

THE DEVONIAN PLANT *REIMANNIA*, WITH A DISCUSSION OF THE CLASS PROGYMNOSPERMOPSIDA

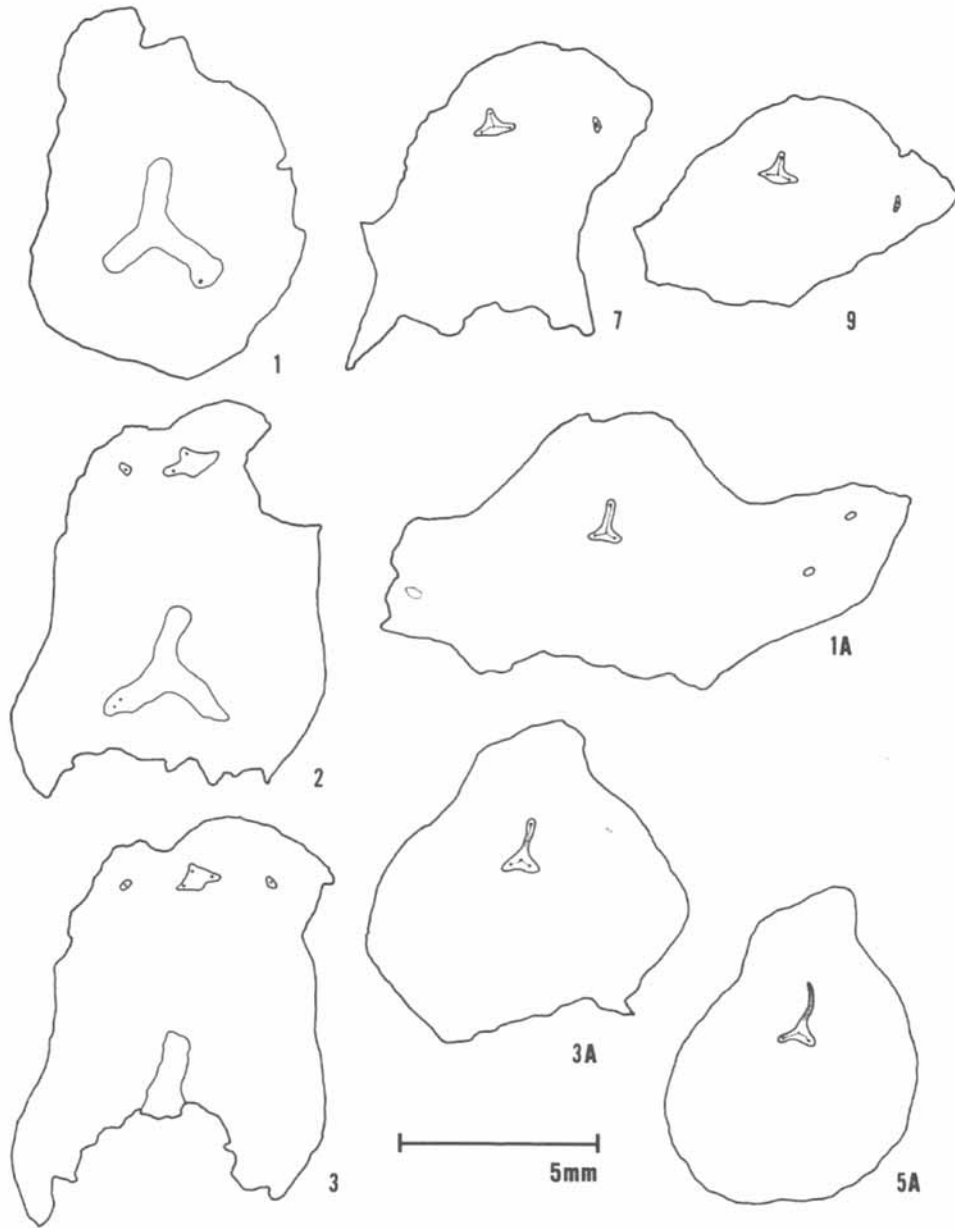
by WILLIAM E. STEIN, JR

ABSTRACT. The type specimen of *Reimannia aldenense*, from the Middle Devonian of New York, was reinvestigated in order to more critically evaluate the anatomy of this poorly understood monotypic genus. Three successive axis orders were observed in organic connection. The first-order axis contains a three-ribbed primary xylem column showing mesarch order of maturation with protoxylem strands along median-radial planes and near the tips of primary xylem ribs. Traces appear to be produced in a helical arrangement. The primary xylem of the second-order axis is proximally elliptical or shallowly four-ribbed, as seen in transverse section, and gives off a sub-opposite pair of traces, supplying third-order axes, which may divide once through the course of their departure. Distally, the primary xylem of the second-order axis assumes an increasingly three-ribbed configuration and probably gives off a single abaxial trace. No evidence for a histologically distinctive 'peripheral loop' has been found.

Although placed within the Iridopteridaceae by Arnold (1940), these features show that *Reimannia* has little in common with the other genera of this group. Instead, *Reimannia* should be considered a form genus for permineralized axes within the Aneurophytales (Progymnospermopsida). Assignment is made to this group even though *Reimannia* shows neither of the diagnostic characters originally used in combination to establish the class: a free-sporing habit and 'typically gymnospermous' secondary vascular tissues. It is pointed out that the definition of the Progymnospermopsida, based upon a combination of primitive and derived characters, is inextricably tied to a prior phylogenetic assessment as the direct ancestors of seed plants. Although such a definition is acceptable on methodological grounds, primitive and derived characters should not be treated equally in the analysis of phylogeny or in the characterization of groups.

REIMANNIA ALDENENSE was established by Arnold (1935) for well-preserved material from the Middle Devonian Ledyard Shale Member of the Ludlowville Formation near Alden, Erie County, New York. Although Arnold referred to several specimens found in more than one concretion (1935, p. 5), the type material consists of axes in a single concretion and apparently this alone formed the basis of his description. Axes of more than one size were included in *Reimannia* but primary emphasis was placed on a single small axis showing the best preservation (Arnold 1935, figs. 1, 6, 9, text-fig. 1). Arnold considered the essential features of *Reimannia* to include: (1) a three-angled primary xylem strand, (2) three protoxylem strands, one of them an 'apparent peripheral loop' (Arnold 1935, p. 7), and (3) the absence of secondary tissues. The three-ribbed configuration of the primary xylem reminded Arnold of *Aneurophyton germanicum* (Kräusel and Weyland 1923, 1926, 1929) but the peripheral loop suggested to him also affinities with the Zygopteridaceae, and doubt was expressed whether real affinities could be determined for such fragmentary material. Subsequently, with the establishment of *Arachnoxylon* (Read 1938) and the discovery of *Iridopteris* (Arnold 1940), Arnold (1940, 1947) placed *Reimannia* in a new suborder, the Iridopteridaceae, within the Coenopteridales as a second genus in the family Iridopteridaceae. The presumed occurrence of