased the level of contrast between morphological features of the plant and the surrounding sediment (particularly with respect to pinnule form). Wet viewing also eliminated signs of glyptal application and reduced the evidence of preparation using the uncovering technique. Cellulose acetate film pulls, using acetone as a solvent, were prepared in order to investigate the cellular details of pinnule laminae.

The internal anatomy of one specimen proved to be petrified by a combination of the minerals pyrite and limonite. Three separate pieces of anatomical material were glued to marked strips of paper (with Duco Cement), and then removed from the specimen using tungsten needles. The paper strips were labelled to insure a permanent record of the petrified material's proximal *vs*. distal orientation. The three segments of anatomy were then embedded in Ward's Bioplastic within a vacuum chamber. Next, the plastic-bound segments were sliced into transverse sections using a diamond-bladed saw. An overall length of approximately 9 cm of anatomical material yielded a total of 68 transverse sections. Each section was subsequently mounted as a slide in a synthetic resin medium. Three additional petrified chunks from this specimen were immediately mounted as slides for longitudinal views.

Anatomical (and some morphological) features were examined and photographed with a Wild M5A/MPS 55 Photoautomat dissecting microscope system. Anatomical specimens were additionally investigated with a Leitz compound microscope system and photographed with a Nikon camera assembly. All photographs were taken using Kodak Panatomic X film.

Chapter IV

GEOLOGIC SETTING

4.1 STRATIGRAPHY

The Nordstrand Point Formation is the youngest accessible member of the Okse Bay Group of formations on Ellesmere Island (Text fig. 1). The Okse Bay Group comprises a Middle to Upper Devonian clastic wedge of the Franklinian geosyncline. Originally recognized by McLaren (1963) as the Okse Bay Formation, this sediment package was raised to group status by Embry and Klovan (1976) and subdivided into five new formations (listed stratigraphically from oldest to youngest): Strathcona Fiord, Hecla Bay, Fram, Hell Gate, and Nordstrand Point. This group of terrigenous formations extends from southern Ellesmere to the more western islands of Devon, Bathurst, and Melville. The Nordstrand Point Formation occurs only on southern Ellesmere (where it conformably overlies the Hell Gate Formation) and the Grinnell Pennisula of Devon (where it is unconformably overlain by the Parry Islands Formation). Farther west (i.e., on Bathurst and Melville), the upper three formations of the Okse Bay Group are replaced by the Beverly Inlet Formation (which with the overlying Parry Islands Formation forms the terrigenous Gripper Bay Subgroup).

The Nordstrand Point Formation represents the upper sandstone and shale member of the formerly recognized Okse Bay Formation described by McLaren (1963). Specifically, this unit consists of alternating fining-upwards cycles, with each cycle consisting of a lower resistant sandstone layer (usually only 3 m thick) and an upper recessive shale-siltstone layer (up to 12 m thick). Thin coal seams are cited as occurring in the upper part of the formation (but these probably represent compressed *Callixylon* logs, as will be discussed later). The sandstone layers are characterized by a gray to white color, whereas the shale-siltstone layers are distinctively gray-green (or occasionally red) in color. The sandstones are quartzose lithic arenites (approximately 69% quartz, 5-10% rock fragments, and 11-13% clays - mainly kaolonite), cemented by calcite and/or authigenic quartz and clay. The shale layers consist primarily of quartz (62%), kaolonite (16%), and illite (13%). Previously, only trace fossils, ostracoderm fragments, and unidentifiable plant fragments were known from this formation (McLaren 1963; Embry and Klovan 1976; Rice 1987; Goodbody, et al. 1988), but Scheckler and Basinger collected samples of fish plates and bone from here as well in 1988. Embry and Klovan (1976) have interpreted the Nordstrand Point Formation to be meandering-stream in origin, based on lithologies, sedimentary forms, fossil information, and the observed cyclicity.

The Nordstrand Point Formation has been palynologically dated as being primarily Middle Frasnian in age, correlating with the *Maclarenii* megaspore zone of Chi and Hills (1976) and with the *ovalis-bulliferous* miospore zone of Richardson and McGregor (1986; see diagnosis section for a list of specific palynomorphs). Only the upper 100-200 m of a total formation thickness of 500-700 m (Embry and Klovan 1976; Goodbody, et. al., 1988) appear to be Late Frasnian in age (falling within the *Devonica* spore zone of Chi and Hills, 1976). All of the specimens herein described (except the petrified axis) derive from a locality (University of Saskatchewan US301; 77^0 06'40"N, 86^0 44'30"W) only 10 m above the contact point with the underlying Hell Gate Formation (Text fig. 1). This locality (which is the type locality of the new species) can thus be safely regarded as Middle Frasnian in age. Specimens specifically derive from the upturning western edge of a small paleochannel bed at this locality. The gray-green siltstone in this area of the bed is characterized by a distinctive orange stain (presumably iron-based) along its exposed vertical face. The concentration of the fossils in this single, small bed (approximately 1 m long and less than 0.5 m thick) suggests that conditions were sufficient for deposition and fossilization of this plant during only a brief moment of time, in a restricted area of the ancient meandering stream channel.

The petrified axis described here was found as an isolated specimen beside an outcrop of the Nordstrand Point Formation, along the modern channel that flows into Bird fiord. The exact original provenance of this specimen cannot be ascertained. Yet, this rock (a gray-green siltstone) is lithologically identical to the shale-siltstone layers of the Nordstrand Point Formation. Furthermore, since the Nordstrand Point is the only formation upstream of the collection site (University of Saskatchewan US310; 77^{0} 06' 30"N, 86^{0} 35'W) of this fossil, the specimen is confidantly interpreted as a product of this formation. Because of the velocity of the stream, transport of this specimen over any significant distance would probably have worn away the pertrifaction from the exposed surface of the rock. Thus, the apparent lack of transport damage to this specimen suggests that its original position lay somewhere within the adjacent outcrop (or one very nearby). The specimen therefore probably eroded from the outcrop (due to seasonal freezing and thawing), and then weathered while lying in the scree. The collection site of this fossil occurs at a higher level of the Nordstrand Point Formation than does the type locality. However, compressed sphenopteroid pinnules of the type described herein occur in association with (but not directly connected to) the petrified specimen, and specimens of *Archaeopteris obtusa* occur at the same collection site. Thus, the petrified specimen and the specimens collected from the type locality appear to be constituents of the same megafloral zone. Evidence linking the anatomy of this petrified specimen with the morphology reported here will be examined subsequently.

4.2 PALEOECOLOGY

During the Mid to Late Frasnian, Ellesmere Island (along with most of the rest of what is now North America) was attached to the ancient continent Laurussia. Based on paleomagnetic data (as well as paleoclimatic, paleobiogeographic, and tectonic data), Bambach, et. al (1980) have suggested that Laurussia straddled the equator at this time, with current North America tipped such that the paleoequator extended approximately from modern Southern California to Maine. Using this model for the Late Devonian world, Ellesmere would have occupied a position of approximately 30^0 N latitude on the eastern coast of Laurussia. The climate of Ellesmere during the Frasnian might therefore be expected to have been similar to that of modern Florida. Specifically, Ellesmere would probably have been subtropical in climate, with warm, wet summers, and moderate, above freezing, but drier winters. More recent analyses of paleomagnetic data for Laurussia by Scotese and McKerrow (1990), and by Kent and Van Der Voo (1990) suggest a slightly more southern paleolatitude ($\pm$ 15^0 N) for Ellesmere during the Frasnian. Yet, despite the latitudinal adjustments of these more recent paleogeographic reconstructions, the paleomagnetic evidence seems to continue to support a subtropical interpretation with respect to the climate of Ellesmere during the Frasnian.

A contrasting world model for the Late Devonian has been proposed by Witzke (1990), which calls into question this interpretation of ancient Ellesmere's climate. The Witzke model departs from those paleogeographic models so far discussed in depending exclusively on lithic evidence. Thus, based on the report by some geologists of coal layers within the Frasnian age Okse Bay Group of Ellesmere, the Witzke model suggests a more northern position for the paleoequator of Laurussia. Specifically, this model places the paleoequator just north of Ellesmere during the Frasnian. This interpretation results from the assumption that the presence of "coal" implies a swamp environment in an equatorial climate. This model thus suggests a year-round hot and humid environment for Late Devonian Ellesmere, which would have been similar to the climate associated with modern tropical rain forests of lower latitudes.

Re-examination of the Okse Bay Group sections from which reports of coal derive has helped clarify this discrepancy concerning the location of the ancient Laurussian continent. In surveying these geologic sections, the Basinger/Scheckler/Hill team discovered that isolated, coalified logs of *Archaeopteris* (= *Callixylon*) have apparently been misinterpreted by previous geologists to represent true, peat-derived coal seams. The coalified nature of these logs derives from the diagenetic compression of individual trees, following transport and deposition in a fluvial system, and is not the product of *in situ* peat accumulation in ancient swamps. Thus, the reports of coal beds upon which Witzke based his equatorial interpretation of the Late Devonian climate of Ellesmere are mistaken. Therefore, the paleogeographic models of Bambach, et. al. (1980), Scotese and McKerrow (1990), and Kent and Van Der Voo (1990), based on paleomagnetic evidence, seem to provide a more accurate depiction of the Devonian world in which the new taxon, herein called *Ellesmeria*, lived.

Embry and Klovan (1976) have interpreted the depositional environment of the Nordstrand Point Formation to have been a terrestrial fluvial system, specifically of a meandering-stream type. The sandstone sediment in which fossils of *Ellesmeria* occur is thus allochthonous in nature, having been transported hydrologically some distance prior to deposition within the river channel. The preservational state of the specimens in the current collection suggests that deposition occurred quickly. In particular, the laminated ultimate appendages seem relatively free of the effects of decomposers, and therefore probably were not suspended for very long in the fluvial system. *Ellesmeria* clearly grew somewhere on the flood plain, but the exact ecologic setting of its habitat (levee vs. drier floodplain, etc.) cannot currently be ascertained.

The apparent low diversity flora of the flood plain generally resembled contemporaneous floras of lower latitudes. Thus, *Archaeopteris* was the dominant plant and aneurophytes had become rare. Three species of

Archaeopteris occurred on the flood plain, with *A. obtusa* being more abundant than either *A. macilenta* or *A. fissilis* (a dominant species lower in the section, and found only in former ± 30^0 N paleolatitudes). Associated specimens of *Callixylon* presumably represent the larger branches and trunks of these *Archaeopteris* species. Aneurophytes were absent (but were numerous or dominant in formations lower in the section). Arborescent lycopods (consisting of at least two new species) composed an additional element of the flora. Unlike their later relatives of the Carboniferous, these lycopods were not inhabitants of peat-accumulating swamps. It should be noted that none of these lycopod species were the source of coalified logs mistakenly attributed by some to represent coal beds. Another member of the flora is *Barinophyton*, which may have been a storm-derived coastal contaminant. This flora was thus similar in its general composition to more equatorial, time-equivalent floras, but it was depauperate as a result of its lack of herbaceous lycopods and other fern-like groups (such as *Asteropteris* and *Cladoxylon*), as well as in its lack of diversity of *Archaeopteris* (*A. halliana* and *A. hibernica* are missing) and aneurophyte progymnosperms.

With regard to specific plant species, the Nordstrand Point Formation flora consisted of a number of unique endemics not known to have occurred anywhere else in the world at this time. This flora was clearly not just an extension of the Late Devonian equatorial flora, but rather had developed its own unique forms in response to a subtropical environment. Therefore, by the Frasnian, the global terriginous ecosystem (which had been characterized by apparent uniform vegetation since at least the Mid Silurian) was beginning to be partitioned. This subdivision into regional ecosystems, as an adaptive response to local physical and climatic factors, initiated a process of global evolution. This process eventually culminated in the production of biomes, characterized by plants with distinctive, climate-controlled form and density, such as are seen in the modern world.

Chapter V

SYSTEMATIC SECTION AND DIAGNOSES

5.1 SYSTEMATIC SECTION

Class	Pteridopsida
Order	Zygopteridales
Genus	*Ellesmeria*, gen. nov.
Species	*Ellesmeria sphenopteroides*, sp. nov.

5.2 DIAGNOSES

Ellesmeria, gen. nov.

GENERIC DIAGNOSIS: Three orders of branch known. First order axes (i.e., main axes) demonstrating only slight distal taper. Second order laterals (i.e., primary pinnae) distichous and alternate in arrangement; usually borne quadriseriately (i.e., in pairs), but rarely biseriately (i.e., singly). Third order laterals (i.e., secondary pinnae) sub-opposite to alternate in arrangement, and aligned parallel to the first order axis; bear laminate pinnules alternately. Dichotomous pinnule-like organ (or aphlebia) borne proximally by each primary pinna, in the catadromic position. Roots apparently adventitious in nature. Longitudinal groove present in compressed main axes and primary pinnae, corresponding to the internal vascular pattern. Vasculature of both main axis and primary pinna mesarch and bipolar. Primary xylem of main axis elongate (in cross section), ribbon-like to clepsydroid in shape. Each primary pinna pair supplied by crescent-shaped initial trace of primary xylem, that may become four-ribbed prior to dividing. Small, circular, centrarch traces (perhaps supplying aphlebiae) also present. All known tissues primary. Reproductive structures unknown.

TYPE SPECIES: *Ellesmeria sphenopteroides* sp. nov.

SPECIFIC DIAGNOSIS: Plants as described in the generic diagnosis. Main axes 8-11 mm in greatest diameter, to 2-3 mm wide distally; primary pinnae 5-8 mm at proximal base, 1-3 mm distally; secondary pinnae 0.5-1 mm. Bases of primary pinnae taper in cornute manner. Pinnules broadly lobed, often with three main lobes. Pinnules narrow at base, sometimes decurrent and slightly fused. Venation anisotomous proximally, isotomous more distally; vein endings expanded and tear-drop in shape. Aphlebiae 5-7 times dichotomous; perhaps somewhat planated and slightly webbed. Vegetative pinnule-like structures of uncertain form occasionally present along main axes. Surface of main axes sometimes demonstrating micro-ribbing, suggesting somewhat fibrous cortex (but not of sparganum, nor dictyoxylon-type). Adventitious root-like structures occasionally present along one side of main axes and primary pinnae. Main axis stele bipolar, ribbon-like to clepsydroid in shape;

2.4-3.0 mm in length, 0.4-0.9 mm in width (in cross section). Protoxylem poles of main axis stele and of primary pinna trace composed completely of tracheids, consisting of 3-10 cells. Bipolar primary pinna trace initially elliptical (length 0.5 mm and width 0.2 mm); soon becoming crescentic in shape, and eventually four-ribbed (expanding to 0.9-1.0 mm in length, 0.4-0.8 mm in width). Four-ribbed stage of primary pinna trace produces from its catadromic ribs a pair of small (0.2 mm in diameter), centrarch traces that probably supply the aphlebiae. Protoxylem tracheids annular to helical; 8-26 um in diameter, at least 1.7 mm in length. Early metaxylem cells scalariform-bordered pitted; 17-43 um in diameter, at least 2.1 mm in length. Late metxylem tracheids circular-bordered, multiseriate pitted (pit apertures often elliptical and slanted diagonally); 22-56 um in diameter, at least 2.0 mm in length. Secondary xylem unknown. Phloem not preserved. Inner cortical cells parenchymatous, 34-86 um in diameter, thick-walled, and elongate (0.6-1.0 mm in length). Intercellular space abundant. Outer cortex , where preserved, of small, rectangular cells (31 um diameter radially, 21 um tangentially) with thickened walls (possibly the source of external surface micro-ridging). Epidermis not preserved.

HOLOTYPE: Virginia Polytechnic Institute and State University Paleobotanical Collection (VPISUPC) #110.1.1 (specimen on loan from

University of Saskatchewan, where it will be permanently stored). Compression of first order axis 16 cm long, with four nodes preserved. Three orders of branching and ultimate appendages present. Figs. 1, 7, 10-11, 18-19, 22, 27, 29, 33.

PARATYPES: VPISUPC # 111.1: Compression of two orders of branching, including petrified first order axis. Three segments of the this axis (totaling 9 cm) were cut into 68 transverse sections (111.1.1 is proximal, 111.1.68 is distal), whereas the three remaining segments were mounted as longitudinal sections (111.1.1 L - 111.1.3L). Figs. 34-71. VPISUPC #110.1.2: Compression of three orders of branching and ultimate appendages, Figs. 14, 16-17, 32. VPISUPC #110.2.1: Compression of three orders of branching and ultimate appendages, Figs. 2, 8, 12-13, 20, 24. VPISUPC #110.2.2: Isolated compressed primary pinna, with secondary pinnae and laminated pinnules, Figs. 2, 12-13, 23. VPISUPC #110.3.1: Compression of three orders of branching and ultimate appendages, Figs. 3-5, 28. VPISUPC #110.3.2: Isolated secondary pinna with laminated pinnules, Figs. 21, 25-26. VPISUPC #110.4: Compression of three orders of branching and ultimate appendages - counterpart of specimen #110.3.1, Fig. 15. University of Saskatchewan Paleobotanical Collection (USPC) #4342A: Compression of two orders of branching, Figs. 31. USPC #4342B: Compression of three orders of branching - counterpart of specimen #4342A, Figs. 9, 30. USPC #434: Compression of two orders of branching, Fig. 6.

TYPE LOCALITY: North side (77^0 07'N, 86^0 45'W) of braided river channel that drains into Bird Fiord, Ellesmere, N.W.T., Canada.

HORIZON: Level of a small paleochannel, about 2 m above the base of the outcrop (where outer edge of rock assumes a yelowish color). This horizon falls within the Nordstrand Point Formation in the Okse Bay Group of the Upper Devonian Stage, Frasnian Series (Embry and Klovan 1976), about 10 m above its conformable contact with the Hell Gate Formation.

BIOSTRATIGRAPHIC HORIZON: The sedimentary matrix of rocks from the type locality is unsuitable for palynological study. However, the type locality is only 10 m above the base of the formation and therefore correlates with the *Maclarenii* megaspore zone (Embry and Klovan 1976). This spore zone is interpreted by Chi and Hills (1976) as Middle Frasnian in age and is characterized by an abundance of *Ocksisporites maclarenii* and *O. connatispinosus* , with additional species including *Nikitinsporites canadensis*, *Lagenicula devonica*, and all the species of the *Medius* zone (except *Trichodosporites delicatus*, *Hystricosporites expandus*, *Restusotriletes distinctus*, *Verruciretusispora primus*, and *Grandispora microfoveolatus*).

The *Maclarenii* megaspore zone correlates with the Middle to Upper Frasnian age *Archaeoperisaccus ovalis-Verrucosisporites bulliferous* miospore zone of Richardson and McGregor (1986). The *ovalis-bulliferous* zone is characterized by the co-occurrence of the following species: *Archaeoperisaccus ovalis, Verrucosisporites bulliferus, Ancyrospora furcula, A. melvillensis, Aneurospora greggsii, Archaeoperisaccus opiparus,* cf. *Archaeozonotriletes laetus, Diaphanospora reticulata, Geminospora lemurata, Hymenozonotriletes deliquescens,* and *Lophozonotriletes media* (as well as the megaspore species *Nikitinsporites canadensis*)(Richardson and McGreggor, 1986). Associated megafossils (including *Archaeopteris obtusa, A. macilenta,* and *A. fissilis*) from the type locality indicate that this portion of the Nordstrand Point Formation correlates with megafossil floral assemblage zone VI (the *Archaeopteris* zone) of Banks (1980).

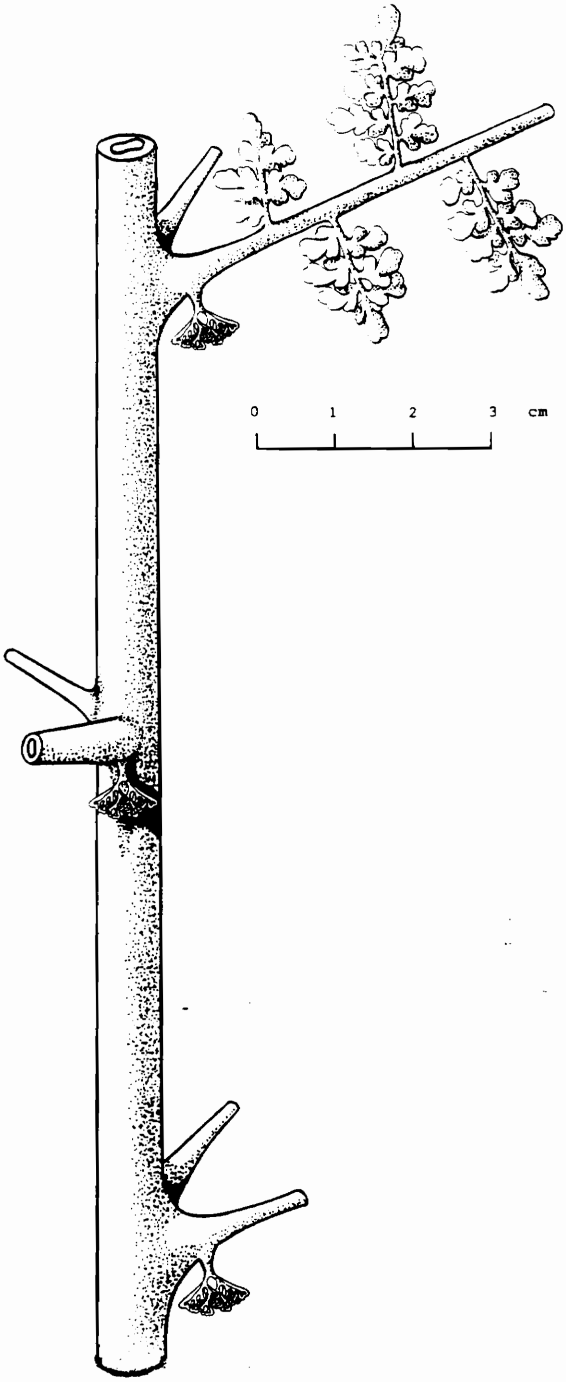
DERIVATION OF NAME: Generic name established in recognition of the arctic island from which the plant derives. Specific epithet named for the sphenopteroid nature of the plant's laminated ultimate appendages.

Chapter VI

RECONSTRUCTION

This new plant is incompletely known. Its preserved portions consist of a pinnate branching system, with three orders of branching and laminate ultimate appendages of a general sphenopteroid type, as demonstrated by the holotype specimen (fig. 1). Axes of the first branch order will hereafter be referred to as main axes; those of the second order as primary pinnae; and those of the third order as secondary pinnae. The term pinnule will be used in reference to an ultimate appendage. For the most part, this is the standard terminololgy used in the description of fossil plants with frond-like vegetative branching systems. No attempt is made in this thesis to distinguish between cauline branching (i.e. that associated with a stem) and foliar branching with respect to this new plant. This issue is intentionally being avoided, as the distinction between a branching system evolving towards leaf status and a truly foliar system is often unclear (and somewhat controversial) in fragmentary fossils of this age.

A partial reconstruction of the plant *Ellesmeria sphenopteroides* has been prepared based upon the succeeding observations reported here (Text fig. 2). A portion of a typical sterile first main axis, with subtending primary pinnae, secondary pinnae, and pinnules is depicted. The bilobed



Text figure 2: Proposed Reconstruction for *Ellesmeria sphenopteroides* stele patterns of the main axis and a primary pinna are also indicated. This reconstruction does not attempt to show the habit nor growth position of the plant, as the evidence for these features remains unclear (i.e. more proximal orders of branching and stem unknown). Thus, the orientation of the main axis in the drawing is not meant to imply orthotropic (i.e. vertical) growth. In reality, the main axis may have largely been oriented horizontal to the substrate (as will be reviewed in the succeeding comparison and discussion sections).

Chapter VII

DESCRIPTION - MORPHOLOGY

7.1 MAIN AXIS

Main axes are identified in the suite of specimens by the laterals that they bear. Known primarily from fragments only 10-15 cm in length, the main axis of this new plant is preserved in one specimen for a length of 33 cm. The diameter of the plant's main axis is quite variable, perhaps depending on the developmental provenance (proximal vs. distal) of a specimen. For example, the main axis of one specimen (fig. 2) is 9 mm wide, whereas the holotype specimen's main axis (fig. 1) is only 3 mm wide proximally and 2 mm distally. Yet, the main axes of these and all other specimens in the collection are interpreted as equivalent organs of morphology based upon the following evidence (which will be fully examined and illustrated in subsequent sections):

1) the main axis normally gives rise to quadriseriately arranged primary pinnae (i.e. occurring in alternate pairs), which themselves produce alternate secondary pinnae. There is no evidence suggesting that a quadriseriate arrangement of laterals occurs in multiple branch orders of this plant. Thus, this arrangement of the primary pinnae is a key identifying feature of the main axis.

2) the form of the attachment base connecting a primary pinna to a main axis is also diagnostic of this level of the plant's morphology. Proximal to a primary pinna node, the main axis swells (to a width of about 10 mm in fig. 6), curving gradually outward to yield the catadromic (i.e. lower) surface of a pinna. Then, just distal to the node, the anadromic (i.e. upper) surface of the pinna curves rapidly inward, such that the original width of the main axis (8 mm in fig. 6) is almost immediately re-established.

3) Dichotomous aphlebioid structures occur only where primary pinnae emerge from the main axis.

4) Normal laminate pinnules are borne solely by the ultimate order of branch (the secondary pinnae). The pinnules thus serve as another key morphological reference point, from which the identification of the main axis (as well as the primary and secondary pinnae) can be verified.

The main axes of the specimens in figures 1 and 2 thus appear to be morphologically equivalent, and demonstrate a fairly wide range in the diameter of the plant's main axis. The greater width of the main axis shown in figure 2 is interpreted as the result of a more proximal location within the whole plant (the extent of which is unknown) - as opposed to the narrower, probably more distal main axis of the holotype specimen.

The specimen with the longest main axis in the collection (33 cm) is incompletely preserved with respect to width, and does not contribute information regarding axis taper (fig. 3). However, as previously mentioned, the holotype specimen's main axis tapers from 3 to 2 mm along its 16 cm length. If the robust, presumably more proximal main axis of figure 2 tapered in width at a rate comparable to that of the holotype specimen (1 mm/16 cm), then a length of approximately 112 cm would be required to achieve a distal taper of just 2 mm. We cannot determine whether these specimens represent fragments of the same axis, or are separate but homologous axes. Yet, the robust width of the main axis in figure 2 - associated with no evidence of rapid taper - suggests that the main axis of this plant could achieve quite sizeable lengths.

An analysis of internode length along the main axis of this plant has yielded some information (though of disputable significance) regarding the developmental history of this organ. Previous developmental studies have shown the growth systems of most early land plants (such as *Lepidodendron, Calamites, Tetraxylopteris,* and *Archaeopteris*) to have been determinate in nature (Eggert 1961, 1962; Scheckler 1976, 1978). Under such a system, a plant axis has a finite growth potential, resulting from sequential reduction in the size of its apical meristem (apoxogenesis). Ultimately, the apical zone reaches a minimal size at which it can no longer function meristematically, and growth ceases. As has been shown for the aneurophyte*Tetraxylopteris,* a sequential pattern of decrease in internode length can be an important indicator of a determinate growth system (Scheckler 1976).

In the holotype specimen, no appreciable change in length occurs along a series of four internodes (fig. 1). However, other specimens may demonstrate a series of internodes which decrease in length distally. For example, in addition to an indisputable proximal internode 6.7 cm in length, the specimen in figure 2 may display a more distal, 5 cm long internode. However, this interpretation assumes that the isolated axis at the top of the figure is actually a distal primary pinna of this specimen. The specimen in figure 3 also seems to exhibit a distal series of decrease in internode length (note: the proximal-most lateral, indicated by the lower arrow in fig. 3, is shown to be in full attachment to the specimen in fig. 5). Yet, there are also problems associated with this interpretation. In the upper left corner of the figure, the specimen appears to bend almost 90^0 to the right. This area is interpreted as a bend, and not a node, because the tissue is torn here, and the main axis does not continue towards the upper edge (nor towards the left edge) of the rock. Furthermore, there is no indication here of the characteristic attachment base of a primary pinna. Based on the assumption that the main axis bends to the right, the series of three evident internodes shows a distal decrease in length (6.2 cm, 4.2 cm, 3.8 cm, respectively).

This evidence suggests that the branching system of this plant was produced by a determinant developmental program. However, this analysis is based on only a few specimens, each with no more than four primary pinna nodes preserved. A larger sample would be required to assess whether the observed decrease in internode length truly derived from a determinant growth system, or from some other cause of morphologic variation (seasonal response, response to light availabilty, etc.)

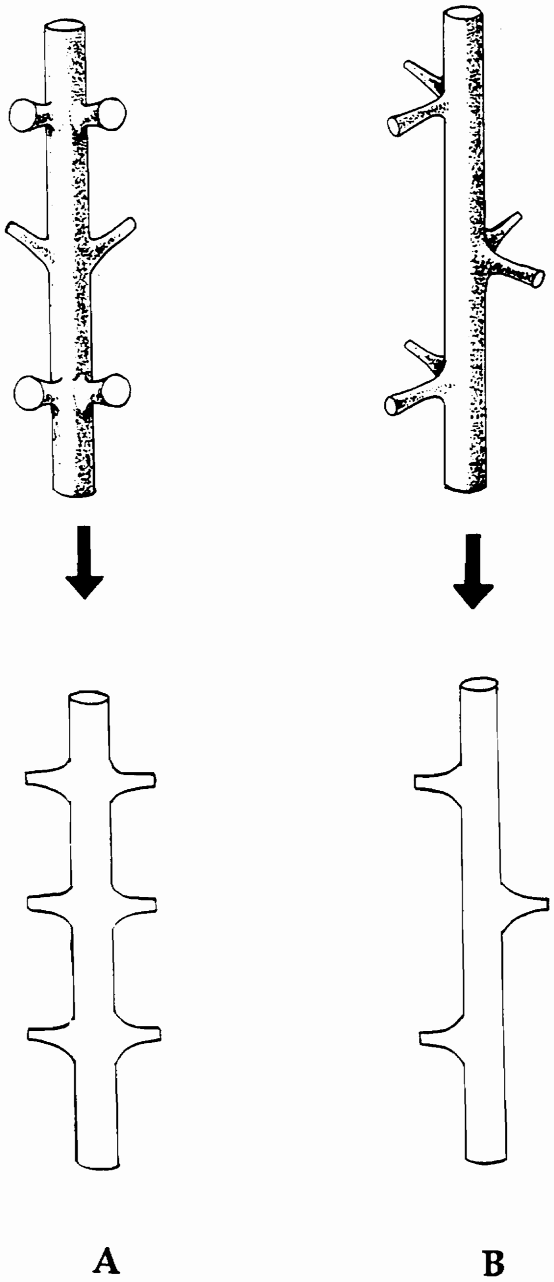
Finally, a characteristic feature of morphologically preserved main axes (and primary pinnae) is a distinct central groove (fig. 4, 6-8, 15, 34). This groove, which is often seen to be double ridged (fig. 4, 8) or double indented (fig. 15), is interpreted to be a product of sediment compaction of the plant's vasculature. The details of the relationship between the external groove and the internal stele of this plant will be examined in the anatomy section. The presence of a vascular groove of this type permits quick recognition of this plant from other elements of the Nordstrand Point Formation flora.

7.2 PRIMARY PINNA ORGANIZATION AND ORGANOTAXIS

Incomplete primary pinnae are known from fragments up to 10 cm long. Each primary pinna emerges from the main axis in a characteristic tapering fashion (as previously described), resulting in a somewhat cornute attachment base (fig. 2, 4). In larger specimens, primary pinnae are on the average about 7 mm wide at the proximal base, but quickly taper to a width of 2-3 mm within the next 1-2 cm of length (fig. 2). From this point, any additional distal taper in a pinna is minimal. Primary pinnae of the holotype specimen are much more slender, tapering from an average width of just over 1 mm at the proximal base to a width of just under 1 mm distally (fig. 1).

Typically, primary pinnae diverge in pairs from the main axis in a quadriseriate manner (i.e., alternating, distichous arrangement/organotaxis of paired laterals - Text fig. 3). Prior to entombment in sediment, each member of a pair of primary pinnae probably diverged at an angle of at least 90 degrees with respect to the other member of the pair, while each individual pinna departed from the main axis at an angle between 60 to 90 degrees. Commonly, a pair of primary pinnae is slightly offset in its attachment to the main axis, such that the attachment site of one pinna of a pair is slightly distal to that of its sister pinna (fig. 1-2, 9, 18-19).

The quadriseriate arrangement of primary pinnae is most apparent in the holotype specimen (fig. 1, 10-11). The distal-most pair of primary pinnae (node "D" of fig. 1) ascend from the horizontal plane on which the main axis resides (i.e., come out of the plane of the plate). The left primary pinna of the next more proximal node (node "C") departs into the plane of the plate, descending from the horizontal plane of the main axis (the right



Text figure 3: Comparison of Branch Orientation for a Quadriseriate System Before and After Compression and Fossilization.

A = life orientation that leads to artifactual opposite branch arrangement following compression
B = life orientation that leads to artifactual alternate branch arrangement following compression

lateral of this node is torn proximally, and appears not to lie in its original growth position - fig. 19). Recapitulating the pattern of node "D", the right primary pinna of node "B" ascends out of the plane of the plate (the distal portion of the left lateral being absent). Finally, the left primary pinna of node "A" (following the pattern of node "C") descends from the horizontal plane of the main axis into the plane of the plate. Figures 10 and 11 corroborate these interpretations, providing low-angle views which document the three- dimensionality of the branching system. The organotaxis of this specimen therefore compares most closely to a quadriseriate-type.

The specimen in figure 2 demonstrates an identical insertion pattern of primary pinnae. The paired primary pinnae of this specimen's node "B" (fig. 2) descend from the horizontal plane of the main axis, into the plane of the plate. Figure 12 verifies this observation and demonstrates the downward pitch of the pinnae as viewed from the distal end of the specimen. The right lateral of node "A" (fig. 2), however, ascends from the plane of the main axis (the left lateral being absent). The three-dimensional orientation of this specimen's primary pinnae becomes clearly evident when the fossil is viewed from the side (fig. 13). Thus, the primary pinnae of this specimen also appear to be arranged in distichous pairs. Other specimens (fig. 6, 9), though not preserved extensively enough to verify an overall quadriseriate organotaxis, nonetheless corroborate the general paired organization of primary pinnae - and are therefore consistent with a quadriseriate-type of branch system.

Due to the orientation of these specimens in the surrounding sediment - with the paired laterals of each node departing to the left and right of the main axis (Text fig. 3 A) - the quadriseriate arrangement of laterals is somewhat obscured. The primary pinnae of a specimen oriented in the sediment in this manner would be compressed slightly, distorting the three-dimensional, quadriseriate organization of laterals, and producing an artifactual pattern that simulates a strictly opposite system. However in figures 1 and 2, the subtle, yet unmistakable alternation of nodes where the laterals ascend into the surrounding sediment with those where the laterals descend into the sediment clearly indicates the three-dimensionality of the branching system. A quadriseriate-type of organotaxis best accounts for these observations.

7.3 PRIMARY PINNA VARIATION

An intriguing aspect of the morphology of this plant, however, is the variation evident with respect to primary pinna arrangement. Two specimens appear to demonstrate a reduced quadriseriate to alternate arrangement of primary pinnae. In the case of the specimen seen in figure 3, both part and counterpart (fig. 15) have been thoroughly examined for the possiblity of a quadriseriate arrangement of primary pinnae. For a quadriseriately branched axis that is preserved in the orientation indicated by Text figure 3 B, the plane of fracture of a specimen is likely to pass through the thin layer of intervening sediment between a pair of primary pinnae. In such a situation, the compression surface of one primary pinna of a pair (at any given node) would tend to remain attached to the part, while that of the other member of the pinna pair would tend to remain attached to the counterpart. As a result, specimens would display an artifactual alternate arrangement of primary pinnae. However, no evidence of this condition was detected with respect to the specimen in figure 3. The lower arrow of figure 4 does indicate an axis which seems to be associated with the primary pinna axis above. However, the counterpart specimen reveals that these axes are unrelated (fig. 15). Thus, prior to preparation of this specimen by the uncovering technique, the main axis of this specimen appeared to give rise to only a single primary pinna at each node - in an overall alternate manner.

However, with careful uncovery of the overlying sediment, node "B" of this specimen (fig. 3) was found to possess an additional primary pinna of greatly reduced size (0.5 mm greatest width *vs.* normal primary pinna width of 2.5 mm) to the left of the main axis (figs. 4, 28). This dwarf primary pinna, preserved for a length of only 4 mm, bears a single secondary pinna with normal laminate pinnules. This node is therefore interpreted to have produced a true pair of primary pinnae, with one being of greatly reduced stature. Preparation of this specimen has also revealed a more proximal node (node "A" of fig. 3), where a single primary pinna departs to the right of the main axis (fig. 5). The primary pinna of this node thus occurs along the same side of the main axis as does the fully expressed primary pinna of the next more distal node. The overall insertion sequence of primary pinnae for this specimen is therefore not simply alternate. The occurrence of a dwarf primary pinna at node "B", and the departure at node "A" from an otherwise alternate organotaxis suggests that this specimen demonstrates a reduction sequence from a typical quadriseriate-type branching system. Each node appears to have developed a true pair of primary pinnae, with one member of the pair being of reduced size.

Since this specimen does not show a consistent alternation pattern of normal-sized primary pinnae, perhaps the reduced expression of any given pinna was not predetermined by the overall developmental program. Instead, pinna reduction may have been a local response to the influence of environmental parameters (in particular - light conditions, and the orientation of the plant to light). This situation might have occurred in an individual in which the main axis (or some segment of this organ) was oriented parallel to the ground, such that each primary pinna of a nodal pair was produced along the same side of the main axis. Exposure to direct sunlight under these conditions might have restricted the development of the upper primary pinna of a pair - leading to pinna reduction, and consequently reduced levels of self-shading (with respect to the lower member of the pinna pair). A developmental response of this type is a well documented feature of many modern plants, as illustrated by the dorsal *vs.* ventral leaf forms of *Selaginella* (Scagel, et al. 1966; Mauseth 1991). Thus, the developmental shift from a normal quadriseriate branching system to a more or less biseriate system may have been a photoreception strategy that served to reduce self-shading.

The specimen seen in figure 14 (occurring adjacent to the holotype specimen) also is interpreted to exhibit reduction from a quadriseriate-type of organotaxis to a biseriate system, with regard to primary pinna arrangement. The pinnules attached to this specimen are identical to those of other specimens - documenting that these fossils indeed derive from the same plant (fig. 17). Except for the distal-most node, the entire specimen was uncovered *via* the uncovering technique. Thus, with respect to the two more proximal nodes, there is no chance that primary pinna pairs were overlooked due to separation onto part and counterpart (as earlier discussed). With the uncovery method, if either of these nodes possessed a fully developed pair of primary pinnae, then both pinnae would have been found in attachment to the main axis. Yet, each of these nodes displayed only a single primary pinna (of normal dimensions) in attachment. The middle node was found to overlie an axis, thus creating the artifactual appearence of a node emitting a pair of primary pinnae (fig. 16). However, uncovering of this specimen has revealed that the underlying axis is completely separate from and unrelated to the main axis. Here again, the biseriate (specifically alternate) arrangement of primary pinnae of this specimen may be explained as a reduction from a general quadriseriate-type of system, perhaps as a strategy for improved photoreception efficiency.

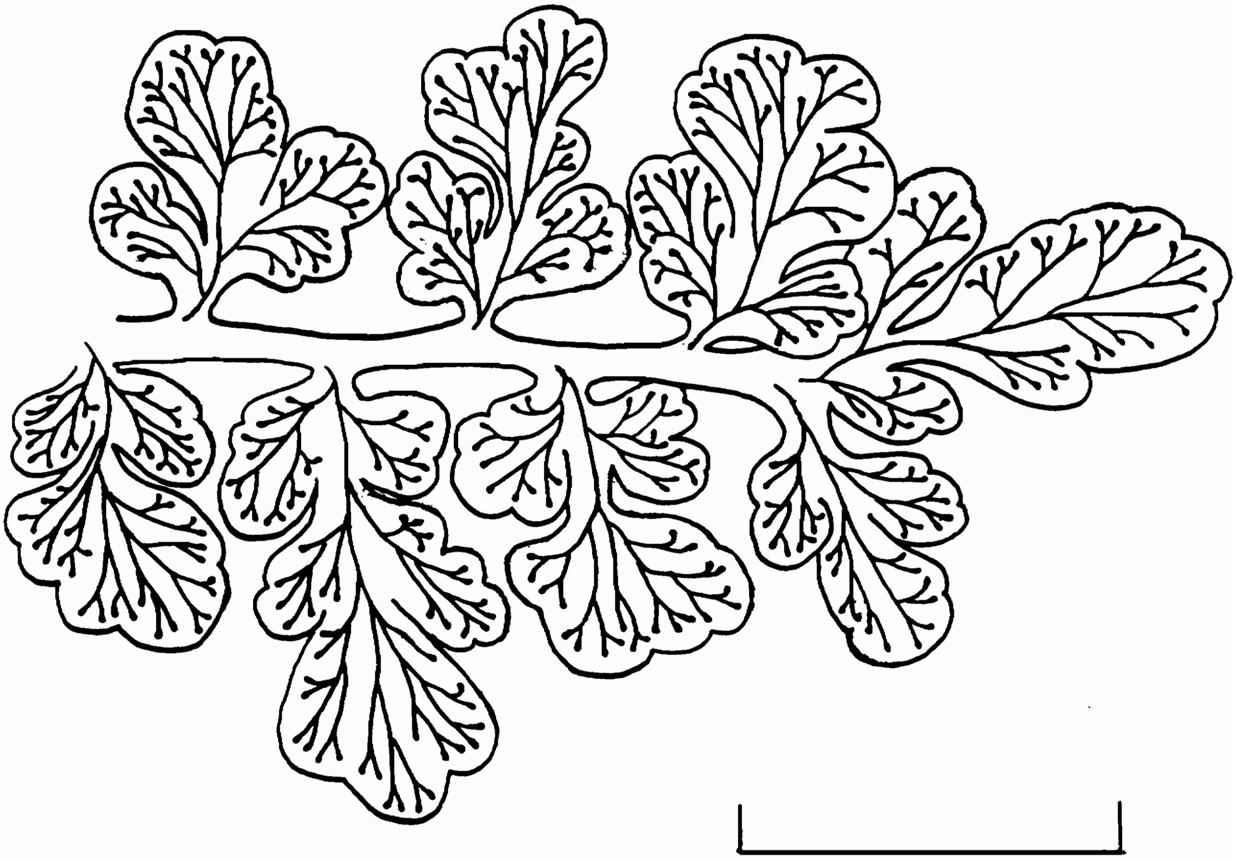
7.4 SECONDARY PINNAE

Primary pinnae give rise to secondary pinnae alternately, usually beginning along the anadromic side (figs. 18-20). Secondary pinnae are borne in the same plane as the main axis (i.e. these pinnae run parallel to the main axis). The initial secondary pinna occurs on the average 9 mm from the base of each primary pinna. The average distance between consecutive secondary pinnae in the same rank (i.e. on the same side of a subtending primary pinna) is 13 mm. However, a secondary pinna is on the average only 5 mm from the closest secondary pinna in the opposing rank (*vs.* an expected average of 6.5 mm for a truly alternate system). Thus, the arrangement of secondary pinnae may be better described as ranging from sub-opposite to alternate. No trend towards increase or decrease of internodal distance is detectable along the length of preserved primary pinna fragments.

Secondary pinnae occur in lengths of up to 1.4 cm. In larger specimens, they are approximately 1 mm wide basally, tapering to less than 0.5 mm wide distally. There is some indication, moving distally along a single primary pinna, of an increasing size gradient with respect to secondary pinnae - perhaps as a result of epidogenesis (fig. 20). However, primary pinnae are not preserved for lengths great enough to allow a rigorous assessment of this feature. One isolated pinna fragment, which is thought to be of the secondary order (based upon the presence of attached pinnules), measures 2.2 cm in length and is approximately 0.75 mm in width (fig. 21). The secondary pinnae of complete specimens might demonstrate even greater sizes.

7.5 PINNULES

Each secondary pinna generally bears six to seven laminated pinnules in an alternate manner, and terminates in a single pinnule (figs. 21-24, 27). A composite reconstruction of pinnule form is presented in Text figure 4, based primarily on the relatively large pinnules illustrated in figure 21, but also on all other available pinnule specimens of *Ellesmeria sphenopteroides*. With respect to these pinnules, the only remnant of the original lamina tissue is an organic residue, gray to golden brown in color.



Text figure 4: Reconstruction of Secondary Pinna With Laminate Pinnules for *Ellesmeria sphenopteroides*

scale bar = 1cm

Pinnule margins, though not very well preserved, are believed to have been somewhat broadly lobed (a shape commonly associated with the form genus *Sphenopteris*). Three main lamina lobes are often detectable (figs. 21-24, 27). Pinnule bases (fig. 21-27) are fairly narrow (relative to more distal regions of the lamina), and are perhaps weakly decurrent and weakly fused (i.e. interconnected by a thin layer of lamina). However, some uncertainty remains with respect to these last two features due to poor preservation. Cellulose acetate film pulls revealed no information regarding stomata form or cellular pattern.

In larger specimens, a pinnule can occupy an area approximately equal to that of a rectangle 9 mm in length and 5 mm in width. All the pinnules borne by a single secondary pinna can encompass a combined area equal to that of a rectangle 2.1 cm in length and 1.6 cm in width. If, as suspected, the isolated pinna fragment in figure 21 is of the secondary order, then the preceding area estimates are probably fairly conservative in relation to the maximum values possible for this plant.

The submergence of specimens in liquid (water used here) significantly enhances the details of pinnule form, particularly with respect to venation. Secondary pinnae initially supply each pinnule with a single vein (fig. 21). This main vein then divides anisotomously three to five times, generally corresponding to the main lobes of the pinnule (Text fig. 4, figs. 21, 23-27). The resulting secondary veins then continue to divide - initially anisotomously, but in an increasingly dichotomous manner towards the distal margin of the lamina. Ultimately, a single vein ending can be the product of up to 8 total vein branchings. Vein endings are quite distinctly enlarged and demonstrate a characteristic teardrop-shaped lobing pattern (Text fig. 4, figs. 21, 23-27).

7.6 APHLEBIAE

Each primary pinna bears at its proximal base a small aphlebia-like appendage (hereafter referred to as an aphlebia) in the catadromic position. This appendage, though apparently equivalent to a secondary pinna, is dichotomous in organization - unlike a normal secondary pinna. One such structure attached to the holotype specimen appears to exhibit a total of six dichotomous branchings (figs. 18, 29). Furthermore, this aphlebia is significantly smaller than a normal secondary pinna of the same specimen (6 mm *vs.* 12 mm in length, respectively). The total area enclosed by this aphlebia specimen is approximately equal to that of a rectangle 6 mm long and 4 mm wide.

The spatial arrangement of the ultimate tips of this organ is somewhat equiviocal. However, an aphlebia attached to one specimen seems to demonstrate some degree of planation in the arrangement of its ultimate tips (figs. 16, 32). Additionally, a very narrow band of golden-brown colored residue (which is quite similar to the preserved lamina residue of a normal pinnule) surrounds the tips of this organ (fig. 32). This observation suggests that the distal tips of an aphlebia of this plant may be slightly laminated. With the exception of only a few specimens, the preservation of this structure is generally poor - because of the apparently delicate nature of its construction. Thus, often only the bases of aphlebiae remain attached to a specimen of this plant (fig. 33).

7.7 MAIN AXIS PINNULES

In addition to primary pinnae, a few main axis specimens directly give rise to pinnule-like structures (figs. 9, 15). These organs are always poorly preserved, and therefore difficult to characterize. They appear to occur randomly, as they exhibit no regular pattern of arrangement on the main axis and are not associated with any other structure (such as primary pinnae or aphlebiae). They can be up to 1.2 cm in length, and usually display a relatively thick base (in comparison to normal pinnules). In one specimen, this base is 2 mm wide proximally, tapering to less than 0.5 mm wide distally (arrow "B" of fig. 30). This organ quickly dichotomizes, yielding what seem to be vein-like branches. These branches appear to be surrounded by an extremely thin film which may represent a lamina. In the same area of this specimen's counterpart, a cluster of normal laminate pinnules occurs (fig. 31). Their point of origin could not be ascertained, and their relationship to the pinnule-like organ of figure 30 is unclear. Approximately 1.7 cm proximal to this organ, a similar but smaller structure occurs along the same side of the main axis (arrow "A" of fig. 30). This structure dichotomizes twice, and may be the vascular strand of a pinnule-like organ. Clearly, these enigmatic structures are difficult to interpret. They seem to be pinnule-like in nature (rather than root-like), but they are quite different from normal pinnules (particularly in regard to the sparcity of branching and lamination).

7.8 ROOTS

Root-like structures occur in association with several specimens. The specimen in figure 20 provides the clearest example of such objects, which seem to emanate from the catadromic side of a primary pinna. These structures range from 5 mm to 1.3 cm in length. However, these presumed adventitious roots could not be verified to be in full attachment to the specimen. Roots may also extend from the specimen seen in figures 35-37. These root-like objects appear to form a dense mat along only one side of this specimen's main axis. This observation is consistent (as will become evident in the discussion section) with a system in which laterally extending branch units contact the ground, take root, and then reiterate the vegetative body of the plant.

Chapter VIII

Description - Anatomy

8.1 INTRODUCTION

Knowledge of the internal anatomy of this plant comes from a single pyrite and limonite petrified axis from another site of the Nordstrand Point Formation, upstream from the type locality. Unfortunately, the counterpart of this specimen was not recovered. Although it is somewhat poorly preserved as a result of exposure to weathering, there is little doubt that this specimen represents the species herein described. This interpretation is corroborated by a number of morphological and anatomical features of this specimen. Before fully examining the anatomical evidence, a brief discussion of the key morphological aspects of this argument is necessary.

8.2 MORPHOLOGY OF THE PETRIFIED SPECIMEN

The most important morphological evidence linking this specimen to those already dicussed is the quadriseriate arrangement of its primary pinnae. Under conditions of direct lighting and low magnification (figs. 34-35), this specimen appears to possess three alternately arranged lateral appendages (interpreted as primary pinnae). However, with low angle illumination under higher magnification, a second primary pinna becomes apparent at each of the two more proximal nodes. In figure 38, the arrows indicate the raised impression surfaces of two overlapping axes deriving from the proximal most node. The right arrow designates a primary pinna which retains a distal segment of compressed carbon (figs. 34-35). This pinna is clearly a product of the proximal-most node of this specimen. However, the sleeve of carbon at the base of this node (fig. 34) actually belongs to a second primary pinna, fully attached to the main axis of the specimen (fig. 38). Similarly, the middle node of the specimen also appears to give rise to two overlapping primary pinnae. The carbonized base of one pinna is clearly attached to the main axis at this node (fig. 35-36). However, higher magnification reveals the raised impression surface of another axis overlying this pinna (fig. 39). An even higher magnification view confirms this observation and illustrates a "criss-crossing" cell pattern that results from the overlap of the two axes (fig. 40). Both the overlying and underlying axes seem to emanate from the middle node, and are therefore interpreted as a pair of primary pinnae. Thus, this specimen appears to demonstrate an overall distichous arrangement of paired primary pinnae, preserved in the orientation illustrated by Text figure 3 B.

The morphology of this specimen compares closely with those previously described in a number of other key areas. The main axis of the specimen displays a prominent, double indented groove (figs. 34-35) that corresponds to the vascular groove of all other specimens of this plant. It is important to note that no other known element of this flora demonstrates a vascular groove of this configuration (which will be explained in greater detail later). Additionally, the primary pinnae of this specimen display attachment bases of the same type (i.e., cornute, as previously described) seen only in specimens of this plant - and not in any other known element of this flora (figs. 34-36). Furthermore, the axis dimensions, internodal distances, and primary pinna angles of attachment compare closely to those of other specimens in the collection. Although pinnules of the type previously discussed have not been found attached to this specimen, the veins of such pinnules do cover the impression surface of the main axis. The vein patterns of these pinnules are identical to those of *Ellesmeria sphenopteroides*, with anisotomous divisions proximally, dichotomous forks distally, and expanded, lobed tips terminally (fig. 41-43). These pinnules, which seem to occur in an alternate series, probably represent a distal primary pinna that had bent back along the main axis. Finally, our confidence in the attribution of this specimen is bolstered by the certainty that it cannot represent any of the other known taxa from this extensively sampled, low diversity flora.

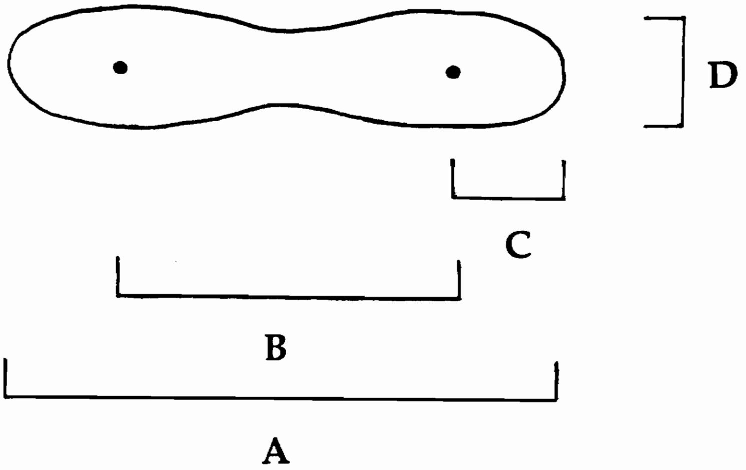
8.3 ANATOMY OF THE PETRIFIED SPECIMEN

The petrifaction removed from this specimen had a total length of 12.5 cm. Of this length, 9 cm came from three pyrite and limonite petrified segments surrounded by compressed carbonized material (representing the compressed external tissues of the specimen). These segments served as the source of the 68 transverse sections. Within these sections, the cell lumens appear to have been replaced almost exclusively by pyrite, while the cell walls are composed of limonite in combination with some of the original, but degraded, organic wall material. The remaining 3.5 cm of the petrifaction consisted of three segments without an external carbonized sheath. These segments appear to have been subjected to more extensive weathering and oxidation - resulting in a higher proportion of limonite to pyrite content. As the preservation of these segments seemed relatively poor (highly oxidized state, incomplete preservation of vascular strand, general absence of external tissues, etc.), they were reserved for longitudinal views.

8.3.1 MAIN AXIS STELE

The transverse sections provide a great deal of information concerning main axis and primary pinna stele form, as well as some information regarding cortical tissues. The main axis stele, although incompletely preserved throughout these sections, is seen in enough detail to permit reconstruction of its overall form. This vascular strand is an elongate (2.4-2.8 mm long, 0.4-0.9 mm wide), ribbon to clepsydroid-shaped protostele (Text fig. 5). The stele is bipolar, with the two protoxylem poles occurring at opposite ends of the vascular strand (each being inset approximately 0.3-0.5 mm from the end of the strand). The distance between protoxylem poles is interpreted to be at least 1.4 mm (and perhaps as much as 2 mm). The stele demonstrates a mesarch pattern of vascular development, such that the protoxylem poles are completely surrounded by metaxylem. The intervening area of metaxylem between these poles includes no additional protoxylem. The vascular tissue of this single petrified specimen is composed solely of primary xylem tracheids. Whether the species as a whole was capable of developing a vascular cambium is unknown.

As noted above, these conclusions concerning main axis stele form are based upon fragmentary, yet nonetheless compelling evidence. Both ends of the stele are never visible within the same section. However, each end, with its associated protoxylem pole, is preserved at some point within the complete series of sections. Figures 47-48 demonstrate the left half (as viewed from the proximal end of the specimen) of the main axis stele, with a single protoxylem pole (composed of 3-5 preserved cells). The left arrow of figure 47 indicates a subtle, yet unmistakable area of smaller cells interpreted as protoxylem surrounded by larger diameter metexylem cells. Figure 48



Text figure 5: Reconstruction of Bipolar Main Axis Stele for *Ellesmeria sphenopteroides.*

A (strand length) = 2.4-2.8 mm

B (distance between protoxylem poles) = 1.4 mm (at least)

C (distance from protoxylem poles to strand edge) = 0.3-0.5 mm

D (maximum strand width) = 0.4-0.9 mm

provides a higher magnification view of the protoxylem pole associated with the left end of the main axis stele. Figures 47 and 48 also clearly show the elongate, ribbon-like nature of the stele. Furthermore, the arrows to the far right of both figures 47 and 48 indicate a slight invagination of the strand (approximately 1.4 mm from the strand's end) which may define the mid-region of an overall, somewhat clepsydroid-shaped (i.e., hour-glass) stele. Additionally, these figures show that towards the outer edge of the stele, metaxylem cells are smaller.

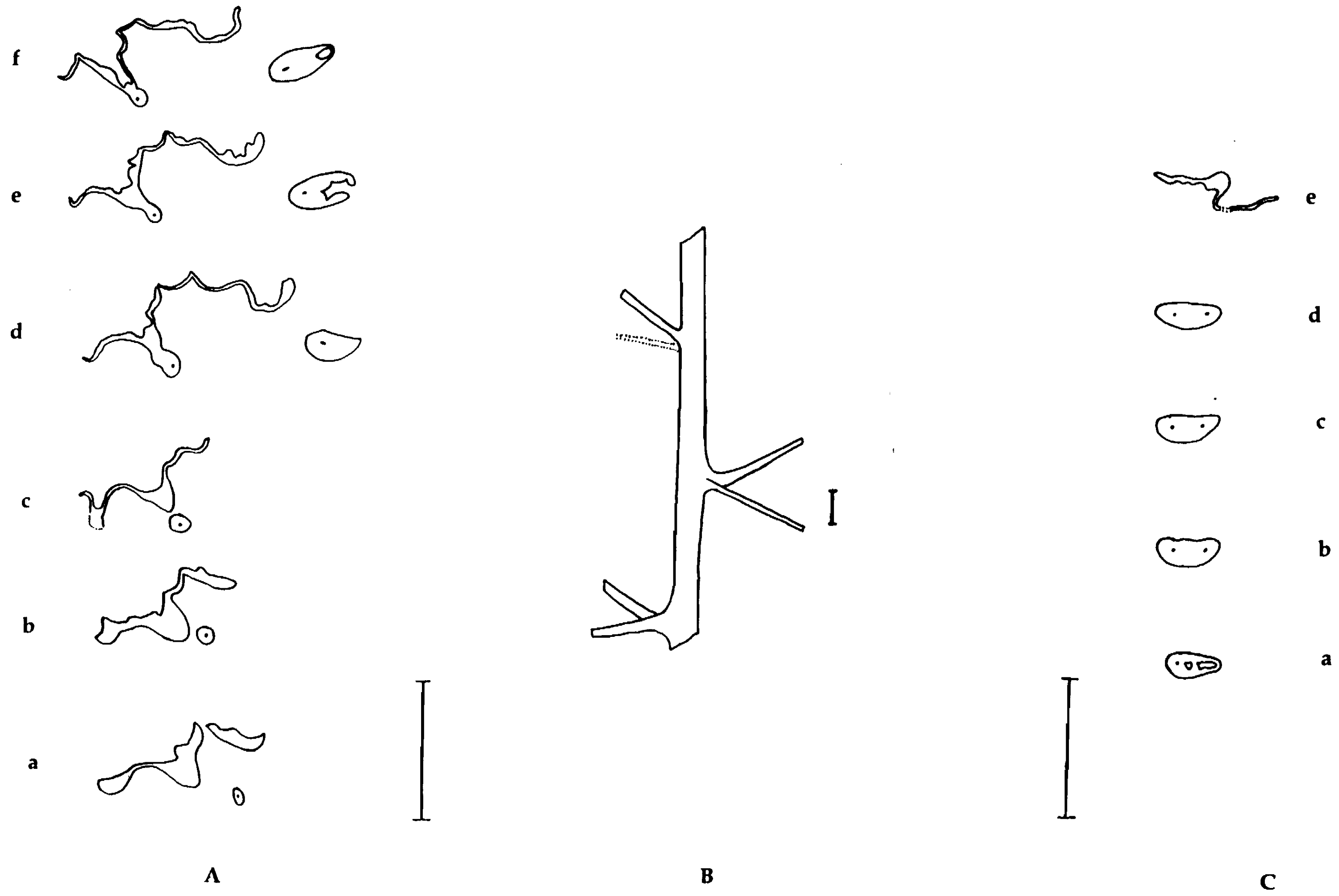
The right end of the main axis stele is preserved in more proximal sections of the specimen, as demonstrated by figures 49-50. The right end of the stele appears to be a mirror image of the left end, thus conforming to the interpretation of the stele as bilobed in form. The arrows of figures 49-50 indicate the single protoxylem pole of the right half of the stele. This protoxylem pole consists of approximately 10-15 cells. Weakly defined rows of metaxylem radiate from this area of protoxylem. Additional sections (figs. 44-46) further substantiate the bilobed, bipolar reconstruction of the main axis stele. In figure 51, the elongate strand is preserved only along its edge, suggesting its overall length to be at least 2.8 mm. This length is approximately twice the distance from the end of the strand to the aforementioned invagination area seen in other sections (figs. 47-48, and even more clearly in fig. 44), suggesting that this cleft does indeed mark the mid-region of a bilobed stele.

When compressed by sediment, a plant axis with a bilobed stele often makes an impression in the surrounding matrix, such that during the process of fossilization a central groove is permanently imprinted on the surface of the axis (as seen in specimens of the Late Devonian fossil plant *Rhacophyton ceratangium* - Pl. 1, fig. 1, Andrews and Phillips 1968). Thus, the external occurrence of a central vascular groove in specimens of *Ellesmeria* (especially the petrified specimen) provides morphological corroboration of the bilobed nature of this plant's stele. In larger main axis specimens, this groove is often bordered by two ridges, which represent the two lobes of the original stele (fig. 4, 8). Consequently, counterparts of such specimens display a groove that is double indented in form (fig. 15). The groove of an axis that is less robust in size is often marked by only a single ridge or indentation (which relates to the central cleft of the bilobed stele), because of the more diminutive size of the original vascular column (fig. 6-7).

8.3.2 PRIMARY TRACE DEVELOPMENT

The mode of primary pinna trace formation for this plant cannot be ascertained, because of the lack of preservation in the petrified specimen of the junction between the primary pinna and main axis vasculatures. However, a few primary pinna traces are themselves preserved in enough detail to provide a basic understanding of their form and developmental history, subsequent to separation from the main axis stele. The main axis stele supplies each node with a vascular trace which initially recapitulates the general features of the main axis vasculature. Thus, this trace is relatively elongate (0.5-0.7 mm long/0.2-0.3 mm wide), ribbon-like, bilaterally symmetrical, and bipolar (fig. 49). This form is also suggested by the edge of a trace in figure 52. Protoxylem poles usually consist of less than 10 cells. As will be discussed later, this trace (which will be referred to as a primary trace) is believed to have divided in half, yielding a pair of traces which then supplied the pair of primary pinnae at any given node.

Text figure 6 correlates specific cross sectional views with their position within the whole specimen. The primary trace that supplies node "B" originates proximally to node "A", and extends through the cortex of the main axis for the length of the entire internode between nodes "A" and "B" (approximately 4.2 cm). This trace is initially somewhat elliptical in shape, and its one evident protoxylem pole consists of only one to a few cells (fig. 53, Text fig. 6). The other protoxylem pole of the trace is not preserved at this level. At this point, just proximal to node "A", the trace measures 0.5 mm long by 0.2 mm wide. As the trace continues distally through the cortex of the main axis, it expands epidogenetically, attaining a length of 0.7 mm by a width of 0.3 mm (fig. 49, Text fig. 6). At this level, the trace exhibits a slightly more



Text figure 6: Drawings of the Petrified Axis of *Ellesmeria sphenopteroides* and Selected Anatomical Cross Sections crescentic shape, while maintaining a bipolar form. The trace remains visible through several more distal sections and continues to expand in size. The trace ultimately appears to achieve a length of at least 1 mm and a width of 0.4 mm (fig. 54, Text fig. 6). However, the poor preservation at this level of the petrifaction obscures the overall form of the trace just proximal to the node that it supplies (i.e. node "B" of Text fig. 6).

The primary trace that supplies the proximal-most node (i.e. node "A" of Text fig. 6) yields additional details of the final stages of primary trace development. The incomplete and somewhat distorted preservation of the trace (as well as of the main axis) complicates its reconstruction, resulting in the somewhat speculative nature of the following conclusions. Yet, comparison of the associated anatomical and morphological data yields a coherent and convincing overall interpretation.

Figure 55 illustrates this trace, just proximal to node "A". The uppermost arrow in this figure indicates the separation of this trace from the poorly preserved main axis stele. The trace supplying node "A" is at this point multilobed, with three ribs visible of an overall apparent four-ribbed outline. Thus, this primary trace, which presumably was bilobed in form initially, apparently developed a four-ribbed pattern prior to dividing to yield two secondary traces (which then supplied the pair of primary pinnae). The primary trace is at this point (just proximal to the node that it supplies) approximately 0.9 mm long and 0.6 mm wide. This trace therefore compares quite closely in its dimensions to the later stages of the trace that supplies node "B" (fig. 54).

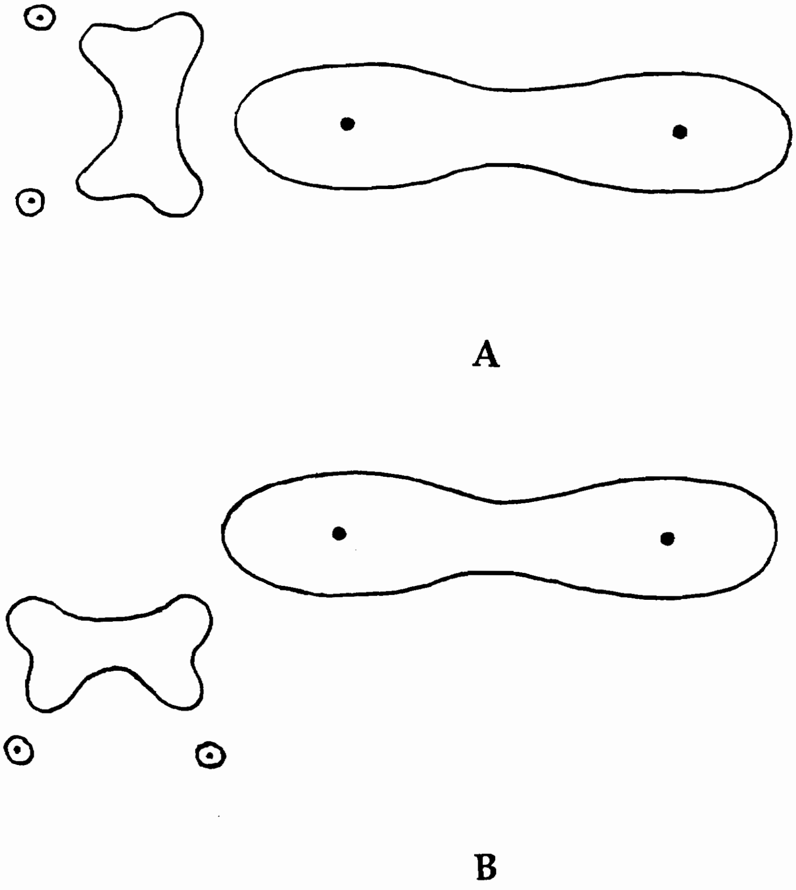
8.3.3 APHLEBIA TRACE DEVELOPMENT

Text figure 6 illustrates a series of sections which track developmental modifications of the two lower ribs of this trace (these illustrations correspond to figs. 55-61). At some point within this series, each of these two lower ribs demonstrates a single protoxylem pole, indicating the site of an incipient circular trace. Moving distally through this series of sections, a small, centrarch, circular trace (0.2 mm in circumference) approaches (figs. 55-58) and eventually merges (figs. 59-61) with the lower right rib of the primary trace supplying node "A" of Text figure 6. The proximal to distal developmental orientation of this circular trace thus runs opposite to that of the main axis as a whole. The orientation of this trace in such a manner suggests the vascular supply of an appendage borne in the catadromic position by a primary pinna. This anatomical evidence thus corroborates the aforementioned morphological observation that primary pinnae bear small, catadromic pinnules (i.e. aphlebiae).

Simultaneously, the four-ribbed primary trace appears to be in the process of producing a second circular trace. Although incomplete preservation prevents documentation of its entire developmental history, the lower left rib of the primary trace is also interpreted to be an incipient circular trace. In preparation for the production of a circular trace, this rib becomes rounded (0.2 mm in circumference) and develops a central protoxylem pole, which is implied by the radiating rows of the surrounding metaxylem cells (figs. 55-56). The resulting centrarch trace would therefore have been identical (in size, shape, and presumably developmental history) to the catadromic aphlebia trace associated with the lower right rib of the primary trace. Thus, this pair of circular traces, associated with node "A" of text figure 6, is believed to represent the vasculature of a pair of catadromic aphlebiae.

This interpretation requires the assumption that torsional twisting of the primary trace occurred during the process of fossilization (because of the compaction and defluidization of sediment). Thus, a 90 degree counter-clockwise rotation resulted in the reorientation of the trace, such that its catadromic side now lies parallel to the long axis of the main axis stele (Text fig. 7). The crushed/distorted and poorly preserved state of cortical tissues in this series of sections is consistent with this interpretation and suggests that the cortex would have provided little or no restriction to such twisting effects.

If this interpretation is correct, the occurrence of a pair of circular aphlebia traces on the same side of the main axis at this location substantiates the morphological observation that this specimen bears pairs of primary



Text figure 7: Comparison of Primary Trace Orientation (With Respect to Main Axis Stele) Before (=A) and After (=B) Fossilization

Catadromic side of primary trace designated by an associated pair of circular aphlebia traces. Black dots represent protoxylem.

pinnae at each node. Furthermore, the two ribs (fig. 55) that produced the aphlebia traces form an angle which closely approximates that formed at any given node by a pair of primary pinnae. Thus, the primary trace seems to produce a pair of catadromic pinnule traces before dividing in half to form the vasculature of the two primary pinnae at a node.

More distal sections of this specimen show a small, isolated, terete trace, identical to the one shown in figure 56 (fig. 70, distal to node "C" of Text fig. 6). The relationship of this trace to a primary trace or the main axis stele is not evident. However, based on its marked similarity to the aphlebia traces already discussed, this centrarch trace probably supplied an aphlebia of a more distal node (i.e. distal to node "C" of Text figure 6).

8.3.4 SECONDARY TRACE DEVELOPMENT

Upon the division of a primary trace, the resulting secondary traces probably re-established a bipolar, bilobed form. An internal stele of this type is suggested by the external form of the vascular groove (identical to that observed for main axis specimens) which occurs in association with most primary pinna specimens (fig. 2-4, 5, 7, 23). The observed distichous arrangement of secondary pinnae, with respect to their subtending primary pinna, further substantiates this interpretation. A pair of secondary traces may actually be visible in more distal sections (between nodes "B" and "C" of

Text fig. 6), in association with a more fully preserved segment of the main axis stele. Two narrow strips (one to two cell layers thick) of tissue, potentially xylary in nature, occur above and below, respectively, the main axis stele in this area of the petrifaction (fig. 48). These elongate strips could possibly represent the outer edges of a pair of bilobed secondary traces.

8.3.5 XYLEM PITTING AND CELL DIMENSIONS

Protoxylem consists of tracheids that range from 8 um to 26 um in diameter, and can achieve lengths of at least 1.7 mm. The annular to helical wall thickenings of these cells are visible in longitudinal views through a protoxylem pole (figs. 63-64). No parenchyma was seen in any protoxylem pole. The walls of early metaxylem tracheids (close to a protoxylem pole) possess scalariform-bordered pits (figs. 63-67). These cells are 17 um to 43 um in diameter, and can attain lengths of at least 2.1 mm. However, later formed metaxylem tracheids (farther from a protoxylem pole) are larger (ranging from 22 um to 56 um in diameter), and some possess walls with circular-bordered pits that are two- to four-seriate (figs. 63-64, 68-69). These pits appear to be slightly elliptical, and they often slant diagonally in a parallel orientation (fig. 68). Late metaxylem tracheids can achieve lengths of at least 2 mm.

8.3.6 CORTICAL ANATOMY

A zone of relatively thick-walled parenchyma characterizes the inner cortex (figs. 49-50, 53, 59-62). These cells, which are generally large in comparison to xylem cells, range in diameter from 34 um to 130 um. In longitudinal view, these cells appear elongate, with lengths ranging from 0.6-1 mm (fig. 71). The lower end of the diameter range of these elongate cells probably results from their slight distal taper. The presence of a significant amount of intercellular space indicates that this tissue could perhaps have been chlorenchymatous in nature. This tissue is very fragmentary in its preservation - often being almost completely absent from a cross-section. In addition to the parenchymatous inner cortex, an outer cortical layer of fibrous cells may have occurred. The best evidence for this fibrous tissue comes from morphological specimens, which commonly display a microscopically ridged surface (somewhat visible in fig. 30). Additionally, a few cross-sections seem to indicate a thin outer strip of small diametered, relatively thick-walled cells (fig. 62). These cells tend to be somewhat rectangular in shape, exhibiting on average a radial plane diameter of 31 um and a tangential plane dimeter of 21 um. Such a tissue could perhaps, when compressed and coalified, be the source of the outer surface ridging. However, this outer cortical layer does not demonstrate the pronounced wall thickenings nor the anastomosing pattern characteristic of the fiber bundles of a sparganum/dictyoxylon-type of cortex.

Also absent from this plant is the external surface ridging and pitting patternindicative of an underlying sparganum/dictyoxylon-type of cortex.

Chapter IX

COMPARISONS WITH OTHER TAXA

9.1 INTRODUCTION

Upon the discovery of *Ellesmeria,* the significance of this plant's foliage was immediately recognized, due to its Frasnian dating. The presence of sphenopteroid foliage in Late Devonian to Early Mississippian-age strata is almost exclusively interpreted as evidence of gymnospermous vegetation (Galtier 1981; Galtier and Scott 1985; Rothwell and Scheckler 1988). This interpretation derives from the assumption that ferns (excluding members of the cladoxylales) lagged millions of years behind pteridosperms in the development of well-laminated foliage. Ferns are thus not thought to have developed *Sphenopteris*-like pinnules until the Upper Visean or later (Galtier and Scott 1985). Since currently the earliest recognizable gymnosperms are Mid and Late Famennian in age (Rothwell and Scheckler 1988), the Mid Frasnian dating of *Ellesmeria* suggests the possibility that this plant represents the oldest yet discovered form of pteridosperm. However, despite the resemblance of its foliage to that of some early gymnosperms, additional aspects of the morphology of *Ellesmeria* are simultaneouly reminiscent of zygopteroid ferns. Furthermore, *Ellesmeria* demonstrates at least superficial similarities to a number of other plant types of the Late Devonian. Thus, from the earliest stages of this project, it has been clear that the evidence bearing upon the evolutionary affinities of this plant would require intense scrutiny, against the background of a broad range of Devonian plant types.

9.2 PROGYMNOSPERMS

Except for laminate foliage and the suite of pitting types of primary xylem, *Ellesmeria* has no similarity of organization with members of the Archaeopteridales. No further comparison is necessary. *Ellesmeria,* however, does share many organizational features with members of the Aneurophytales, so that more substantial comparisons are necessary.

The ultimate appendages of some aneurophytes (e.g., *Triloboxylon* and *Proteokalon;* Scheckler and Banks 1971a, 1971b; Scheckler 1975, 1976) are planated and thus regarded as "pinnule"-like. However, the laminated pinnules of *Ellesmeria* , that are multiple-veined with anisotomous proximal vein divisions, are very different from the non-laminated, strictly forked ultimate appendages of aneurophytes.

Successive branch orders with repetitive vascular form characterize both *Ellesmeria* and aneurophytes, and probably other trimerophyte descendants as well. Yet, the distichous arrangement of paired laterals borne by main axes that then bear secondary pinnae that are oriented parallel to the main axis, seen in *Ellesmeria,* is quite different from the three-dimensional, helical or decussate branching of the Aneurophytales (Beck and Wight 1988).

Furthermore, the rachial pinnules of *Ellesmeria* have no counterpart in the Aneurophytales where the forked ultimate appendages are borne only by the ultimate branch order (Scheckler 1976). Nor do the catadromic pinnules, borne by primary pinnae of *Ellesmeria* , compare with the positions of the first, basal-most ultimate appendages of any aneurophytalean. The basal ultimate appendages of Aneurophytales are always lateral or anadromic; they are never catadromic. Internally, the bipolar, ribbon-like vascular strand of the main axes and primary pinnae of *Ellesmeria* is wholly unlike the three- or four-ribbed actinosteles of Aneurophytales with multiple mesarch protoxylem strands (Beck and Wight 1988).

In conclusion, although three-dimensional branching systems of many Devonian trimerophyte derivatives appear superficialy similar, a careful analysis of its branch pattern shows that *Ellesmeria* is wholly dissimilar to any progymnosperm.

9.3 PTERIDOSPERMS

As mentioned previously, the possession of sphenopteroid foliage (referred to here in a general sense) stands out as a fundamental similarity between *Ellesmeria* and early gymnosperms (i.e., pteridosperms of the orders Elkinsiales, Calamopityales, and Lyginopteridales). Given the fact that the stratigraphic position of this new plant lies within the Upper Devonian - when only gymnosperms were thought to have yet achieved foliage of this type - the potential gymnospermous affinity of *Ellesmeria* cannot be overlooked. In fact, if the Frasnian-aged *Ellesmeria* were known solely from its pinnules, most paleobotanists would probably accept its foliage as evidence for the oldest yet discovered gymnosperm (the oldest known gymnosperms being *Moresnetia zalesskyi* Stockmans and *Elkinsia polymorpha*Rothwell, Scheckler and Gillespie of the Mid Famennian order Elkinsiales, Rothwell and Scheckler 1988; Rothwell, et al. 1989). The most obvious feature that unites the foliage of *Ellesmeria* to that of early pteridosperms is the broadly-lobed outline of its fully laminated pinnules. Pinnules of this shape, attributable to the form genus *Sphenopteris*, characterize many species of pteridosperms (ranging in stratigraphic age from the Mid Famennian to the Upper Pennsylvanian - Galtier and Scott 1985; Rothwell and Scheckler 1988). Additionally, the venation pattern of the pinnules of *Ellesmeria* , like that of the pinnules of early pteridosperms, is largely dichotomous in nature. Furthermore, in both *Ellesmeria* and early gymnosperms, pinnules are borne biseriately (with one or more intervening orders of pinnate branching) on a bifurcating "frond unit". If *Ellesmeria* were proven to be a pteridosperm, this bifurcating "frond unit" (i.e., what has herein been described for this new plant as paired primary pinnae) would actually be a dichotomizing frond petiole, or rachis. The main axis that bears this bifurcating frond would therefore be recognized as the morphological stem of the plant.

Yet, a careful comparison of the constructional details of *Ellesmeria* and early gymnosperms calls into question the homology of "frond units" in these plants (note that the following analysis utilizes the seven points of comparison for sphenopteroid foliage presented in the preceding background section):

1) The most fundamental distinction between the foliage of *Ellesmeria* and early pteridosperms is the organotaxis of the axis bearing the bifurcating "frond units". The bifurcating "frond units" of *Ellesmeria* are arranged in a distichous, quadriseriate pattern. However, in almost all known pteridosperms, the stem produces fronds in a helical pattern (usually in a 1/3 or 2/5 phyllotaxis, as for *Elkinsia, Tristichia, Laceya,* and *Calamopitys*) or in a decussate fashion (as for *Tetrastichia* and *Quaestora*)(Taylor 1981; May and Matten 1983; Stewart 1983; Serbet 1991).

2) Viewed from the exterior, each of the primary pinnae of *Ellesmeria* is completely independent of its nodal partner for its entire length. In contrast, the morphological bifurcation of the frond of pteridosperms normally occurs several centimeters distal to the point of attachment of the frond to the stem. Viewed from an anatomical perspective, the frond trace of

Tristichia may sometimes fork while still within the cortex of the stem, but the petiole base of this plant remains united and does not divide until after separation from the stem (Matten and Banks 1969). The primary pinnae of pteridosperm fronds (including those of *Tristichia*) thus share a common petiole base of significant length.

3) *Ellesmeria* exhibits a dichotomous, catadromic pinnule (or aphlebia) at the base of each primary pinna (i.e., a single pair of aphlebiae for each pair of primary pinnae). Pteridosperms do not possess pairs of aphlebiae of this type at the base nor point of bifurcation of the frond. However, they can display pinnules that have been termed "aphlebiae" [that range in form from dichotomous (*Sphenopteris*) to ovoid (*Cyclopteris*)] along their petioles and/or primary pinnae (Gensel 1973).

4) The anatomical pattern of the main axis that bears the "frond units" in *Ellesmeria* differs dramatically from that seen in pteridosperms. The main axis of *Ellesmeria* displays a protostele with two lobes - each with a single area of protoxylem. This organ in early pteridosperms (i.e., the stem) demonstrates a protostele as well, but with typically at least three lobes (as in *Elkinsia, Tristichia, Laceya,* and *Stenomyelon*), and sometimes four or more lobes (as in *Tetrastichia*)(Galtier 1988; Rothwell and Scheckler 1988). Multiple areas of protoxylem are always present in the stem stele of pteridosperms (Taylor 1981; Stewart 1983). Thus,

the main axis stele of *Ellesmeria* is bilaterally symmetric in orientation, whereas the stem stele of early gymnosperms tends to be radially symmetric.

5) The anatomy of the bifurcating "frond units" of *Ellesmeria* is fundamentally distinct from that of pteridosperms. For *Ellesmeria,* the traces that supply the primary pinnae (i.e., its "frond units") appear to recapitulate the bilobed, bipolar form of the clepsydroid stele of the subtending main axis. Thus, the internal anatomy of both the main axis and the primary pinnae is bilaterally symmetric in orientation. As described previously, the initially bilobed, crescent-shaped primary pinna trace may become four-ribbed prior to bifurcating (i.e., yielding the vasculature of a primary pinna pair). However, the ultimate stele of each primary pinna seems to be clepsydroid in shape, based on the distichous arrangement of the secondary pinnae, as well as on the observation for primary pinna specimens of an external vascular groove identical to that associated with main axis specimens.

The anatomy of the "frond units" of early gymnosperms (i.e., their dichotomizing fronds) differs significantly from the pattern described for *Ellesmeria sphenopteroides.* In typical early pteridosperms, the radially symmetric stem produces a frond trace which usually, like the primary pinna trace of *Ellesmeria,* is bilaterally symmetric with respect to internal anatomy. Yet, the frond trace anatomy of early pteridosperms is unique in design, with two basic types evident - conforming to the form genera *Lyginorachis* and

Kalymma. Anatomy of the *Lyginorachis*-type (associated with the pteridosperm orders Elkinsiales and Lyginopteridales - Taylor 1981; Rothwell and Scheckler 1988) commonly demonstrates a flat or concave adaxial suface and a corrugated, convex abaxial surface. Each abaxial ridge is associated with a protoxylem area - such that multiple protoxylem poles occur within a trace. The multipolar petiole traces of *Tristichia* and *Tetrastichia* greatly resemble the *Lyginorachis*-type, but they display only two abaxial ridges, and are therefore referred to as butterfly or papilionoid in shape (Galtier 1988). A *Kalymma*-type trace (associated with the order Calamopityales - Taylor 1981) exhibits a circle or semicircle (concave towards the adaxial side) of independent vascular bundles, each with a separate zone of protoxylem. In some species (such as *Lyginorachis papilio*), a *Kalymma*-like trace actually fuses distally to form a *Lyginorachis*-type trace (Long 1963). At the point of frond bifurction, petiole traces of both the *Lyginorachis*-type and the *Kalymma*-type divide, and sometimes become C-shaped (resembling somewhat the probable bilobed shape of primary pinna traces of *Ellesmeria*), but they always maintain multiple areas of protoxylem (Taylor 1981). Thus, in summary, the primary pinna anatomy of *Ellesmeria* is significantly different in development and form from the frond anatomy of early pteridosperms.

6) The basic lamina form displayed by pinnules of *Ellesmeria* appears to be distinct, on close examination, from that of the pinnules of Late

Devonian and Early Carboniferous pteridosperms. The lamina of *Ellesmeria*'s pinnules appears quite thin and delicate (non-sclerenchymatous), with venation that is proximally overtopped. The pinnule form and venation of some later Carboniferous pteridosperms (such as *Palmatopteris alata* and *P. sarana*) approximate those of *Ellesmeria* fairly closely (Ramis et al. 1979). However, the pinnules of early pteridosperms (which are more time equivalent to this new plant) do not seem to resemble very closely those of *Ellesmeria*. Pinnules of early pteridosperms display mainly isotomous forkings and seem to exhibit a fairly tough, perhaps sclerenchymatous lamina that often obscures the primarily dichotomous venation (as shown by various gymnospermous pinnule specimens reported by Stockmans 1948 from the Evieux Formation of Belgium, and by the *Sphenopteridium*-like specimens illustrated by Long (1964) from Berwickshire, as well as by the *Sphenopteris*-like pinnules reported by Rothwell and Erwin 1987, Rothwell and Scheckler 1988, and by Rothwell, et al. 1989 from the Famennian of West Virginia).

7) The stems of all known early pteridosperms display a sparganum/dictyoxylon-type of outer cortex (Galtier 1988). This sclerenchymatous tissue zone consists of radial bands of anastomosing fibers. Clearly visible in anatomical sections, this tissue layer is also typically evident in morphologically preserved specimens - in the form of a characteristically ridged and pitted surface pattern (as has been shown for *Laceya* - fig. 3, May

and Matten 1983). No evidence, either from morphologically or anatomically preserved specimens, suggests that *Ellesmeria* possessed such a sparganum/dictyoxylon-type of cortex.

8) An additional distinction between the foliage of *Ellesmeria* and pteridosperms is the plane of orientation of secondary pinnae. *Ellesmeria* bears its secondary pinnae in the same plane in which the main axis lies (i.e., parallel to the main axis). However, the secondary pinnae of all known pteridosperms are apparently borne perpendicular to the plane in which the stem occurs (as in *Heterangium*, Shadle and Stidd 1975).

The absence of any knowledge regarding the reproductive structures of *Ellesmeria* prevents a definitive assessment of the gymnospermous *vs.* non-gymnospermous affinities of this plant. Clearly, the basic foliar morphology of *Ellesmeria* bears some similarity to that of early gymnosperms. However, the greater weight of evidence suggests that these similarities do not represent homologies, but rather result from convergent evolution.

9.4 *Schopfiastrum decussatum*

Schopfiastrum decussatum Andrews, a presumed seed fern with sphenopteroid foliage from Middle Pennsylvanian localities of Illinois, stands apart from typical pteridosperms with regard to basic patterns of morphology and anatomy (Rothwell and Taylor 1972). *Schopfiastrum* in fact bears a great deal of morphologic and anatomic resemblance to *Ellesmeria,* in that both its main axis (i.e., stem) and fronds demonstrate bilateral symmetry. Thus, the stem of *Schopfiastrum* produces biseriate fronds in two ranks (as opposed to the three or more ranks of other pteridosperms). Since each frond bifurcates quickly (relative to other pteridosperms), the stem exhibits an overall distichous arrangement of paired rachides. This pattern of branching is reminiscent of the distichous and quadriseriate system of *Ellesmeria.* However, the paired rachides of a *Schopfiastrum* frond can share a common base for up to 11 cm, and the rachis dichotomy is never immediate (i.e., at the point of attachment to the main axis) as in *Ellesmeria.* Also, *Schopfiastrum* bears its primary pinnae in a plane perpendicular to that in which the stem occurs, like other lyginopteridalean gymnosperms (not parallel to the plane of the main axis, as in *Ellesmeria*). Pinnules of *Schopfiastrum* (which have been compared to those of the form genus *Mariopteris*) are slightly lobed, but not nearly so much as those of *Ellesmeria* (Stidd and Phillips 1973). Pinnules of *Schopfiastrum* further differ from those of *Ellesmeria* in their broadly decurrent attachment to the subtending pinna, and in their entirely dichotomous venation.

Like the main axis of *Ellesmeria,* the stem of *Schopfiastrum* possesses an elongate, bilobed protostele. Yet, whereas the stele of *Ellesmeria* exhibits only two protoxylem poles, the stem stele of *Schopfiastrum* always displays at least four areas of protoxylem (Rothwell and Taylor 1972). The stele of the frond rachis of *Schopfiastrum*, like that of the primary pinnae of *Ellesmeria*, is bilaterally symmetric. However, the rachis stele of *Schopfiastrum* is of the *Lyginorachis*-type (i.e., with abaxial ribs and multiple protoxylem points), and is therefore not clepsydroid (i.e., bilobed and bipolar) as in *Ellesmeria*. As stated earlier, *Schopfiastrum* has not been proven definitively to be a gymnosperm (because of the absence of attached seeds) - but the occurrence in this plant of a sparganum/dictyoxylon-type of outer cortex, as well as a gymnospermous bifacial vascular cambium, lend strong support to this interpretation. These tissue systems, which are diagnostic of pteridosperms (but are also found in aneurophytalean progymnosperms), are not known for *Ellesmeria*.

Of the known pteridosperms, Late Pennsylvanian *Schopfiastrum* clearly bears the greatest superficial resemblance to the organization of Late Devonian *Ellesmeria*, producing sphenopteroid fronds in roughly a quadriseriate manner and possessing a bilobed stem stele. However, despite these marked similarities, the two genera are fundamentally distinct with respect to specific details of anatomy and morphology. These plants therefore are clearly unrelated. The comparison of these plants from radically different ages thus emphasizes yet again the truly remarkable degree of convergence for photoreception achieved in plant groups with sphenopteroid foliage.

9.5 *Stenokoleos*

Ellesmeria shares a number of important structural features with *Stenokoleos,* a genus of enigmatic plants ranging from the Middle Devonian (Givetian) to the Lower Mississippian of North America. *Ellesmeria* is most similar externally to *S. bifidus* Matten and Banks, from the lower Frasnian age Oneonta Formation of New York. A reconstruction of this species (based on only a few specimens) by Matten and Banks (1969) demonstrates a stem giving rise alternately to pairs of rachides. Furthermore, each pair of rachides is the product of an immediate dichotomy at the base of a node. Thus, the arrangement of paired rachides on a stem of *S. bifidus* is similar to the quadriseriate arrangement of primary pinnae exhibited by *Ellesmeria.* Also, in both plants, third order lateral branches (secondary pinnae of *Ellesmeria*) develop alternately, producing a planated system (though for *Ellesmeria,* this plane is parallel to the main axis, whereas this plane is perpendicular to the stem for *S. bifidus*). The ultimate appendages of *S. bifidus* remain unknown.

Despite these morphological similarities, the organization of the stem and rachis steles of *S. bifidus* is significantly different from the clepsydroid stele design of *Ellesmeria.* In *S. bifidus,* the stem displays a lobed or ridged protostele (with multiple protoxylem points, including one often in the axis center) that is constantly transforming in shape, in association with the development of rachis traces. In internodal regions, this stele can be more or less bilobed in form. Then, just proximal to a node, the lobe of the stele associated with the next pair of rachides sometimes begins to divide, resulting in a trilobed stele configuration. These two new lobes soon pinch off separately to form a pair of rachis traces. At other nodes, a multiple-ridge pattern can occur in the stem stele that is difficult to interpret Rachis traces can also assume variable shapes, ranging from an initial V-shape to a bilobed, rectangular, or four-ribbed state more distally (with multiple areas of protoxylem occurring throughout). The stele of third order laterals is ellipsoid or clepsydroid in shape, and bipolar. Significantly, protoxylem areas at some levels of anatomy of this plant often show a mixture of parenchyma and tracheids, reminiscent of what have been termed peripheral loops in zygopterid ferns (Scheckler 1974). Metaxylem tracheids display both scalariform and circular-bordered pitting types. In summary, the anatomy of *S. bifidus* does bear a superficial resemblance to that of *Ellesmeria* (occasional occurrence of bilobed, even clepsydroid, stele pattern, with scalariform and circular pitting). However, the degree of divergence between these plants in regard to overall anatomical pattern, as well as in specific details, implies that their external similarities are probably the result of convergence towards a similar photoreception strategy.

The evolutionary affinities of *Stenokoleos* remain uncertain. Initially, the fern-like characteristics of the genus were emphasized (Hoskins and Cross 1951; Beck 1960), but later authors have stressed its progymnospermous and pteridospermous features. Matten and Banks (1969) have suggested that *Stenokoleos* compares most closely to the lyginopterid pteridosperms *Tristichia* and *Tetrastichia.* Matten's recent work with a new Givetian age species of *Stenokoleos* has even led him to suggest that the Stenokoleaceae - and not the progymnosperms, as currently recognized (i.e., the Aneurophytales and Archaeopteridales) - represent the long sought ancestral stock of pteridosperms (Matten, in press). Matten reconstructs the stem of this plant as possessing a three-ribbed stele throughout its length, which produces pairs of ellipsoid rachis traces in a helical sequence. The stem stele of this species is in fact very similar to the intermittent three-ribbed state described for *S. bifidus.* Perhaps in the future, the implied distichous phyllotaxis of *S. bifidus,* suggested by its reconstruction, may actually be shown to be helical as well. It should also be noted that Rothwell and Erwin (1987) have illustrated specimens of an axis from the Mid to Upper Famennian Hampshire Formation (near Elkins, West Virginia) that bear a striking resemblance to *Stenokoleos.* They interpret these fossils (which include fronds with *Lyginorachis*-type petiole anatomy, *Sphenopteris*-type pinnules, and a sparganum cortex) as evidence of a link between aneurophytalean progymnsosperms and pteridosperms. Though the evolutionary position of *Stenokoleos* is obviously still in a state of flux, the question has become one of just how closely related to progymnosperms and gymnosperms this genus is. As has already been discussed, these groups of plants and their relatives do not seem to be important for understanding the phyletic history of *Ellesmeria,* although the convergence of their foliar morphology is certainly interesting.

9.6 *Chlidanophyton dublinensis*

Chlidanophyton dublinensis Gensel is an element of the Lower Mississippian Price Formation of southwestern Virginia which, like *Stenokoleos,* demonstrates both fern-like and progymnospermous/ gymnospermous characteristics (Gensel 1973). The main feature of similarity between this plant (for which no anatomy is known) and *Ellesmeria* is the occurrence of dichotomizing aphlebiae at the base of fronds. In both plants, aphlebiae seem to exhibit up to seven or eight successive dichotomies. However, *Chlidanophyton* exhibits a pair of aphlebiae at the base of each order of branching, whereas *Ellesmeria* only possesses one aphlebia for each primary pinna. With regard to other aspects of their morphlogy, *Chlidanophyton* and *Ellesmeria* share little in common. Most importantly, *Chlidanophyton* does not demonstrate a distichous nor quadriseriate arrangement for any order of branching. First order branches are borne in a helical sequence on the erect main axis, and they do not fork. Subsequent branch orders develop alternately in a plane perpendicular to the main axis (not parallel to the main axis, as in *Ellesmeria*). The ultimate appendages of *Chlidanophyton*, like the aphlebiae, are completely dichotomous in nature and non-laminated. Finally, fertile material demonstrates ovoid sporangia terminating both ultimate appendages and second order aplebiae (no fertile information is available for *Ellesmeria*). To summarize, clearly the number of distinctions between *Ellesmeria* and *Chlidanophyton* outweigh the similarities. The absence of any knowledge of the anatomy of the latter plant complicates its systematic attribution. However, should *Chlidanophyton* eventually be proven to be unrelated to ferns, the phyletic significance of the association of aphlebiae with the bases of "frond units" (herein treated as a non-progymnospermous/gymnospermous character) may be called into question.

9.7 *Protopteridophyton* and Cladoxylalean Ferns

Ellesmeria bears some resemblance to *Protopteridophyton devonicum* Li and Hsu, a probable early fern from Givetian and Frasnian age strata of southern China (Li and Hsu 1987). The main feature of similarity between these plants is the quadriseriate organization of lateral appendages. Arising from a rhizomatous stem, the aerial main axis of *Protopteridophyton* produces paired first order branches alternately. This level of the plant's organization compares quite closely with the quadriseriate primary pinnae of *Ellesmeria*. However, unlike those of *Ellesmeria*, branches of the second order of *Protopteridophyton* also develop in a quadriseriate manner. Furthermore, second order branches demonstrate a series of dichotomous divisions, terminating in recurved, non-laminated branch tips (which can bear ovoid sporangia).

The anatomy of this plant, although not very well known, resembles that of *Ellesmeria* in some respects. Incomplete petrifactions of the stele of *Protopteridophyton* display two ribs arranged in a V-shape. In this configuration, the stele generally resembles prepared sections of *Ellesmeria* in which a primary pinna trace lies adjacent to one end of the main axis stele (fig. 50). Yet, clearly in *Protopteridophyton* the two xylem ribs are both components of the main axis stele. Li and Hsu (1987) suggest that these two ribs are perhaps part of a multi-ribbed stele. Each rib of this stele possesses an ellipsoid, mesarch area of protoxylem - which apparently divides radially, and then again tangentially in preparation for the production of a first order branch trace. Li and Hsu infer the stele to have produced first order branch traces in a helical sequence (an interpretation, however, which does not seem to correlate with the observed quadriseriate morphology). First order branch traces are clepsydroid in form (much like the anatomy of *Ellesmeria*), with a mesarch area of protoxylem at each end. Also as with *Ellesmeria,* metaxylem tracheids display both scalariform and circular-bordered pitting types.

Despite the shared features noted above, *Ellesmeria* is quite distinct from *Protopteridophyton* in both anatomy and morphology. In particular, the occurrence in *Ellesmeria* of only one order of quadriseriate branching, clepsydroid steles in multiple branch orders, and catadromic aphlebiae - as well as laminated pinnules - suggests that *Ellesmeria* is not very closely related to *Protopteridophyton*. Li and Hsu (1987) have compared *Protopteridophyton* with a number of Devonian and Carboniferous fern groups, drawing no firm conclusion as to its exact affinities. Perhaps this plant will eventually prove to be a close evolutionary associate of cladoxylalean ferns. Like *Protopteridophyton,* cladoxylalean ferns tend to exhibit deeply lobed (to dissected), mesarch steles, some with multiple peripheral loops of protoxylem (associated with parenchyma - Scheckler 1974). With regard to morphology, these plants usually display a combination of digitate and/or helical branching proximally and dichotomous branching more distally. Ultimate appendages are non-laminated, or only weakly so. Overall, cladoxylalean ferns and *Protopteridophyton* seem to resemble each other more closely than either does *Ellesmeria*.

9.8 Stauropteridales

The quadriseriate arrangement of *Ellesmeria*'s primary pinnae finds no parallel within the old coenopterid fern complex, except within the Stauropteridales (*sensu* Stewart 1983) and the Zygopteridales (to be discussed in a subsequent section). The Stauropteridales includes the genera *Stauropteris, Gillespiea,* and *Rowleya* (Erwin and Rothwell 1989).

Stauropteris, with several species, is associated with Mississippian and Pennsylvanian age coal ball strata of Europe and North America (Cichan and Taylor 1982). *Stauropteris* greatly resembles *Ellesmeria* in combining a quadriseriate branch arrangement (in all but the biseriate species *S. biseriata,* Cichan and Taylor 1982) with the development of catadromic, dichotomous aphlebiae (Stewart 1983). However, unlike *Ellesmeria* (but like *Protopteridophyton*), quadriseriate members of this genus display this type of branch organization in multiple branch orders. Also, the aphlebiae of *Stauropteris* occur in association with multiple branch orders. Furthermore, ultimate appendages are non-laminated, and a three- to four-ribbed protostele pattern is maintained throughout the branching system. Each rib of the stele possesses a single mesarch protoxylem pole, such that a total of four areas of protoxylem occur at any given level. This stelar pattern stands in contrast to the anatomy of *Ellesmeria,* except where an initial primary pinna trace appears to become four-lobed (prior to dividing to yield a pair of primary pinna traces -

fig. 55). Unlike that of *Ellesmeria*, metaxylem pitting of *Stauropteris* is solely scalariform-bordered. Sporangia (which are unknown for *Ellesmeria*) develop at the tips of ultimate appendages in *Stauropteris*, which includes both homosporous and heterosporous species.

Gillespiea randolphensis Erwin and Rothwell derives from the Late Devonian specifically Mid to Upper Famennian) Hampshire Formation, near Elkins, West Virginia (Erwin and Rothwell 1989). As with *Ellesmeria*, only one order of branching of this small plant exhibits a distichous, quadriseriate arrangement of laterals. However, unlike *Ellesmeria* (but like *Stauropteris*), *G. randolphensis* displays a three to four-ribbed protostele (that becomes rounded in smaller specimens). This plant differs from both *Ellesmeria* and *Stauropteris* in its lack of dichotomous, aphlebia-like structures. Yet, *G. randolphensis* can possess long, anisotomously branched fertile appendages that depart from the catadromic sides of a given pair of quadriseriately branched lateral axes. Fertile branches of this type also occur at distal levels of the branching system. This plant appears to be heterosporous, and lacks laminated pinnules.

Ellesmeria is fundamentally distinct in both its morphology and anatomy from *Rowleya trifurcata* Long (1976) from coal ball strata of Britain (Long 1976). Unlike the quadriseriately branched main axis of *Ellesmeria*, the slender first order axis of *R. trifurcata* often displays three closely spaced dichotomies, resulting in a lateral trifurcation (where the outer two branches become arrested in growth). Also unlike *Ellesmeria, R. trifurcata* does not possess catadromic aphlebiae. Furthermore, the stele of *Ellesmeria* is quite dissimilar from the tetrarch or triarch protostele of this plant. *R. trifurcata* has been described by Long (1976) to have small, tapering "leaf" appendages, but these appear to be non-laminated, and bear no resemblance to the pinnules of *Ellesmeria*.

In summary, *Ellesmeria* shares with most species of *Stauropteris* two important features, a quadriseriate branching system (also shared with *Gillespiea*) and catadromic aphlebiae. In all other respects of morphology and anatomy, *Ellesmeria* departs from the members of the Stauropteridales (especially with respect to ultimate appendage form and stele design). Since the Stauropteridales may represent an unnatural assemblage (Erwin and Rothwell 1989), based primarily on a shared stele shape, the relationship of *Ellesmeria* to the group as a whole is somewhat ambiguous. Yet, for the reasons mentioned above, *Ellesmeria* and *Stauropteris* may be viewed as components of relatively close evolutionary lines, linking trimerophytes to the coenopterid complex. The distinctions noted between these plants, however, would seem to be of at least ordinal level significance. Furthermore, convergence cannot be overlooked as a possible explanation for the similarity of the branching pattern of *Ellesmeria* to that of *Stauropteris*.

9.9 ZYGOPTERIDALES

With respect to both morphology and anatomy, this new plant compares most closely with members of the order Zygopteridales (*sensu* Stewart 1983). Zygopterid ferns comprise a group of Devonian to Permian age fern-like plants (associated with the old coenopterid complex), which may form an extinct sister group of modern ferns. Based on their methods of pinna trace production, zygopterid ferns are traditionally divided into an etapteroid subgroup (including the genus *Etapteris*) and a clepsydropsoid subgroup (including the genus *Clepsydropsis*). Although various authors (e.g., Leclercq 1954; Andrews and Boureau 1970; Leclercq and Bonamo 1971; Phillips 1974; Barnard and Long 1975; Taylor 1981; Stewart 1983; Meyen 1987) raise the taxa to varying ranks, and may rearrange them slightly, a consensus classification for the zygopterid ferns would be similar to the following:

- Class Zygopteridopsida
  - Order Zygopteridales
    - Suborder Etapteroideae
      - Family Zygopteridaceae
      - Family Rhacophytaceae
    - Suborder Clepsydropsoideae
      - Family Clepsydropsaceae

Ellesmeria compares quite closely to zygopterid ferns of the Etapteroideae. Using the Mid to Late Pennsylvanian age genera *Zygopteris, Etapteris,* and *Alloiopteris,* one can construct a composite model of etapteroid morphology and anatomy. With respect to general organization, these plants were mainly rhizomatous herbs and small shrubs. In most species of *Zygopteris,* the haplostelic rhizome (i.e., stem) gives rise to a frond-like organ, referred to as a phyllophore (Dennis 1974). The internal anatomy of the *Zygopteris* phyllophore (assignable to the form genus *Etapteris*) demonstrates a bipolar, mesarch protostele with bilateral symmetry, of a general etapteroid shape (roughly resembling an "H"). This H-shaped stele probably resulted from modification of the clepsydroid-shaped (i.e., hourglass) stele seen in other zygopterids (*via* tangential lobing of the ends of the stele - Phillips 1974). Parenchyma cells often occur in association with a protoxylem pole, forming a zone referred to as a peripheral loop. The phyllophore produces primary pinnae, arranged in distichous quadriseriate pairs (Hirmer 1933; Phillips 1974). With respect to internal anatomy, primary pinnae maintain the general plan of organization established in the phyllophore (i.e.,a bipolar, mesarch protostele with bilateral symmetry). However, each primary pinna trace displays at least initially a crescent or C-shape. At the base of each primary pinna, usually on the anadromic side, occurs a dichotomously organized, scale-like aphlebia (Barthel 1968; Galtier and Scott 1979). Similar structures often develop along the rhizome as well (Dennis 1974). In the closely related genus *Alloiopteris*, secondary pinnae diverge from the primary pinna in an alternate manner (Galtier and Scott 1979). Secondary pinnae themselves bear laminate pinnules alternately. With regard to form, these pinnules are of a general sphenopteroid type, often being virtually indistinguishable from those of earlier and contemporary gymnosperms (Ramis, et al. 1979). However, usually the venation of *Alloiopteris* pinnules is proximally overtopped, in contrast to the strictly dichotomous pattern of pteridospermous pinnules (Galtier and Scott 1979; Galtier 1981; Galtier and Scott 1985). Some fertile fronds of *Alloiopteris* (=*Corynepteris*) bear clusters of sporangia (each with a distinctive U-shaped, annulus-like band of thickened cells) on the undersides of vegetative pinnules (Galtier and Scott 1979). The fronds of some other zygopterid ferns bear sporangial clusters on non-laminated stalks (as in *Biscaulitheca* and *Musatea*).

The basic elements of etapteroid form also appear to be fundamental to the body plan of *Ellesmeria*. If one assumes that the stem of *Ellesmeria* remains unknown, then all known features of its morphology and anatomy become interpretable based upon the etapteroid model discussed above. According to this interpretation, the main axis of *Ellesmeria* is probably equivalent to the zygopterid phyllophore. Like a phyllophore, the main axis of *Ellesmeria* possesses a bipolar, mesarch protostele of a general clepsydroid shape, produces distichous pairs of primary pinnae in a quadriseriate manner, and demonstrates dichotomous aphlebia-like structures at the base of each primary pinna. As with the zygopterid phyllophore, the vascular trace associated with a primary pinna appears to recaptitulate the basic form of the main axis stele (i.e., a bipolar, mesarch protostele). Additionally, secondary pinnae develop alternately and bear pinnules alternately. The sphenopteroid pinnules of *Ellesmeria* closely resemble those of some *Alloiopteris* species (such as *A. essinghi* and *A. erosa,* Ramiset al. 1979). However, pinnules of *Ellesmeria* appear to display narrower, less decurrent, and less fused bases than do pinnules of *Alloiopteris*. No information as to the nature of the fertile structures of *Ellesmeria* is currently available.

Although *Ellesmeria* clearly bears a striking resemblance to members of the Etapteroideae, it demonstrates some similarity to the other zygopterid group, the Clepsydropsoideae, as well. The Clepsydropsoideae is distinguishable from the Etapteroideae based mainly upon primary pinna arrangement. The primary pinnae of the Clepsydropsoideae are also arranged in a distichous pattern along the phyllophore, but they generally occur singly - not in pairs - in a biseriate manner (Phillips 1974). Some specimens of *Ellesmeria* do seem to demonstrate this clepsydropsoid feature (fig. 3-5, 14-16). However, an etapteroid-like quadiseriate arrangement of primary pinnae is by far the more common condition for this plant. Yet, at least one clepsydropsoid species (*Clepsydropsis leclercqii*) also bears its primary pinnae in a quadriseriate manner (Galtier 1966). The Clepsydropsoideae further differ from the Etapteroideae with respect to primary pinna trace formation. In the Etapteroideae, primary pinna trace formation initiates with the partial detachment of the rim of phyllophore stele tissue just exterior to a peripheral loop (i.e., the peripheral loop "opens" - Phillips 1974). This flap of tissue subsequently becomes fully separated from the phyllophore stele and divides to give rise to a pair of primary pinna traces. However, in the Clepsydropsoideae, the entire primary pinna trace simultaneously pinches off from the phyllophore stele, such that the associated peripheral loop never "opens", but divides at a more proximal level. Lack of specific knowledge regarding the method of primary pinna trace formation in *Ellesmeria* prevents an assessment of its etapteroid *vs*. clepsydropsoid affinities, with respect to this diagnostic characteristic.

Ellesmeria departs from the traditional concept of zygopterid ferns in a few significant respects. Most importantly, with regard to stratigraphic position, *Ellesmeria* (which is Middle Frasnian in age) is significantly older than all other zygopterid ferns interpreted as possessing phyllophore-type fronds with well laminated foliage (i.e., Carboniferous species). Thus, *Ellesmeria* demonstrates well laminated, *Sphenopteris*-like pinnules long before they had been thought to have evolved in zygopterid ferns (i.e., in the

Visean, roughly 30 million years later - Galtier and Scott 1985). In addition, the dichotomous, putative aphlebia of *Ellesmeria* occurs on the catadromic side of a primary pinna base, whereas the aphlebiae of other zygopterids with well laminated foliage tend to be anadromic in position (Barthel 1968; Galtier and Scott 1979). Also, the secondary pinnae of most zygoperids seem to occur perpendicular to the plane in which the phyllophore lies, not parallel to the plane of the main axis as for *Ellesmeria* (Darrah 1941; Barthel 1968). However, Hirmer's 1933 reconstruction of a frond of *Etapteris* does appear to show the secondary pinnae oriented parallel to the phyllophore. Although information concerning the method of primary pinna trace formation (a key character used in distinguishing the two suborders of zygopterid ferns) is inconclusive for *Ellesmeria,* this plant may have departed slightly from the typical zygopterid style. Specifically, following the separation of an initial trace from the main axis stele, this trace may exhibit a unique four-ribbed stage prior to its division to yield the two primary pinna traces at a node (fig. 55). In zygopterids, this initial trace does not become four-ribbed, but instead is bilobed or crescent-shaped throughout its length (Phillips 1974). Furthermore, *Ellesmeria* does not seem to display the typical zygopterid type of peripheral loop (Scheckler 1974). Instead, protoxylem poles in *Ellesmeria* are rather small, consist only of tracheids (usually less than 10 cells), and do not become infilled with parenchymatous tissue. These observations, however, may be biased by the small sample size and the preservational state of the anatomical material (i.e., no preservation of the exact region of trace formation). Additionally, tracheid pitting of previously described zygopterids, unlike that of *Ellesmeria,* has been interpreted to be exclusively scalariform, but can include circular pitting in the secondary xylem of *Zygopteris* (Dennis 1974). Finally, though the main axis of *Ellesmeria* is assumed to have arisen from a true stem, the existence of this organ cannot currently be proven, nor are the fertile organs of this plant known. However, none of the distinctions nor missing pieces of evidence noted here are of such a fundamental nature as to seriously compromise an hypothesis of homologous relationship between *Ellesmeria* and zygopterid ferns. Stratigraphic discrepancies, with respect to the degree of foliar lamination in particular, may be the result of inadequate sampling, because of the paleoecologic bias of previously sampled sites, or the misinterpretation of some Late Devonian and Early Carboniferous foliage types.

9.9.1 RHACOPHYTACEAE

Although zygopterid ferns with extensively laminated foliage have not been thought to have evolved until the Visean (Galtier and Scott 1985), the group itself appears to be well represented in Late Devonian fossil assemblages by non-laminated and more weakly laminated forms. Specifically, many recent classifications have included the family

Rhacophytaceae, a group of common, fern-like plants from the Middle to Late Devonian, within the order Zygopteridales (Leclercq and Bonamo 1971; Barnard and Long 1975; Stewart 1983; Meyen 1987). The precise stratigraphic record of the Rhacophytaceae extends from the Givetian (*Protocephalopteris praecox* of Spitsbergen) to the basal Tournaisian (*Cephalopteris mirabilis* of Bear Island - Schweitzer 1968). Thus, with respect to stratigraphic age, Frasnian age *Ellesmeria* correlates most closely with this Devonian family of zygopterids. Members of this family closely resemble later zygopterids with respect to vegetative form and anatomy, but their fronds display little or no lamina, and their non-laminate fertile structures are unique. The members of the Rhacophytaceae are traditionally grouped (Leclercq 1954; Phillips 1974) with etapteroid zygopterids from the Carboniferous (i.e., the Zygopteridaceae of the suborder Etapteroideae, with respect to the consensus classification presented earlier), based upon a shared method of primary pinna trace production.

9.9.1.1 *Rhacophyton*

Rhacophyton, the type genus of the family, is a cosmopolitan constituent of Late Devonian (Famennian) strata. The genus currently has three species: *R. ceratangium, R. zygopteroides,* and *R. condrusorum.* A fourth potential species, Tournaisian age *R. mirabilis,* is placed by some in a different genus (*Cephalopteris*) and will be considered separately. Most of the differences between the species of *Rhacophyton* are size related, but a few key distinctions emerge upon comparison.

Suzanne Leclercq described *Rhacophyton zygopteroides* in 1951 based upon compressed and petrified material collected from Belgium. The habit of this plant appears to have been very similar to that of later zygopterid ferns. Specifically, Leclercq reconstructed *R. zygopteroides* as a scrambling shrub (probably less than 1 m tall) with long fronds emanating from a rhizomatous stem. Significantly, she was able to identify what she believed to be the stem of the plant, based on a single petrified specimen bearing fronds. Frond rachides are borne in a helical sequence. With respect to internal anatomy, the stem appears to have possessed a pentarch actinostele (based upon Leclercq's careful analysis of a few incompletely preserved sections) .

Fronds are of two types, biseriate sterile and quadriseriate fertile (Leclercq 1951, 1954). Sterile fronds produce distichous primary pinnae alternately, but not in pairs, and are therefore biseriate in organization. Fertile fronds, however, demonstrate distichous pairs of primary pinnae (i.e., quadriseriate organization) along their entire length. Sterile ultimate appendges of *R. zygopteroides* occur alternately (perpendicular to the plane of the rachis) along the primary pinnae of both sterile and fertile fronds . Ultimate appendages (probably the main photosynthetic organs of the plant) display a pseudomonopodially branched main rib, with subsequent divisions being dichotomous. These organs ultimately terminate in recurved, naked (i.e., non-laminated) branchlet tips.

Each primary pinna (including those of both sterile and fertile fronds) bears at its base a three-dimensionlly organized, dichotomously branched aphlebia (Leclercq 1951, 1954). In more proximal regions of a fertile frond and along an entire sterile frond, the terminal ends of aphlebiae are naked and sterile. However, as a fertile frond progresses distally, aphlebiae become more extensively branched and lined with sporangia. Specifically, sporangia occur terminally on the ultimate pinnate divisions of these otherwise dichotomously branched organs. The exannulate sporangia are fusiform, and display a long distal extension, or "beak".

The internal anatomy of rachides consists of a clepsydroid, bipolar protostele, surrounded by a layer of radially aligned xylem cells, interpreted as secondary xylem (Leclercq 1951, 1954). The bipolar nature of this stele is manifested in the external morphology of compressed rachis specimens, in the form of a central, longitudinal groove. The rachis stele generates a single primary pinna trace at each node, in an etapteroid manner (i.e., the peripheral loop opens). This bipolar, crescent-shaped trace soon divides in a fertile frond (thereby supplying the pair of primary pinnae), but remains intact in a sterile frond (as the vasculature of a single primary pinna).

The primary pinna traces of fertile fronds subsequently recapitulate the bipolar, clepsydroid form of the rachis stele. However, the primary pinna traces of sterile fronds may have maintained a more crescent-shaped form.

Leclercq (1954) remarked on the similarity of *R. zygopteroides* to both etapteroid and clepsydropsoid zygopterids with respect to branching pattern. However, despite the plant's combination of quadriseriate and biseriate branching, Leclercq considered *R. zygopteroides* to be most closely related (and probably ancestral) to Carboniferous etapteroids, based on their shared method of primary pinna trace formation. Her claim that branch pattern, without knowledge of the manner of trace formation, holds little value for distinguishing etapteroid and clepsydroid zygopterids has been verified more recently by the discovery of a quadriseriate clepsydropsoid species (*Clepsydropsis leclercqii*, Galtier 1966).

Rhacophyton ceratangium Andrews and Phillips (1968), the species with which North American paleobotanists are probably most familiar, is known best from the Famennian of West Virginia. Krausel and Weyland (1941) first described fossils of this plant from Valley Head, near Elkins, West Virginia as *R. incertum*. Andrews and Phillips (1968) later described a wealth of fresh material (presumably of the same plant) from Valley Head, for which they erected the new specific name *R. ceratangium*. Andrews and Phillips felt confident enough in their understanding of this material to propose a whole plant reconstruction, which subsequently was modified slightly by Cornet, et al. (1976). Their reconstuction depicts the plant as an upright shrub, approximately 3 m in height, with a long trunk-like stem and densely branched lateral appendages.

Putative stem specimens of this plant demonstrate widths of up to 2 cm (Cornet, et al. 1976). The anatomy of these axes consists of a bipolar, clepsydroid protostele, surrounded by a zone of radially aligned xylem cells interpreted as secondary xylem. As in *R. zygopteroides*, this stele pattern results in a longitudinal vascular groove on the exterior surface of morphologically preserved specimens. This anatomical pattern is maintained in each subsequent branch order. Dittrich, et al. (1983) have more recently verified that the zone of radially aligned xylem consists of secondary xylem by demonstrating the presence of vascular rays. They also demonstrated trace formation to have been of the etapteroid type.

According to the interpretation of Cornet, etal. (1976), the apparent stem of this plant gives rise to pairs of second order branches (i.e., rachides) in a quadriseriate manner. Each rachis bears a dichotomous to somewhat anisotomous aphlebia in the catadromic poistion. Distally, a rachis produces primary pinnae in a quadriseriate manner. However, in sterile regions of a rachis, one member of each quadriseriate pinna pair is usually greatly reduced in size, such that these areas appear biseriate in organization (with the plane of planation being perpendicular to the plane of the "stem"). A fertile rachis becomes completely quadriseriate distally, fully expressing each member of each primary pinna pair. Like rachides, all primary pinnae bear basal catadromic aphlebiae. In fertile regions of a rachis, fertile aphlebiae of the type described for R. *zygopteroides* develop. Sporangia appear to be generally of the same form as those of R. *zygopteroides*.

Primary pinnae give rise to secondary pinnae, which may produce an additional pinna order in large fronds (Cornet, et al. 1976). Secondary and tertiary pinnae develop in a general biseriate manner, which may have been the product of evolutionary reduction from a quadriseriate arrangement. Ultimate appendages are generally of the same form as those of R. *zygopteroides*. However, current evidence suggests that pinnule display was more variable in R. *ceratangium*, ranging from a three-dimensional orientation to being planated and flattened.

The Cornet, et al. (1976) reconstruction of R. *ceratangium* as a tall shrub has more recently been called into question by Scheckler (1986). In a paper analyzing in part the paleoecological context of R. *ceratangium*, Scheckler presents a different interpretation of the lifestyle of this species. Based upon the common observation of a dense mat of adventitious roots emanating from one side of a frond, Scheckler believes that this plant possessed long fronds that would reiterate wherever they touched the ground.

He therefore envisions *R. ceratangium* as a scrambling shrub, very adept at clonal propagation (which contributed to its monopolization of paleoequatorial coastal swamps and fluvial backswamps). This reconstruction implies that fronds of this plant derived from an as yet undiscovered ground-level stem of the type observed by Leclercq (1951) for *R. zygopteroides* (i.e., either stunted in its axial growth, or rhizomatous). Thus, the vegetative organ recognized by previous researchers as the stem of *R. ceratangium* may actually represent a proximal branch order of an extremely large frond. This interpretation would help explain why all currently known parts of *R. ceratangium* demonstrate an identical anatomical pattern.

It should be noted that Matten (1974) has reported two petrified specimens (yielding 26 sections) that he attributes to *R. ceratangium*, from the Givetian age Cairo flora of New York. Although generally resembling *R. ceratangium* with respect to primary and secondary xylem form, corroborating morphological evidence for these older specimens is unavailable. Notably, however, in contrast to *R. ceratangium* (and all known zygopterids), Matten reports that these specimens display at least one protoxylem area in between the two main protoxylem poles. Thus, the attribution of these specimens to *R. ceratangium*, or even to *Rhacophyton*, is questionable.

Rhacophyton condrusorum Crepin represents the earliest described species of the genus. Initially described by Crepin (1874, 1875) from the Mid to

Late Famennian Evieux Formation of Belgium (as *Psilophyton condrusorum*), the species has more recently been evaluated by Gilkinet (1922), Stockmans (1948), and Schultka (1978). Notably, the species is treated by Gilkinet (1922) as *Sphenopteris condrusorum*. Based on the earlier studies by Gilkinet and Stockmans, *R. condrusorum* is distinguishable from *R. ceratangium* primarily based upon the greater size of its axes, the shorter beak of its sporangia, and by its possession of an additional order of branching in the frond. Schultka's description of the species conforms even more closely to that given by Cornet, et al. (1976) for *R. ceratangium*, recognizing the proximal-most branch order as the stem of the plant. In a more recent discussion concerning these species, Dittrich, et al. (1983) have suggested that the putative stems of *R. condrusorum* and *R. ceratangium* may actually represent mature rachides. This interpretation is of course consistent with the Leclercq (1951) reconstruction of *R. zygopteroides* and the Scheckler (1986) reconstruction of *R. ceratangium*. Thus, Gilkinet's and Stockmans' earlier interpretations of *R. condrusorum* may prove to be more accurate than that of Schultka (i.e., interpreting the frond as more extensively branched, and the stem as unknown).

Ellesmeria demonstrates a number of fundamental similarities to members of the genus *Rhacophyton*. Features shared by both of these genera include: clepsydroid form of rachis stele (i.e., main axis of *Ellesmeria*); distinct external groove in multiple branch orders of the frond, relating to the internal stele form by compression during fossilization; recapitulation in pinnae of the basic form of the bipolar rachis stele; quadriseriate arrangement of primary pinnae (comparable to what have been called the "rachides" of *R. ceratangium*); and dichotomous, catadromic aphlebia at the base of each primary pinna (as opposed to the anadromic aphlebiae of later zygopteids). Also like the species of *Rhacophyton*, *Ellesmeria* demonstrates a tendency for three-dimensional, quadriseriate fronds to become biseriate, and therefore more or less planated. This trend towards planation is perhaps a shared adaptation for improved photosynthetic efficiency. The absence of any knowledge of the reproductive structures of *Ellesmeria* makes impossible any further comparison with *Rhacophyton*.

Ellesmeria appears to compare most closely to *R. zygopteroides* in its basic morphology. Both of these species demonstrate a quadriseriate arrangement in only one order of branching (specifically, at the level of the primary pinna). *R. zygopteroides* actually only demonstrates a quadriseriate arrangement in fertile fronds (which are proximally sterile), whereas vegetative fronds are biseriate in organization. Perhaps a similar condition may have contributed to the occurrence in *Ellesmeria* of both quadriseriate and biseriate fronds (i.e., preserved quadriseriate specimens may represent proximal sterile portions of fertile fronds). However, the absence of fertile material for *Ellesmeria* prevents an assessment of this possibility. Additionally, both species produce aphlebiae only at the bases of primary pinnae. In contrast, *R. ceratangium* (and perhaps *R. condrusorum*) displays a quadriseriate arrangement, with associated aphlebiae, in multiple branch orders. However, like *R. ceratangium,* as well as *R. zygopteroides,* a frond of *Ellesmeria* may have developed adventitious roots along one side upon making contact with the substrate. This feature may indicate a shared overall type of scrambling habit in these plants.

Ellesmeria is distinct from the genus *Rhacophyton* with respect to key features of anatomy and morphology, especially xylem pitting and foliage lamination. *Ellesmeria* possesses both circular and scalariform-bordered metaxylem pits in its primary xylem, whereas tracheid pitting in *Rhacophyton* has been considered by all previous investigators to be primarily of a scalariform-bordered type (rarely scalariform-reticulate). However, Dittrich, et al. (1983 - pl. III, fig. 5) illustrate a section of secondary xylem from a specimen of *R. ceratangium* in which pits near the ends of tracheids become progressively more rounded, perhaps even circular, in form. Thus the tracheid pitting of *Rhacophyton* may prove not to be so distinct from that of *Ellesmeria* as the current literature suggests. The putative Givetian *R. ceratangium* specimens described by Matten (1974) possess bordered pits of an unknown form.

The most important vegetative distinction between *Ellesmeria* and the species of the genus *Rhacophyton* is the degree of lamination observed in the ultimate pinnules of these plants. The pinnules of *Ellesmeria* are fully laminate and sphenopteroid in form, whereas those of *Rhacophyton* have been described as non-laminate. However, in terms of branching pattern, the veins of *Ellesmeria*'s pinnules compare quite closely to the naked branch tips of the pinnules of *Rhacophyton*. In both cases, initial anisotomous to pseudomonopodial divisions (more or less producing a main vein, or main pinnule axis) give way distally to a series of isotomous divisions. Thus, if a pinnule of *Rhacophyton* were to have developed a lamina, it would probably have been very similar in appearance to a pinnule of *Ellesmeria*. Furthermore, the degree of lamination with regard to pinnules of *Rhacophyton* may have been determined by ecological conditions, and not by genetic restrictions (i.e., absence of genes coding for lamina development). As a facultative swamp inhabitant (Scheckler 1986), *Rhacophyton ceratangium* may have expressed a non-laminate type of pinnule as a xeric response to reduced conductance, because of restricted root growth in an anaerobic swamp substrate. Therefore, the possibility should not be overlooked that *Rhacophyton*, or another member of its clade, was genetically potentially capable of producing a fully laminated pinnule of the type demonstrated by *Ellesmeria*.

9.9.1.2 *Cephalopteris mirabilis*

Cephalopteris mirabilis Nathorst, the youngest known member of the Rhacophytaceae (from the basal Tournaisian, Tn1a to basal Tn1b, of Bear Island), does demonstrate pinnule lamination. The original illustrations of the plant by Nathorst (1900, 1902) clearly depict ultimate appendages with a narrow, but unmistakable band of lamina. Thus, the occurrence in *Ellesmeria* of fully webbed ultimate appendages does not provide so clear a distinction between this new plant and time equivalent members of the Rhacophytaceae as mere words would suggest. With respect to other known morphological features, *C. mirabilis* is very similar to members of the genus *Rhacophyton* (Leclercq 1951). Most notably, *C. mirabilis* demonstrates a main axis that gives rise to primary pinnae in a quadriseriate manner and bears dichotomous aphlebiae (sometimes fertile) at the catadromic base of each primary pinna. Primary pinnae can bear (in the plane perpendicular to the rachis) up to three additional orders of branch, as well as the ultimate appendages (Schweitzer 1968). The anatomy of this plant is unknown, but compressed axes often demonstrate a double longitudinal groove, reminiscent of the vascular groove seen in frond axes of *Rhacophyton*. This grooving pattern in the fronds of *C. mirabilis*,therefore, very likely results from compression of a bipolar protostele. These similarities to *Rhacophyton* led Leclercq (1951) to even formally redescribe *C. mirabilis* as *Rhacophyton mirabilis*.

However, unlike other members of the genus *Rhacophyton*, ultimate appendages of *Cephalopteris* develop along each branch order of the frond, not just along the terminal order of branch (Schweitzer, 1968). Also in contrast to the other species of *Rhacophyton*, the ultimate appendages of this plant, as well as the aphlebiae, bear sporangia. Sporangia are reported to be elongate and short-tipped (like *R. condrusorum*) and lack a sinuous beak (Leclercq 1951; Andrews and Phillips 1968). These collective differences have led Schweitzer (1968) to restore the combination *Cephalopteris mirabilis*. Reproductive information for *Ellesmeria* is not available for comparison, but like *C. mirabilis* this new plant may produce vegetative pinnule-like structures in more proximal branch orders of the frond (fig. 9, 30). With respect to general organization, *Ellesmeria* closely resembles *C. mirabilis*, but demonstrates two fewer orders of branching and bears secondary pinnae parallel (not perpendicular) to the main axis.

9.9.1.3 *Protocephalopteris praecox*

The oldest fossil species attributed to the Rhacophytaceae is *Protocephalopteris praecox* (Hoeg) Ananiev, which was originally described as *Cephalopteris praecox* (Hoeg 1942). Fossils of this plant are known from Givetian age strata (Upper Middle Devonian) of Spitsbergen and Siberia (and possibly also Belgium and South Africa, Ananiev 1960). Our current understanding of *P. praecox* is based on only a small set of morphologic specimens, showing two orders of branching plus ultimate appendages, with no anatomy yet known. Reconstructions of the plant presented by Ananiev (1960) and Schweitzer (1968) display a main axis bearing quadriseriate first order branches, and dichotomous, catadromic aphlebiae - as in the Rhacophytaceae and *Ellesmeria*. However, unlike those of these other plants, first order branches of *P. praecox* also produce ultimate appendages (which are dichotomous and unwebbed) in a quadiseriate manner (Schweitzer 1968). As with *Cephalopteris mirabilis*, sporangia of *P. praecox* occur at the tips of both ultimate appendages and aphlebiae.

The quadriseriate branching pattern and catadromic aphlebiae of *Protocehalopteris* have been regarded as proof of its homology with the Upper Devonian members of the Rhacophytaceae. Photographs in the literature document that paired ultimate appendages do indeed occur in a distichous sequence on the first order branches (Hoeg 1942; Ananiev 1960; Sweitzer 1968). However, indisputable evidence of the quadriseriate arrangement of first order branches has not been forthcoming. Ananiev (1960) depicts extremely fragmentary material that is inconclusive in this regard. In the single specimen of pertinence to the issue illustrated by Schweitzer (1968; pl. 13, fig. 1), only one of two putative first order branches is seen to be clearly attached to the main axis. The present study of *Ellesmeria* demonstrates that a specimen can easily be misinterpreted as being quadriseriate in organization, should an unrelated axis happen to underlie a lateral branch at its point of attachment to a more proximal order of branching (fig. 16). Thus, the specimen illustrated by Schweitzer (1968) should be re-examined.

The absence of any knowledge of the anatomy of *P. praecox* makes the interpretation of this plant even more difficult. If the main axis gives rise to first order laterals in a truly quadriseriate pattern, one would expect its vasculature to be a clepsydroid protostele. As has been shown, such a vascular pattern is commonly manifested in a distinct double groove in external specimens of the Rhacophytaceae, as well as in *Ellesmeria*. Yet in *P. praecox*, the external surface of a main axis specimen displays a multi-ribbed pattern (Hoeg 1942; Ananiev 1960; Schweitzer 1968). A surface architecture of this type in a fossil specimen is commonly the result of compression of a multi-ribbed stele. The possibility that such a stele pattern occurred in the main axis of *P. praecox* calls into question the previously presumed homology between this organ and a zygopterid phyllophore. However, an alternative interpretation might be that the Svalbard and Siberian specimens assigned to the taxon actually represent several plants (at least one of which displayed a multi-ribbed stele).

In summary, *P. praecox* has not been shown conclusively to demonstrate two of the diagnostic features of the Rhacophytaceae (quadriseriate primary pinnae and clepsydroid protostele), although it does display fertile aphlebiae. Numerous authors have used *P. praecox* as a model for the ancestral source of zygopterid ferns and suggested that these plants were primitively quadriseriate at multiple levels (Schweitzer 1968; Cornet et al. 1976; Taylor 1981). Although entirely plausible, this hypothesis is based on reconstructions of *P. praecox* (by Ananiev 1960 and Schweitzer 1968) which may or may not stand up to future testing.

Chapter X

DISCUSSION

10.1 SIGNIFICANCE OF *Ellesmeria sphenopteroides*, gen. et sp. nov.

10.1.1 EVOLUTIONARY ANALYSIS AND TAXONOMIC ASSIGNMENT

Based on the foregoing comparisons between *Ellesmeria sphenopteroides* and potentially related plant groups of the Devonian and Carboniferous, this new plant seems to share the greatest number of homologous features with members of the Zygopteridales. In particular, its main axis appears to be homologous to the zygopterid phyllophore (i.e., the rachis of the Rhacophytaceae), based on numerous shared aspects of vegetative construction, including: quadriseriate organization of primary pinnae; occurrence of a dichotomous aphlebia at the base of each primary pinna; bipolar, bilaterally symmetric, more or less clepsydroid-shaped internal anatomy (with respect to both main axes/phyllophores and primary pinnae); and venation pattern (i.e., proximally anisotomous, distally dichotomous), as well as general lamina form of pinnules. Thus, *Ellesmeria sphenopteroides* is here recognized as a new member of the Zygopteridales.

Although quadriseriate branching (with respect to primary pinna arrangement) is by far the more common condition for this plant, *Ellesmeria* sometimes demonstrates biseriate branching and therefore resembles both etapteroid and clepsydropsoid zygopteroids. Yet, based on the reasoning of Leclercq (1954), lack of information with respect to the method of primary pinna trace formation in *Ellesmeria* prevents an assessment of its etapteroid *vs*. clepsydropsoid affinities.

However, with regard to stratigraphic position and other features (most notably the occurrence of aphlebiae in the catadromic, as opposed to anadromic position), *Ellesmeria* seems to align most closely with the family Rhacophytaceae, within the order Zygopteridales. Understanding the evolutionary position of the Rhacophytaceae thus seems to be important for clarifying the phylogenetic history of *Ellesmeria*. Most recent classification systems regard the rhacophytaceous ferns as a subgroup of the zygopterid ferns. Based on this interpretation, the most common approach is to recognize the Rhacophytaceae as a family of the order Zygopteridales. Taylor (1981), however, has taken a more non-committal stand with regard to the higher taxonomic placement of this family, erecting a separate class (the Rhacophytopsida). Other researchers have chosen to place this group in an artificial order (the Protopteridales of Cornet, et al. 1976, after Hoeg 1942) for enigmatic fern-like plants of the Devonian. However, this taxonomic group was originally conceived by Hoeg as a depository for aneurophytes, in addition to incompletely known fern-like plants. Hoeg thus based the name of the order Protopteridales on the aneurophyte genus *Protopteridium*, for which the name *Rellimia* was offered by Lerclercq and Bonamo (1971). Aneurophytes are now firmly established as an order of the class Progymnospermopsida - which clearly experienced a separate trimerophyte ancestry from that of fern groups. Yet, even today some would include the aneurophytes along with the unrelated rhacophytaceous ferns within the Protopteridales (Schultka 1978). The Protopteridales therefore seems to be a poorly founded group.

However, the concept of a plexus of early ferns (including the Rhacophytaceae) from which zygopterids and other fern groups evolved perhaps does deserve some taxonomic consideration. Based on such a concept, the reproductive morphology of Carboniferous zygopterids (i.e., the Zygopteridaceae of Barnard and Long, 1975) might be viewed as an ordinal level departure from the earlier fern construction-style of the Rhacophytaceae. The marked distinction between the reproductive structures of these groups lends credence to such an interpretation. However, the details of vegetative morphology and anatomy for these plants are so similar that their placement in a single order (i.e., the Zygopteridales) seems equally defendable, and is here preferred. Thus, whether *Ellesmeria* should prove to be more closely related to the Rhacophytaceae, the Zygopteridaceae, or the Clepsydropsaceae (based on the future discovery of reproductive material, etc.), its evolutionary position is here confidantly interpreted as lying within the the Zygopteridales.

Ellesmeria cannot currently be placed in a family (not the Rhacophytceae, the Zygopteridaceae, nor the Clepsydropsaceae), because of missing information with respect to key familial characteristics. Most importantly, the fertile morphology of this plant (whether sporangia are borne by aphlebiae, pinna stalks, pinnules, or some other structure) remains unknown. Also, the lack of information concerning the method of primary pinna trace formation stands as an obstacle. Finally, the lack of conclusive evidence as to the presence or absence of secondary xylem, and the absence of evidence for more proximal branch orders or the stem would severely inhibit any attempt to formally place *Ellesmeria* within a family.

It should be noted that, as is often the case for fossils, these family concepts are not so rigorous in their definition with respect to monophyly as are those of modern systems based on cladistic techniques. In terms of cladistics-based classification, if Carboniferous zygopterids were derived from earlier rhacophytaceous ancestors, then these plants cannot be placed in separate families. Therefore, the current Rhacophytaceae is perhaps paraphyletic in this regard.

10.1.2 THE PROBLEM OF SPHENOPTEROID FOLIAGE CONVERGENCE

Although the sphenopteroid foliage of *Ellesmeria sphenopteroides* bears a striking resemblance to that of early gymnosperms, the details of the external and internal form of this new plant are distinctly zygopterid - not gymnospermous - in nature, as is demonstrated in the comparison section of this thesis. Similarities between pteridosperms and zygopterids (including *Ellesmeria*) with respect to sphenopteroid foliage are the result of convergent evolution, and are therefore insignificant for understanding the phylogeny of this new plant.

However, an understanding of the convergent history of sphenopteroid foliage holds great significance in general for improved accuracy with respect to the evolutionary attribution of ancient fern-like fossils. This study specifically demonstrates that the zygoterid *vs.* pteridospermous affinities of such fossils should not be assessed based solely on pinnule form - even with respect to fossils that are as old as Late Devonian in age. Thus, the presence of well laminated, *Sphenopteris*-like pinnules in Late Devonian strata does not necessarily indicate pteridospermous vegetation. Pinnule venation of Carboniferous zygopterid ferns does tend to be more monopodial in form, and that of pteridosperms more dichotomous (Galtier and Scott 1985), yet some degree of overlap occurs with respect to this characteristic. Based on the form and venation of the pinnules of *Ellesmeria,* the overlap with respect to these features between Devonian zygopterids and pteridosperms was perhaps even more pronounced.

Even when based on the morphology of the rest of the frond, and not just that of the pinnules, taxonomic determination (i.e., zygopterid fern *vs.* pteridosperm) for sphenopteroid specimens is typically extemely difficult or even impossible, because of fragmentation during the processes of deposition and fossilization. Under such conditions, for example, the bifurcate petioles of pteridosperms can prove to be indistinguishable from the paired primary pinnae of quadriseriately branched zygopterid ferns. Thus, only when the external morphology of preserved fronds can be correlated with their internal anatomy may there be a reasonable expectation of discerning the evolutionary affinities of specimens with sphenopteroid foliage. Specific points of comparison that enable distinguishment of zygopterid foliage from that of pteridosperms are examined in detail in previous sections.

10.1.3 EVOLUTION OF THE ZYGOPTERID FROND

Cornet, et. al. (1976) have speculated that the etapteroid zygopterid frond (quadriseriate primary pinnae, biseriate secondary pinnae) evolved via reduction from an organ quadriseriately branched at multiple levels (as in *Protocephalopteris praecox* and *Rhacophyton ceratangium*). The fragmentary nature of available specimens of *Ellesmeria* creates great difficulty in discerning what this species tells us about frond evolution in early ferns. Because no information is available concerning the stem (nor more proximal orders of branching, should they exist) of *Ellesmeria*, one's ability to compare known levels of its morphology with what is known of the architecture of other fossil taxa is restricted. However, as discussd earlier, the main axis of *Ellesmeria* seems to be equivalent to the phyllophore of Carboniferous zygopterid ferns, as well as the rachis of the Devonian Rhacophytaceae. Based upon this hypothesis, the primary pinnae represent the only architectural site for *Ellesmeria* of quadriseriate-type branching. This morphologic evidence, in combination with the observed well laminated pinnules of *Ellesmeria* , suggests that a frond essentially of the type characterizing etapteroid zygopterids (as well as the clepsydropsoid species *Clepsydropsis leclercqii*) of the Carboniferous had already become established by the Frasnian. Although this interpretation does not in any way disprove the Cornet, et. al. (1976) model for the evolution of the zygopterid frond, it does severely restrict the potential stratigraphic range for such a series. Thus by the Frasnian, before *R. ceratangium* (a key intermediate element of the series proposed by Cornet, et.al. 1976) appears in the stratigraphic record, the end member of this series may have already become established. Furthermore, as previously mentioned, some of the evidence advanced in support of *P. praecox* as the ancestral component of this series may prove to be in error.

Galtier (1966) has suggested that the biseriate frond, with permanent peripheral loops, of the Clepsydropsoideae may have derived from the strictly quadriseriate frond, with impermanent peripheral loops, of the Etapteroideae, by means of a transitional form with a quadriseriate frond and permanent peripheral loops (as in Visean age *Clepsydropsis leclercqii*). Galtier emphasized that the pinna trace of *C. leclercqii* remained undivided for a significant length, before then dividing to supply a pinna pair. For a frond of this type, a failure of the pinna apical meristem to dichotomize would then have resulted in the development of a clepsydropsoid-type, biseriate foliar system.

Ellesmeria may also exhibit a transitional pattern between etapteroid and clepsydropsoid zygopterids with respect to frond architecture. Although usually arranged in a strictly quadriseriate manner, the primary pinnae of *Ellesmeria* occasionally display a reduced quadriseriate to even biseriate organization. No anatomical information is currently available for *Ellesmeria* regarding the status of peripheral loop form during primary pinna trace formation. Yet, the morphology of this new plant seems to lend credence to an additional developmental model, suggested by Cornet, et. al. (1976) in regard to *Rhacophyton ceratangium,* for the evolution of a biseriate frond from a quadriseriate progenitor. Specifically, with respect to *Ellesmeria,* arrested growth of one primary pinna of a pair appears to have sometimes resulted in a reduced quadriseriate to biseriate frond arrangement. Thus, although a model based on *C. leclercqii* for the evolution of the clepsydropsoid frond in zygopterids seems reasonable, the possiblity that this frond architecture was the product of multiple evolutionary pathways should not be overlooked. Furthermore, the Frasnian age of *Ellesmeria* suggests that biseriate frond organization was achieved by some zygopterid ferns much earlier than previously recognized.

10.1.4 ZYGOPTERID CHARACTER STATE ASSESSMENT

Ellesmeria currently represents the oldest certifiable zygopterid fern for which anatomical information is known. This plant thus provides important data for establishing anatomical character state polarities within this group. Specifically, the occurrence of circular-bordered pits in the cell walls of primary xylem tracheids of this plant suggests that this feature is ancestral for the group. This interpretation receives additional support from Scheckler's (1977a, 1977b) observation of circular pits in the primary xylem tracheid walls of a Frasnian age trimerophyte from Alberta, Canada. As earlier mentioned, this partially quadriseriately organized trimerophyte, with bipolar, bisymmetrical anatomy, is perhaps representative of the ancestral stock of zygopterids. Until now, circular pitting has been thought to be a derived feature in zygopterids, occurring solely in the secondary xylem of the Pennnsylvanian species *Zygopteris illinoiensis* (Dennis 1974). Although tracheid pitting of Famenian age *Rhacophyton* has previously been reported to be scalariform, there seems to be some evidence of circular pitting in this genus as well, towards the ends of secondary xylem tracheids (Dittrich, et. al. 1983). As previously mentioned, Matten's 1974 report of putative *R. ceratangium* from the Givetian (i.e., predating *Ellesmeria*) does not include information concerning pitting form. These specimens may very well represent a zygopterid fern, but as no morphological corroboration is available, their generic assignment should be regarded cautiously. Thus, *Ellesmeria* is the oldest confirmed, anatomically preserved zygopterid fern currently known, and its circular pitting seems to represent the ancestral form for the group, based on stratigraphic occurrence.

With respect to morphology, *Ellesmeria* demonstrates that by the Frasnian zygopterid ferns displayed both quadriseriate and biseriate branching of primary pinnae. Thus, *Ellesmeria* compares quite closely with younger, Famennian age *Rhacophyton zygopteroides* with respect to this condition. The putative strictly quadriseriate branch form of *Protocephalopteis praecox* remains the ancestral condition for the Zygopteridales. However, the interpretation for *P . praecox* of a quadriseriate arrangement of primary pinnae is based on fragmentary evidence and should be re-examined.

The well laminated pinnules of *Ellesmeria* demonstrate that ultimate appendages of this form had evolved within the Zygopteridales by the Frasnian - much earlier than previously realized. The narrowly laminated pinnules of basal Tournaisian *Cephalopteris mirabilis* (of the Rhacophytaceae) provide the oldest previous record of pinnule webbing for zygopterid ferns. Extensive pinnule lamination had been considered a highly derived feature of zygopterids, not achieved until later in the Carboniferous (Galtier 1981; Galtier and Scott 1985). Yet, now this pinnule form has been shown to be a much more ancestral trait within the group. The well laminated pinnules of *Ellesmeria* in fact predate the non-laminated pinnules of Famennian *Rhacophyton* that have been used as a model for zygopterid foliage of the Devonian. The non-laminated ultimate appendages of Givetian age *Protocephalopteris praecox* still represent the ancestral condition for the group as a whole. However, some question remains as to the validity of the classification of *P. praecox* as a zygopterid fern (especially beacause of the lack of anatomical corroboration). If *P. praecox* should in the future be shown not to belong to this group, the well laminated foliage of *Ellesmeria* would then represent the ancestral form, based on stratigraphic position, for the Zygopteridales as currently known.

10.2 CONCLUSIONS

In addition to the attribution of *Ellesmeria* to the Zygopteridales, a few other key conclusions can be drawn from this study. First, the Frasnian dating of *Ellesmeria* fossils indicates that laminated foliage had been achieved by some zygopterid ferns long before previously recognized. Second, the possession of laminated foliage by itself does not preclude alignment of this plant with the Rhacophytaceae. Third, the occurrence in *Ellesmeria* of circular- bordered pits in the walls of primary xylem tracheids suggests that this feature is ancestral for the Zygopteridales. Fourth, *Ellesmeria* corroborates the interpretation offered by others (Leclercq 1954; Galtier 1966) that branch pattern (i.e., quadriseriate *vs*. biseriate) alone is not a reliable test of etapteroid *vs*. clepsydroid affinities for zygopterid ferns. Finally, and perhaps most importantly, *Ellesmeria* demonstrates that care must be taken in the attribution of sphenopteroid foliage to early gymnosperms.

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Appendix - Plates

Figure 1: Compression of the holotype specimen showing the three orders of branching (i.e. main axis, primary pinnae, and secondary pinnae) and pinnules. A = proximal most primary pinna node, D = distal most primary pinna node. VPISUPC 110.1.1. One unit = 1mm.

Figure 2: Compression showing the three orders of branching and pinnules. Two primary pinna nodes, and possibly a third (arrow), are evident. A=proximal most primary pinna node, B=next more distal primary pinna node. A twig of *Archaeopteris macilenta* occurs to the right of the specimen. VPISUPC 110.2.1. x 0.55.

Figure 3: Compression showing the three orders of branching and pinnules. Four primary pinna nodes apparent, labelled A (proximal most node, indicated by lower arrow) through D (distal most node, indicated by upper left arrow). Torn area of the specimen where the main axis bends to the right is indicated by the upper right arrow. VPISUPC 110.3.1. One unit = 1mm.

Figure 4: Higher magnification view of specimen seen in fig. 3. Left arrow indicates position of reduced primary pinna (with pinnules) associated with node B of fig. 3. Right arrow points to an axis which crosses beneath (and is unrelated to) the main axis of this specimen. Double ridged main axis vascular groove evident. VPISUPC 110.3.1. x 0.77.

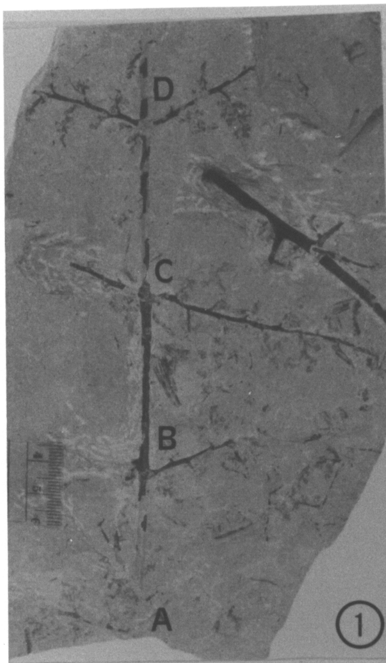
Figure 5: Close up view, following sediment uncovery, of the attachment of the proximal most primary pinna to the main axis of the specimen seen in fig. 3. The main axis runs along the figure's left edge. VPISUPC 110.3.1. x 1.16.

Figure 6: Compression showing a main axis and a single primary pinna node. Main axis vascular groove is evident. USPC 434. x 1.06.

Figure 7: Specimen seen in fig. 1 photographed dry to accentuate the vasular groove of the main axis (at arrow). VPISUPC 110.1.1. One unit = 1mm.

Figure 8: Specimen seen in fig. 2 photographed dry to accentuate double ridged vascular groove of the main axis (at arrow). VPISUPC 110.2.1. x 0.47.

Figure 9: Compression showing the three orders of branching. A node with a pair of primary pinnae (arrows) is evident. Proximal to this node, two pinnule-like structures are seen attached to the right side of the main axis, and another such structure occurs distal to this node. USPC 4342B. x 0.68.



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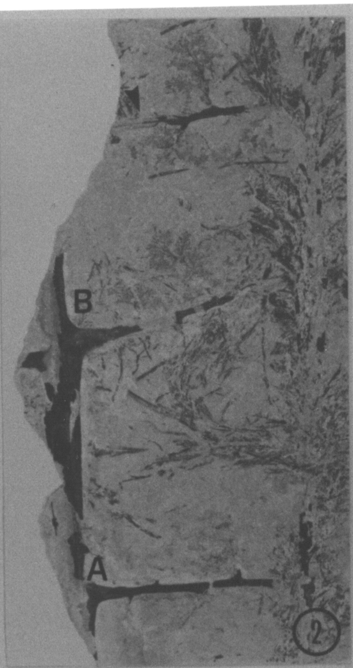

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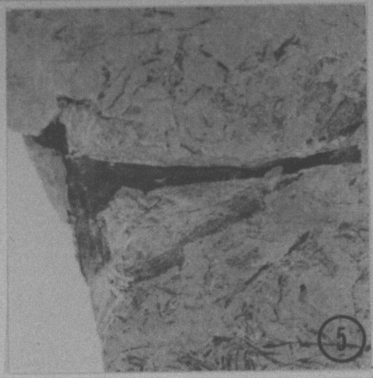

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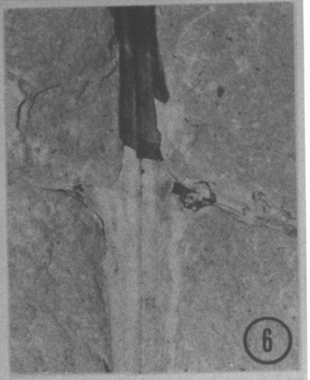

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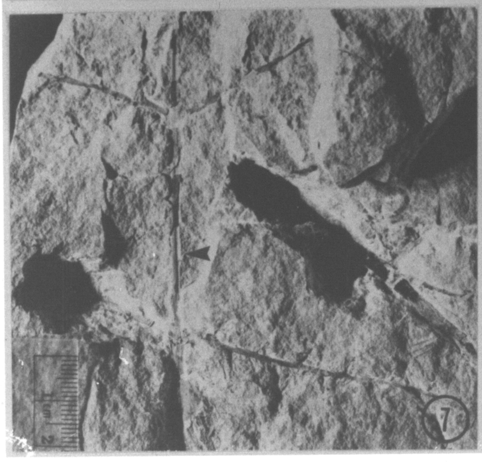

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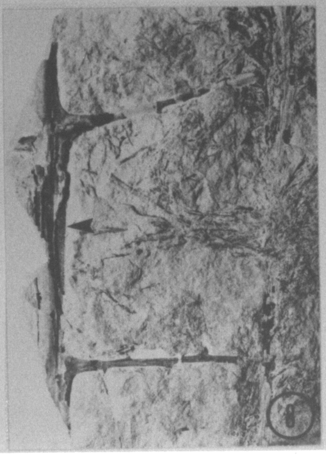

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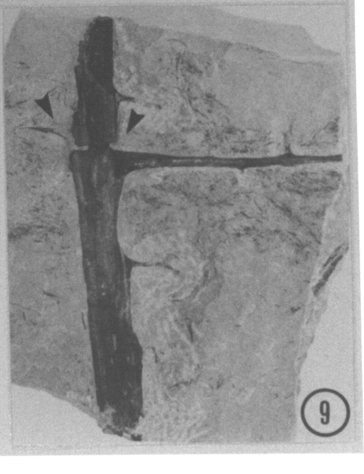

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Figure 10: Holotype specimen viewed from right side, showing quadriseriate arrangement of primary pinnae. The arrows at the far left and far right indicate nodes (B and D, respectively, of fig. 1) where the primary pinnae ascend from the horizontal plane on which the main axis resides. The center arrow points to the intervening node (C of fig. 1), where the primary pinnae descend from the horizontal plane of the main axis. VPISUPC 110.1.1. x 0.46.

Figure 11: Holotype specimen viewed from proximal end, showing quadriseriate arrangement of primary pinnae. The bottom and top arrows indicate primary pinnae (nodes B and D, respectively, of fig. 1) that ascend from the horizontal plane of the main axis, and the middle arrow indicates a pair of primary pinnae (node C of fig.1) that descend from this plane. VPISUPC 110.1.1. x 0.88.

Figure 12: Specimen seen in fig. 2 viewed from distal end. A pair of primary pinnae (arrows), associated with node B of fig. 2, is seen to descend from the horizontal plane of the main axis. VPISUPC 110.2.1. x 0.80.

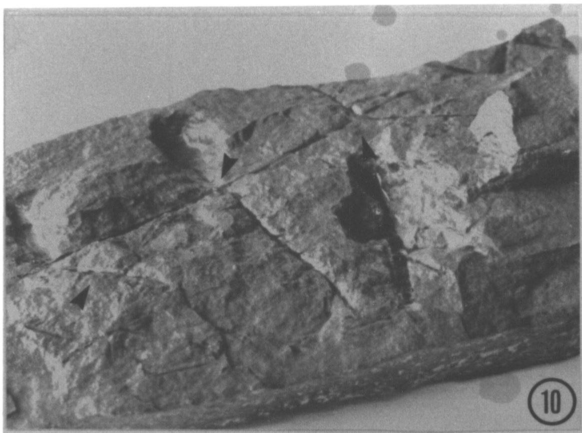
Figure 13: Specimen seen in fig. 2 viewed from left side, showing quadriseriate arrangement of primary pinnae. The left arrow indicates a pair of primary pinnae (node B of fig. 2) that descend from the horizontal plane of the main axis, and the right arrow points to a primary pinna (node A of fig. 2) which ascends from this plane. VPISUPC 110.2.1. x 0.55.

Figure 14: Compression with three orders of branching and pinnules (upper right). Primary pinnae (3 nodes visible) alternately arranged. The distal most primary pinna (with attached pinnules) runs along the top edge of the figure, to the right of the specimen. VPISUPC 110.1.2. One unit = 1mm.

Figure 15: Compression/impression of the three orders of branching and pinnules (counterpart of the specimen seen in fig. 3). Double indented main axis vascular groove evident. The bottom arrow indicates an axis which crosses above, and is unrelated to, the specimen. The top arrow points to a structure of an unknown nature (perhaps pinnule-like) that departs from the main axis. VPISUPC 110.4. One unit = 1mm.

Figure 16: Close up view of the two more proximal primary pinna nodes of the specimen seen in fig. 14. Each primary pinna bears a catadromic pinnule. The arrow indicates an unrelated axis. VPISUPC 110.1.2. One unit = 1mm.

Figure 17: Higher magnification view of laminated pinnules (arrow) attached to the specimen seen in fig. 14. These pinnules are identical to those of other specimens of this plant. VPICUPC 110.1.2. One unit = 1mm.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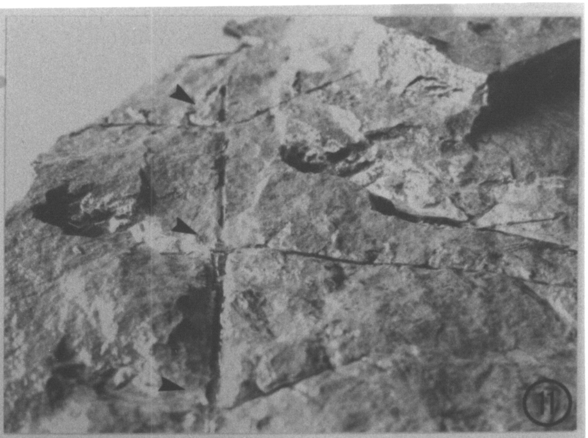
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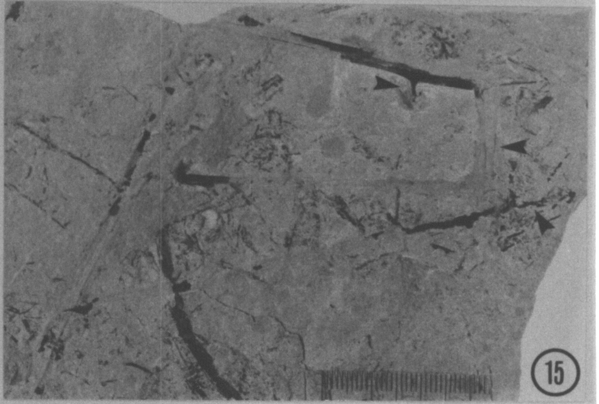
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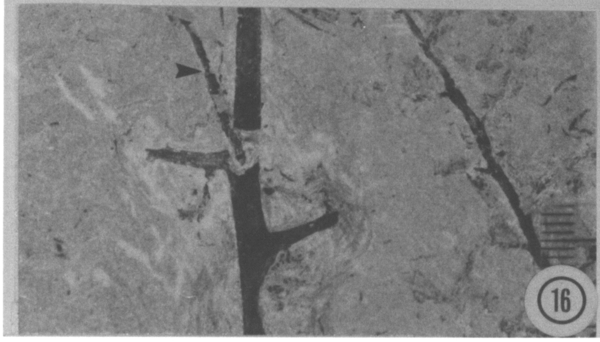
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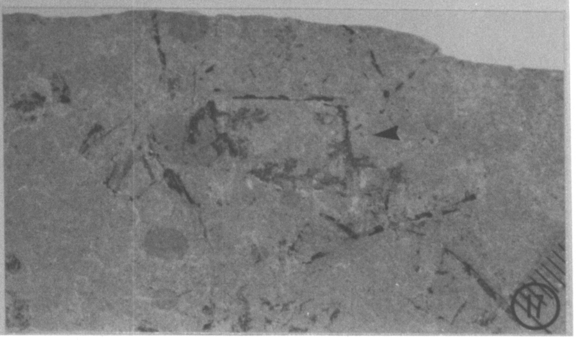
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Figure 18: Higher magnification view of the area seen at D of fig. 1. Alternate to sub-opposite arrangement of secondary pinnae evident. Dichotomous aphlebia (arrow) borne in the catadromic position by the left primary pinna. VPISUPC 110.1.1. One unit = 1mm.

Figure 19: Close up view of the area seen at C of fig. 1. Alternate to sub-opposite arrangement of secondary pinnae evident. Right primary pinna appears to have been torn (just proximal to the first anadromic pinnule) and bent back towards the proximal end of the main axis. VPISUPC 110.1.1. One unit = 1mm.

Figure 20: Close up view of the area seen at B of fig. 2. Two secondary pinnae (with pinnules) occur along the anadromic side of the right primary pinna. The more proximal of these pinnae is smaller in size. The base of another secondary pinna occurs between these pinnae, along the catadromic side of the right primary pinna. Probable rootlets also depart from the catadromic side of the right primary pinna. VPISUPC 110.2.1. One unit = 1mm.

Figure 21: Isolated secondary pinna with laminated pinnules. The pinnules display three main lobes (arrows). VPISUPC 110.3.2. One unit = 1mm.

Figure 22: Secondary pinna with laminated pinnules, attached to the holotype specimen. VPISUPC 110.1.1. One unit =1mm.

Figure 23: Isolated primary pinna (seen at arrow of fig. 2) with two secondary pinnae and laminated pinnules. VPISUPC 110.2.2. One unit = 1mm.

Figure 24: Close up view of the secondary pinnae and pinnules seen in fig. 20. VPISUPC 110.2.1. x 1.6.


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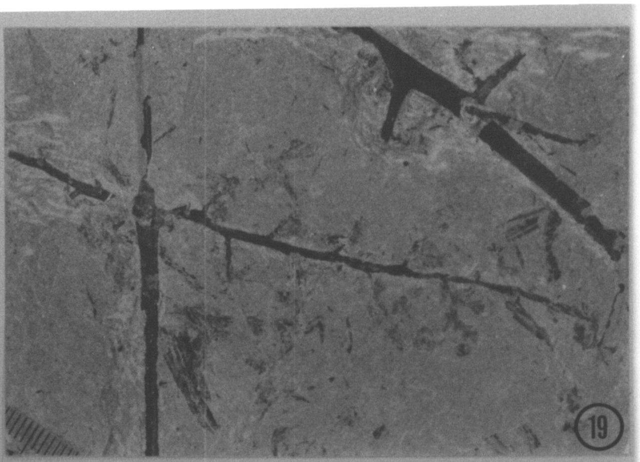
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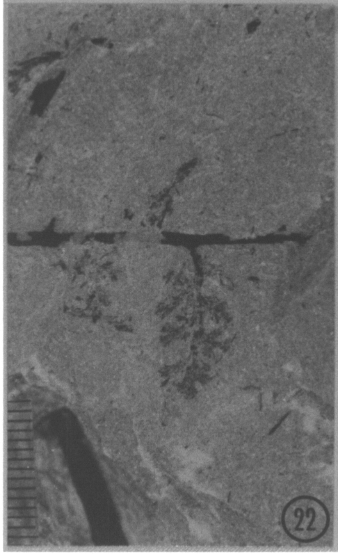
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Figure 25: Higher magnification view of tri-lobed pinnules seen in fig. 21. Venation anisotomous proximally, dichotomous distally. Vein endings (arrows) expanded and tear-drop shaped. VPISUPC 110.3.2. x 6.61.

Figure 26: Higher magnification view of tri-lobed pinnules seen in fig. 21. Venation anisotomous proximally, dichotomous distally. Vein endings (arrows) expanded and tear-drop shaped. VPISUPC 110.3.2. x 6.20.

Figure 27: Higher magnification view of secondary pinna and pinnules seen in fig. 22. Pinnules are three lobed (arrow). VPISUPC 110.1.1. x 5.26.

Figure 28: Higher magnification view of reduced primary pinna with pinnules indicted by left arrow of fig. 4. The edge of the main axis is seen along the right edge of the figure. The top of the figure is proximal, and the bottom of the figure is distal, with respect to the main axis. VPISUPC 110.3.1. x 6.17.

Figure 29: Higher magnification view of dichotomous catadromic aphlebia (arrow) seen in fig. 18. VPISUPC 110.1.1. x 2.33.

Figure 30: Close up view of pinnule-like structures (A=proximal and B=distal) seen in fig. 9. VPISUPC 4342B. One unit = 1mm.

Figure 31: Counterpart of specimen seen in figs. 9 and 30. A group of laminated pinnules (with tear-drop shaped vein endings) occur to the left of the main axis (arrow), in the same area as the pinnule-like structure seen at B of fig. 30. VPISUPC 4342A. One unit = 1mm.

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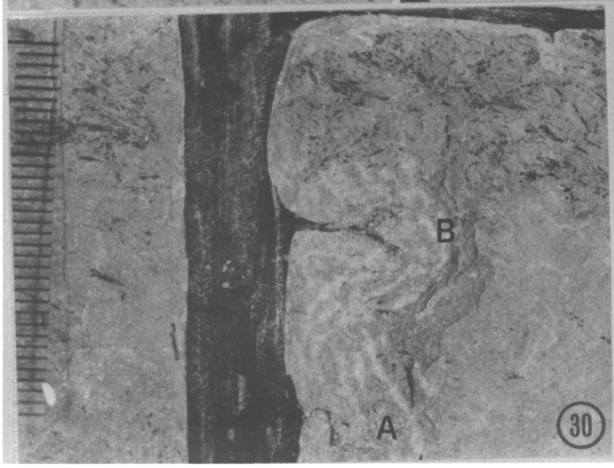

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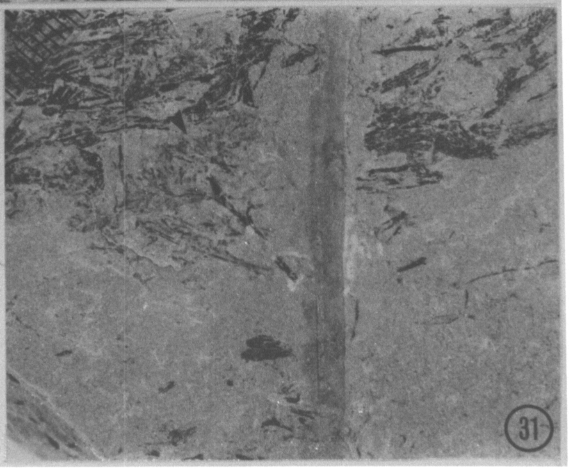

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Figure 32: Close up view of catadromic pinnule borne by middle node of the specimen seen in fig. 14. The tips of this structure appear to be somewhat planated and slightly laminated. VPISUPC 110.1.2. x 12.67.

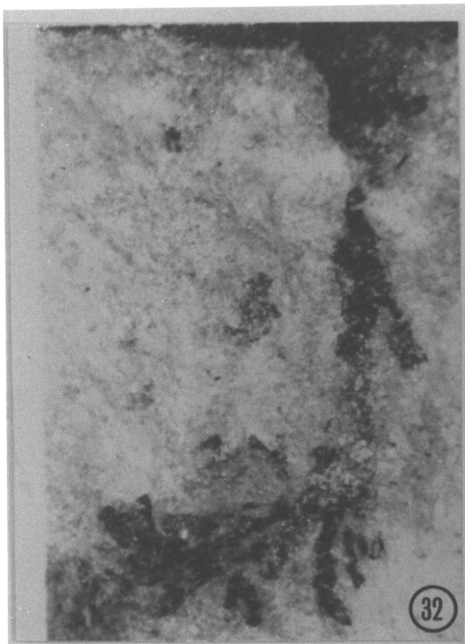
Figure 33: Higher magnification view of the base (arrow) of an aphlebia borne by the left primary pinna associated with node B of fig. 1. VPISUPC 110.1.1. x 10.53.

Figure 34: Impression surface of the petrified specimen, following removal of the petrifaction. Main axis with three primary pinna nodes. The arrows indicate a pair of primary pinna that depart in a quadriseriate manner from the proximal most node (node A of fig. 35). Photographed dry to accentuate double indented vascular groove, which is particularly visible towards the middle of the specimen. VPISUPC 111.1. One unit = 1mm.

Figure 35: The petrified specimen, prior to removal of the petrifaction. Main axis with three primary pinna nodes visible (A=proximal, C=distal). Probable rootlets visible along the bottom side of the specimen. VPISUPC 111.1. One unit = 1mm.

Figure 36: Close up view of probable rootlets along the bottom side of the petrified specimen (near node B of fig. 35). VPISUPC 111.1. One unit = 1mm.

Figure 37: Higher magnification view of probable rootlets along the bottom side of the petrified specimen (near node B of fig. 35). VPISUPC 111.1. x 1.82.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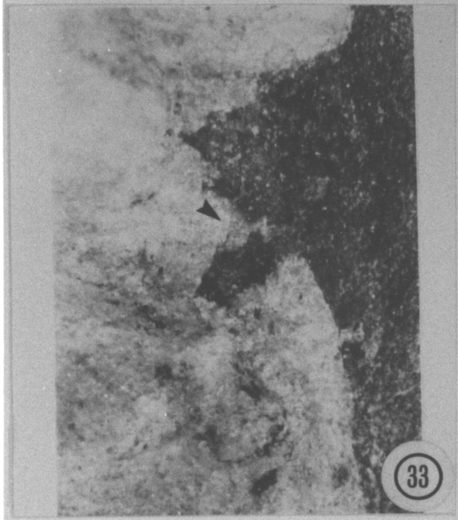
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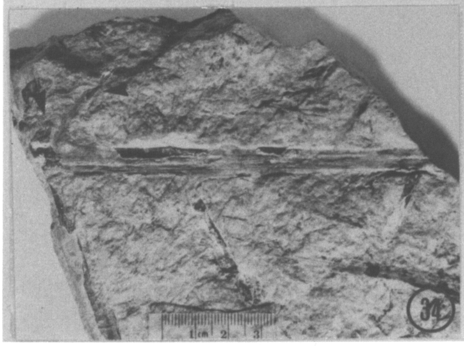
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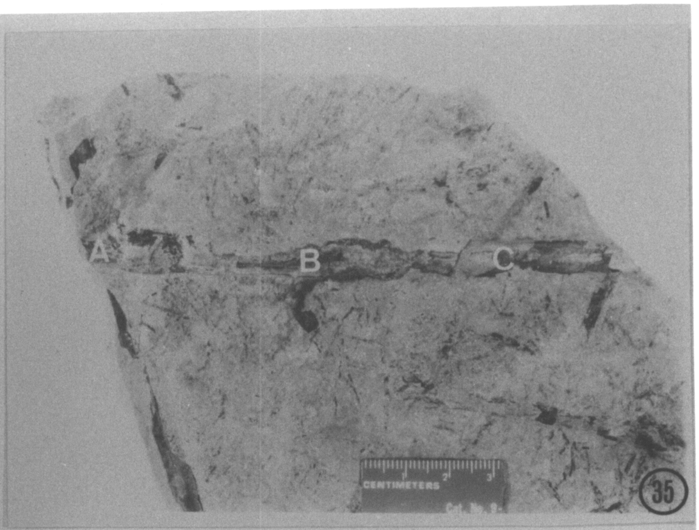
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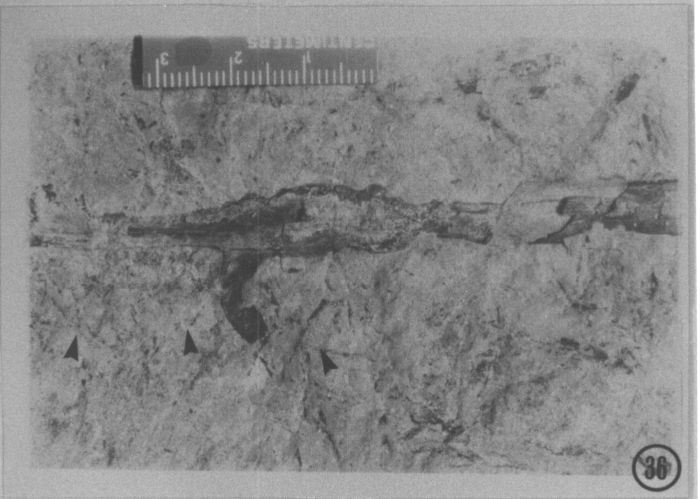
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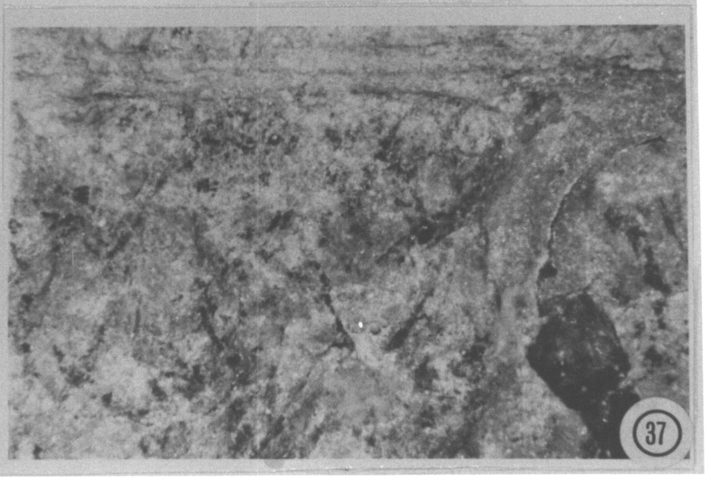
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Figure 38: Higher magnification view of area seen at A of fig. 35. A pair of overlapping primary pinnae that departs from node A is indicted by the arrows (which point to the outer edges of the pinnae, and are directly across from each other). The overlying pinna extends to the upper left corner of the figure, and the underlying pinna extends to the upper right corner of the figure. VPISUPC 111.1. x 6.33.

Figure 39: Higher magnification view of area seen at B of fig. 35. A pair of overlapping primary pinnae that departs from node B is indicted by the arrows. The three left arrows designate the outer edge of one pinna, whereas the arrow at the lower right points to the carbonized surface of an additional pinna (seen in fig. 35 to be attached to the main axis at B). VPISUPC 111.1. x 6.33.

Figure 40: Higher magnification view of area seen at B of fig. 35. A "criss-crossing" cell pattern (arrows) is evident that results from the overlap of the pair of primary pinnae that depart from node B. VPISUPC 111.1. x 13.5.

Figure 41: Close up view of isolated pinnules underlying the petrified specimen. The bottom arrow indicates the proximal end of the main vein. The next two higher arrows indicate the anisotomous nature of more proximal vein branchings. The top two arrows point to expanded, tear-drop shaped vein endings. VPISUPC 111.1. x 12.5.

Figure 42: Close up view of isolated pinnules underlying the petrified specimen. The lower arrow indicates a more distal, dichotomous vein branching, and the upper arrow points to an expanded, tear-drop shaped vein ending. VPISUPC 111.1. x 12.5.

Figure 43: Close up view of isolated pinnules underlying the petrified specimen. The bottom arrow indicates a more distal, dichotomous vein branching, and the middle and top arrows point to expanded, tear-drop shaped vein endings. VPISUPC 111.1. x 12.5.

Figure 44: Transverse section of the main axis stele. The arrow indicates the slightly invaginated mid-region of an overall bilobed strand. VPISUPC 111.1.15r (=reverse side). x 30.

Figure 45: Transverse section of the elongate main axis stele. VPISUPC 111.1.15o (=obverse side). x 30.


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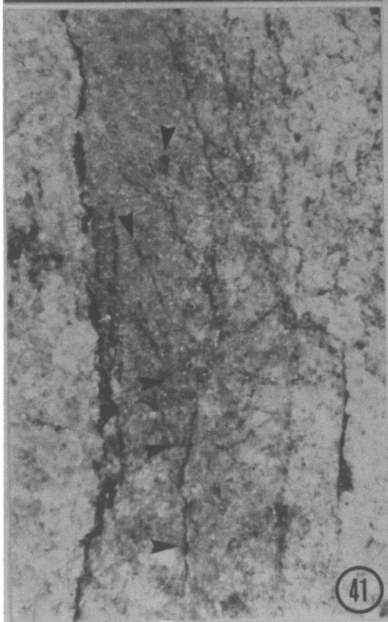
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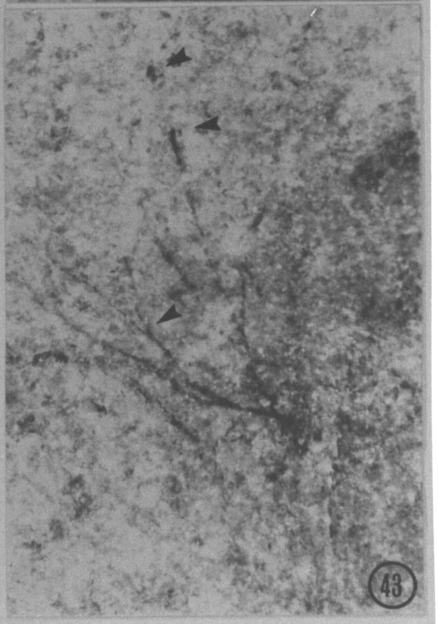
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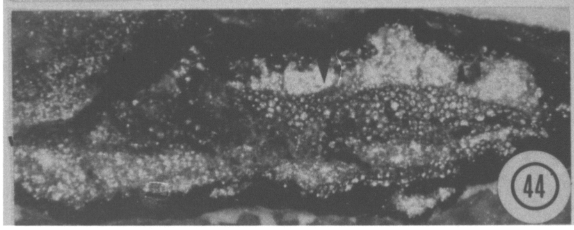
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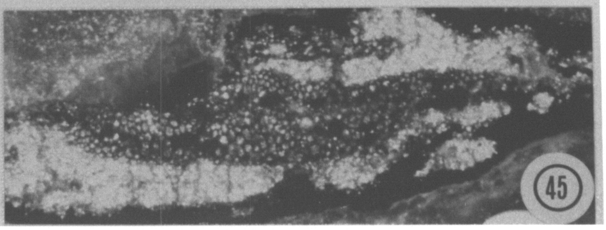
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Figure 46: Transverse section of the elongate, ribbon-shaped main axis stele. The left end of the stele evident (left edge of figure). VPISUPC 111.1.16r. x 30.

Figure 47: Transverse section of the elongate main axis stele. The left end of the stele is seen near the left edge of the figure. The bilobed nature of the strand is indicated by its mid-region invagination (right arrow). A single mesarch protoxylem pole (left arrow) occurs. VPISUPC 111.1.16o. x 30.

Figure 48: Higher magnification view of the left end of the main axis stele in transverse section. The strand's bilobed shape indicated by its mid-region invagination (far right arrow). Single mesarch protoxylem pole (upper left arrow) present. The edges of two probable secondary traces indicated by arrows in the lower left and upper right. VPISUPC 111.1.16o. x 60.

Figure 49: Transverse section of the right end of main axis stele (top) and underlying bipolar primary trace. Single mesarch protoxylem pole of the right end of the main axis stele indicated (arrow). Inner cortex visible (lower left). VPISUPC 111.1. x 60.

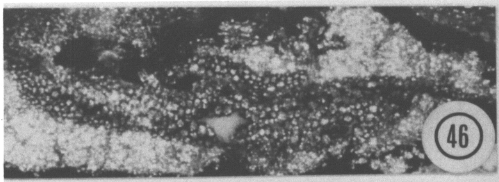
Figure 50: Transverse section of the right end of main axis stele (top) and underlying mesarch bipolar primary trace. Single mesarch protoxylem pole of the right end of the main axis stele indicated (arrow). Inner cortex visible (lower left). VPISUPC 111.1. x 60.

Figure 51: The upper edge of the elongate main axis stele (in transverse section) apparent (arrow). The lower edge of a primary trace occurs at the top of the figure. VPISUPC 111.1. x 30.

Figure 52: The lower edge of a primary trace (in transverse section). The bilobed nature of the trace indicated by its mid-region invagination (arrow). VPISUPC 111.1. x 30.

Figure 53: Transverse section of an early stage in the development of a primary trace (right arrow). The trace is at this point somewhat elliptical. Inner cortical parenchyma occurs to the left (arrow). VPISUPC 111.1. x 60.

Figure 54: Transverse section of a more distal stage (lower two arrows) of the primary trace seen in fig. 53. The trace appears multi-ribbed at this stage (corresponding to the form of the primary traces in figs. 55-58). The main axis stele is indicated by the upper right arrow. The lower arrow indicates an apparent (although poorly preserved) extension of the trace towards the right. The upper left arrow indicates an area where the primary trace touches the main axis stele. VPISUPC 111.1. x 60.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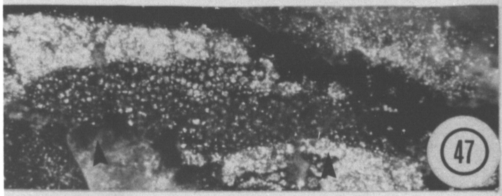
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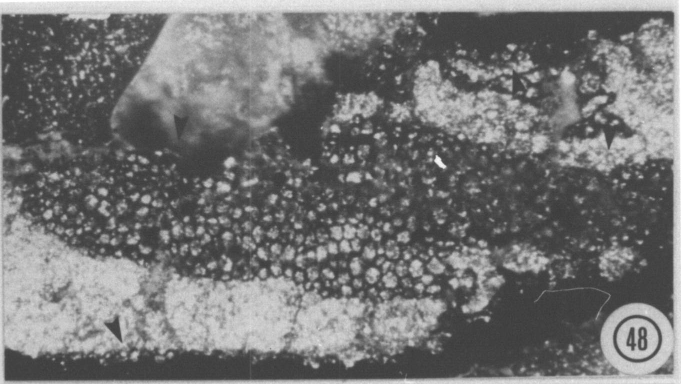
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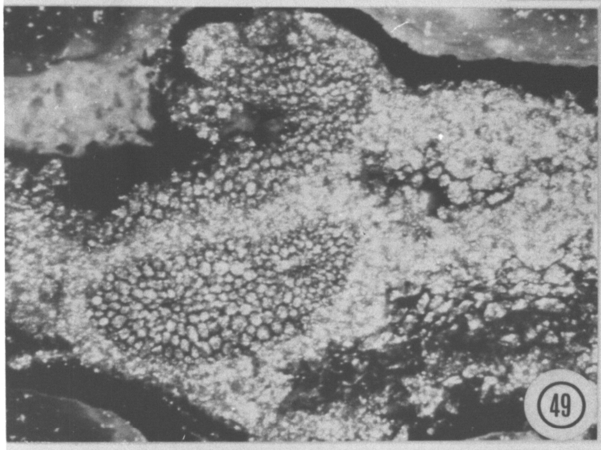
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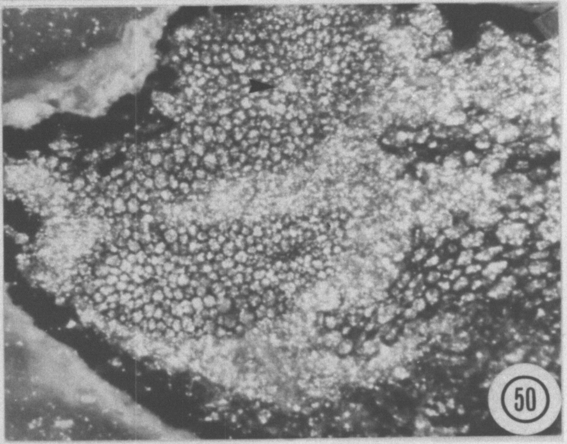
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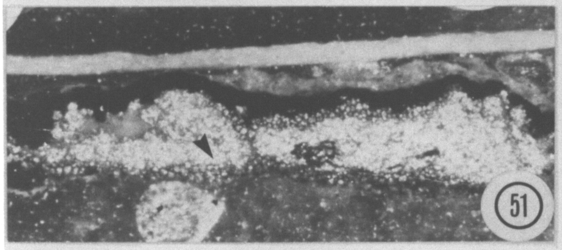
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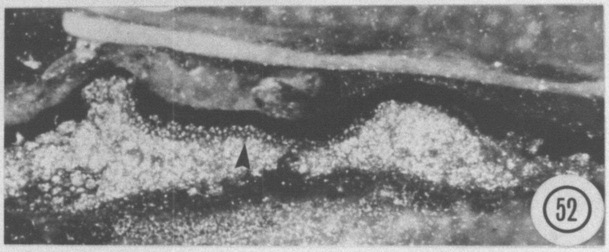
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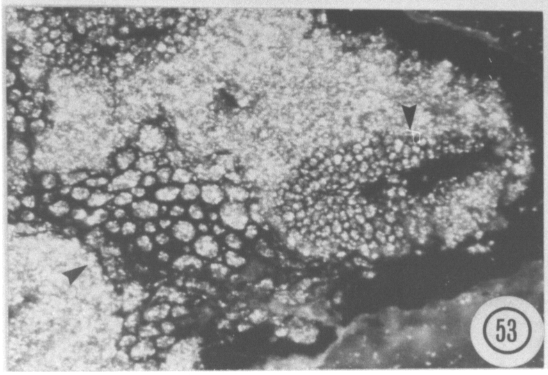
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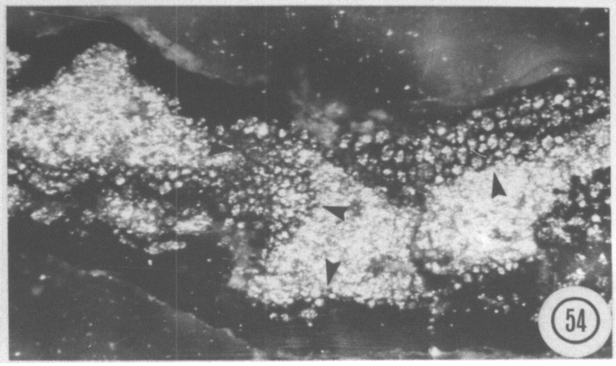
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Figure 55: Transverse section of primary trace, with three ribs visible (left three arrows) of probable four-ribbed form. Upper most arrow indicates the independence of the trace from the main axis stele, a segment of which occurs to the trace's right. Far right arrow points to a circular centrarch aphlebia trace, produced by the primary trace's lower right catadromic rib (lower middle arrow). Far left arrow indicates radiating rows of metaxylem, suggesting the presence of a second incipient centrach trace, associated with the primary trace's lower left catadromic rib. VPISUPC 111.1.1o. x 60.

Figure 56: Same as fig. 55. The right centrarch trace is clearly evident in this section, and the incipient centrarch trace (two lower left arrows) associated with the lower left catadromic rib is more fully visible. The upper left arrow points to the right anadromic rib of the primary trace, and the upper right arrow indicates a strand of the main axis stele. VPISUPC 111.1.2o. x 60.

Figure 57: More distal transverse view of the catadromic ribs of the primary trace of figs. 55-56. The arrow indicates the centrarch trace approaching the lower right catadromic rib of the primary trace. VPISUPC 111.1.5r. x 60.

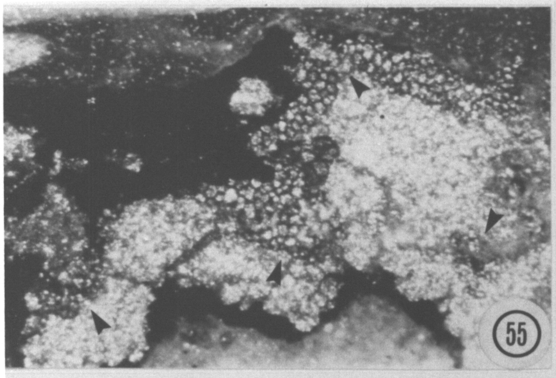
Figure 58: More distal transverse view of the catadromic ribs of the primary trace of figs. 55-57. The arrow indicates the centrarch trace approaching the lower right catadromic rib of the primary trace. VPISUPC 111.1.5o. x 60.

Figure 59: More distal transverse view of right catadromic rib (far left arrow) of primary trace of figs. 55-58. The incipient aphlebia trace is here in attachment to the rib. The middle arrow indicates inner cortical parenchyma. The far right arrow points to the main axis stele' edge. VPISUPC 111.1.6r. x 60.

Figure 60: More distal transverse view of right catadromic rib (arrow) of primary trace of figs. 55-59. The incipient aphlebia trace is seen here to be attached to this rib. A single mesarch protoxylem pole is visible in the middle of the rib. Inner cortical parenchyma occurs to the right of the figure, and the main axis stele is visible at the top of the figure. VPISUPC 111.1.7r. x 60.

Figure 61: More distal transverse view of the right catadromic rib (arrow) of the primary trace of figs. 55-60. The incipient aphlebia trace is seen here to be in attachment to this rib, and a single mesarch protoxylem pole is visible in the middle of the rib. Inner cortical parenchyma occurs to the right of the figure. VPISUPC 111.1. x 60.

Figure 62: Transverse section of a narrow strand of fibrous outer cortical tissue (bottom arrow). Inner cortical parenchyma occurs above (upper arrow). VPISUPC 111.1. x 60.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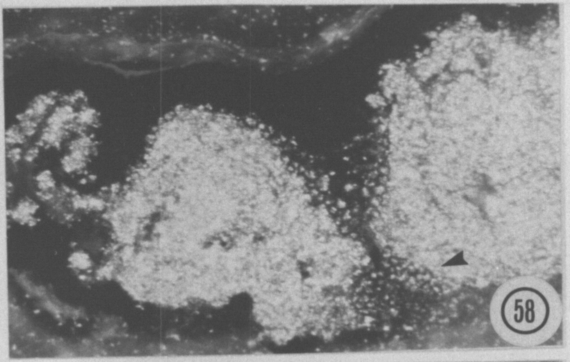
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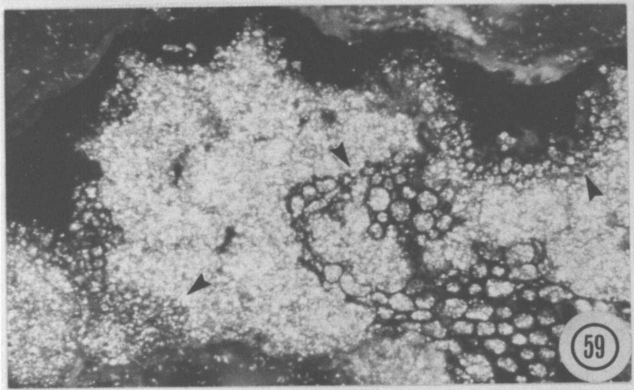
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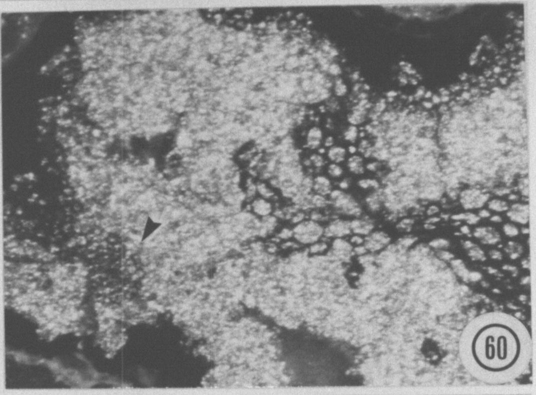
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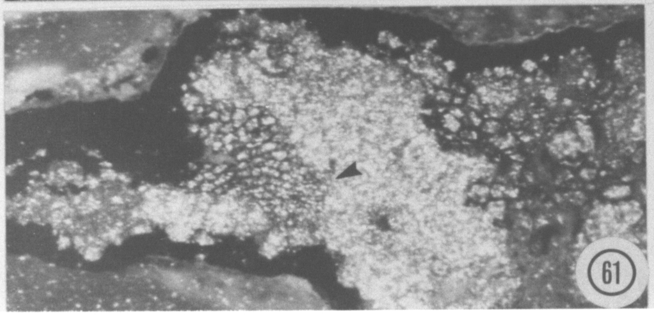
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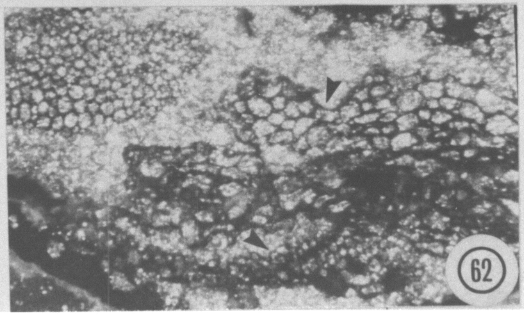
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Figure 63: Longitudinal section through a protoxylem pole (right arrow), showing its mesarch nature. Annular to helically thickened protoxylem tracheids immediately surrounded by scalariform bordered pitted metaxylem tracheids (zone of cells between arrows). Scalariform metaxylem surrounded by larger diameter circular bordered pitted metaxylem tracheids (to the left of the left arrow). VPISUPC 111.1.2L x 73.68.

Figure 64: Longitudinal section through a protoxylem pole, showing its mesarch nature. Helically thickened protoxylem tracheids (center arrow) immediately surrounded by overlying scalariform bordered pitted metaxylem tracheids (left arrow). Scalariform metaxylem surrounded by larger diameter circular bordered pitted metaxylem tracheids (two cells at far right, and four cells at far left). VPISUPC 111.1.1L x 125.

Figure 65: Longitudinal section showing scalariform bordered pitted metaxylem bordered by larger diameter circular bordered pitted metaxylem tracheids to the left. VPISUPC 111.1.2L x 140.83.

Figure 66: Longitudinal section showing scalariform bordered pitted metaxylem tracheids. VPISUPC 111.1.2L x 140.83.

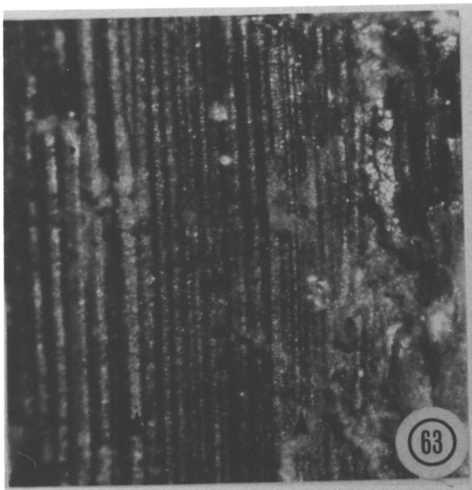
Figure 67: Longitudinal section showing scalariform bordered pitted metaxylem tracheids, borderd by larger diameter circular bordered pitted metaxylem tracheids to the left. VPISUPC 111.1.2L x 140.83.

Figure 68: Longitudinal section showing circular bordered pitted metaxylem tracheids. Cells are two to four seriate with respect to pitting. Pit inner apertures often slanted diagonally, and aligned in a parallel fasion (arrow). VPISUPC 111.1.1L x 140.83.

Figure 69: Longitudinal section showing circular bordered pitted metaxylem tracheids. Cells are two to four seriate with respect to pitting. Pit inner apertures often slanted diagonally, and aligned in a parallel fasion (arrow). VPISUPC 111.1.1L x 140.83.

Figure 70: Transverse section through isolated centrarch trace, interpreted as supplying an aphlebia. VPISUPC 111.1 x 60.

Figure 71: Longitudinal section showing elongate, large diameter, thick walled nature of inner cortical parnchyma. Cells taper towards their ends (arrow). VPISUPC 111.1.1L x 62.24.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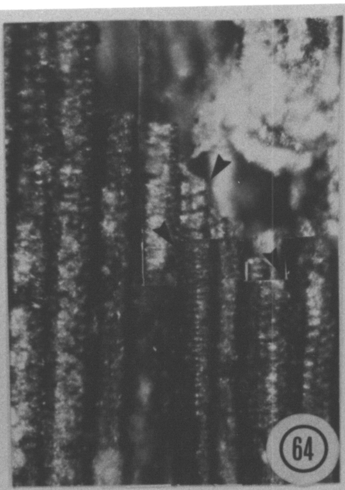
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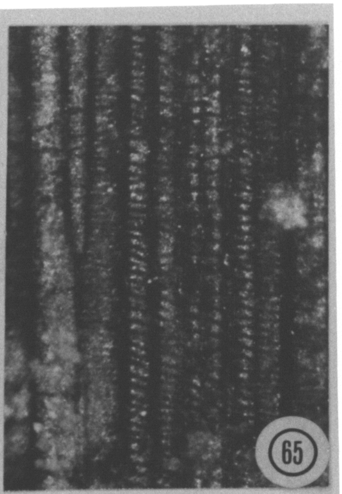
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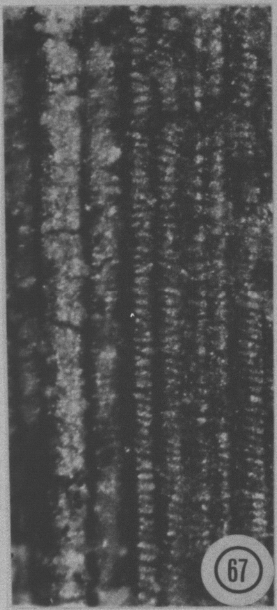
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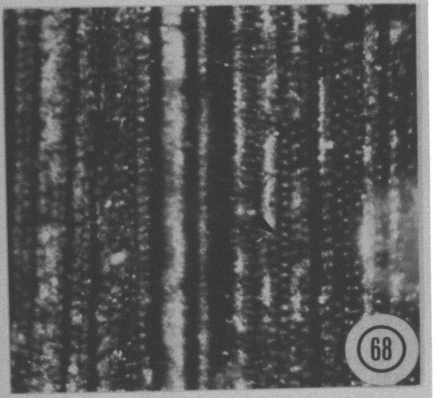
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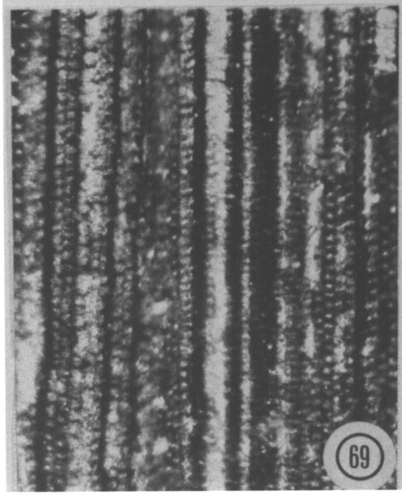
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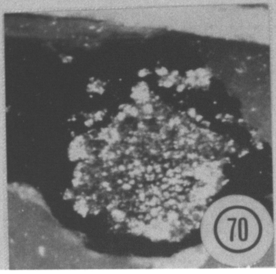
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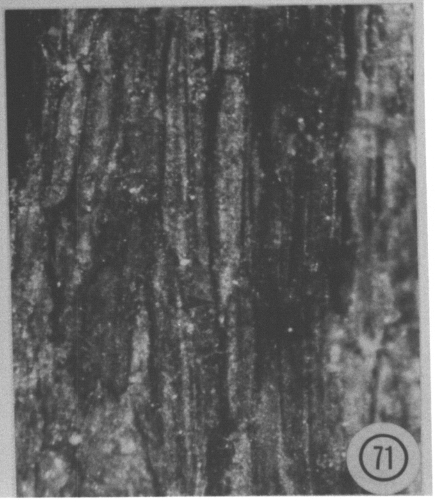
(71)

CURRICULUM VITAE

August 1992

Stewart Adams Hill

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Born April 23, 1966.

Birthplace Sibley Memorial Hospital, Washington, D.C.

Academic Degrees

Bachelor of Science (Biology) from Roanoke College, Salem, Virginia, 1988.

Master of Science (Biology) from Virginia Polytechnic Institute and State University, Blacksburg, Virginia, 1992.

Professional Experience

Field Archaeology Internship, James Madison University, summer 1986.

Internship in Paleobotany at the Museum of Natural History, Smithsonian Institution, Washington, D.C., summer 1987.

Research Assistant for the University of Saskatchewan and VPI&SU, Ellesmere Island, N.W.T., Canada, summer 1989.

Teaching Assistant for the Department of Biology, VPI&SU, fall 1988, spring 1989, fall 1989, fall 1990, fall 1991, spring 1992, and fall 1992 academic sessions (fall 1991 and spring 1992 funding through a grant by SCHEV to Dr. Stephen E. Scheckler and the Learning Resources Center at VPI&SU).

Research Assistant for the Department of Biology, VPI&SU and The Virginia Museum of Natural History, spring 1990 and first summer 1991 academic sessions.

Graduate Assistant for the Department of Biology, in cooperation with the VPI&SU Learning Resource Center (charged with contributing to the development of a computer-interactive Plant Biology Laboratory program), spring 1991, fall 1991, and spring 1992 academic sessions (funding through a grant by SCHEV to Dr. Stephen E. Scheckler).

Memberships

Botanical Society of America
Virginia Academy of Sciences
International Organization of Paleobotanists
Archaeological Society of America

Publications

Abstracts and Presentations at Professional Meetings:

Fossil Plants of the High Arctic. Stephen E. Scheckler and Stewart A. Hill. Virginia Academy of Sciences Spring Meeting, Richmond, Virginia, May 26, 1989.

A *Rhacophyton*-like plant from the Lower Upper Devonian (Frasnian) of Ellesmere, NWT, Canada. Stephen E. Scheckler, Stewart A. Hill, and James F. Basinger. Botanical Society of America Summer Meeting, Toronto, Ontario, August 6-10, 1989.

An Ancestral "Prefern" from the Upper Devonian of Arctic Canada. Stewart A. Hill, Stephen E. Scheckler, and James F. Basinger. Southeastern Fern Conference Annual Meeting, Boone, North Carolina, September 29-October1, 1989.

Floristic Evolution in the Devonian Okse Bay Group of Ellesmere, Arctic Canada. Stephen E. Scheckler, James F. Basinger, and Stewart A. Hill. Botanical Society of America Summer Meeting, Richmond, Virginia, August 5-9, 1990.

Convergence in the Evolution of Megaphyllous Leaves. Stewart A. Hill, Stephen E. Scheckler, and James F. Basinger. Virginia Academy of Sciences Spring Meeting, Blacksburg, Virginia, May 26, 1991.

A New Member of the Zygopteridales from the Lower Upper Devonian (Frasnian) of Ellesmere, N.W.T., Canada. Stewart A. Hill, Stephen E. Scheckler, and James F. Basinger. Botanical Society of America Summer Meeting, San Antonio, Texas, August 5-9, 1991.

Poster Presentations at Professional Meetings:

Convergence of Sphenopteroid Foliage Types. Stewart A. Hill and Stephen E. Scheckler. Mid-Continental Paleobotanical Conference, Columbus, Ohio, April, 26, 1991.

Articles in Preparation For Publication:

Stephen E. Scheckler, James F. Basinger, and Stewart A. Hill. Floristic Evolution in the Devonian Okse Bay Group of Ellesmere N.W.T., Canada. Review of Paleobotany and Palynology.

Stewart A. Hill, Stephen E. Scheckler, and James F. Basinger. A New Member of the Zygopteridales from the Lower Upper Devonian of Ellesmere, N.W.T., Canada. American Journal of Botany (tentative).

Stewart A. Hill and Stephen E. Scheckler. Convergence in the Evolution of Sphenopteroid Foliage Types. Taxon (tentative).

Stewart A. Hill and Stephen E. Scheckler. A Cladistic Analysis of Some Fossil Plants With Sphenopteroid Foliage. American Journal of Botany (tentative).

Stewart A. Hill and Stephen E. Scheckler. Additional Information on the Anatomy of *Rhacophyton ceratangium*. American Journal of Botany (tentative).

Invited Seminars

Roanoke College, Beta Beta Beta (honorary biological fraternity), November, 1989.

Teaching Experience

General Biology Laboratory Instructor (Teaching Assistant), VPI&SU, 1988-1989, fall 1989 academic sessions.

Plant Anatomy Laboratory Teaching Assistant, VPI&SU, fall 1990, fall 1992 academic sessions.

Plant Biology Teaching Assistant, VPI&SU, fall 1991 academic session.

Plant Biology Laboratory Teaching Assistant, VPI&SU, spring 1992 academic session.

Awards

Valedictorian, Roanoke College, 1988
Gary Wesley Leonard Memorial Award in Biology, Roanoke College, 1988
Dr. George G. Perry Beta Beta Beta Achievement Award, Roanoke College, 1987 and 1988
Junior Scholar, Roanoke College, 1987
Senior Scholar, Roanoke College, 1988
The Rev. John E. Bushnell Memorial Award (outstanding campus leadership and scholarship), Roanoke College, 1988
Salem Lion's Club Freshman Award (outstanding campus freshman), Roanoke College, 1985
Alpha Lambda Delta (freshman scholarship fraternity); Senior Award, Roanoke College, 1988
Phi Society (junior scholarship fraternity), Roanoke College
Alpha Chi (senior scholarship fraternity), Roanoke College
Beta Beta Beta (honorary biological fraternity), Roanoke College
Tau Sigma Rho (honorary mathematics fraternity), Roanoke College
Phi Alpha Theta (honorary history fraternity), Roanoke College
Who's Who Among Students in American Universities and Colleges, 1988
Cunnigham Summer M.S. Fellowship Departmental Nominee, VPI&SU, spring 1990
Department of Biology Instructional Fees Scholarship, VPI&SU, fall 1992

Research Interests

Plant evolution
Plant systematics
Plant anatomy and morphology
Paleoecological reconstruction

References

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Stewart Adams Hill

A NEW MEMBER OF THE ZYGOPTERIDALES FROM THE LOWER UPPER DEVONIAN (FRASNIAN) OF ELLESMERE, N. W. T., ARCTIC CANADA

by

Stewart Adams Hill

(ABSTRACT)

A newly discovered fern-like fossil plant is described from the Lower Upper Devonian of southern Ellesmere. This plant occurs as an element of an *Archaeopteris* dominated flora preserved in sediments of the Nordstrand Point Formation (mid-late Frasnian) at Bird Fiord. The plant demonstrates a pinnate vegetative system with three orders of branch and laminate pinnules, of a general sphenopteroid type. Primary pinnae usually diverge from the main axis in distichous pairs (i.e., in a quadriseriate manner), but rarely depart singly (i.e., in a biseriate manner). Each primary pinna bears an aphlebia in the catadromic position. Laminate pinnules are broadly lobed with a proximally overtopped vein system. Anatomically, this plant is characterized by an elongate, mesarch, bipolar protostele that is ribbon to clepsydroid in shape. Proximal to each primary pinna node, an initially crescent-shaped, bipolar pinna trace diverges from the main axis stele. This trace appears to become four-ribbed before dividing to yield a pair of bipolar primary pinna

traces. A pair of circular, centrarch aphlebia traces depart from the catadromic ribs of a primary pinna trace in its four-ribbed stage. Protoxylem is helically thickened, with metaxylem pitting ranging from scalariform to circular. Secondary xylem is unknown. Both the morphology and anatomy of this plant are non-gymnospermous and suggest affinity instead with zygopterid ferns. Within the Zygopteridales, this plant seems to align most closely with the Rhacopytaceae. The Frasnian dating of this plant suggests that laminated foliage had been achieved by some zygopterid ferns long before previously recognized. The presence of *Sphenopteris*-like pinnules in this Frasnian plant also shows that one should be careful in attributing such foliage to early gymnosperms.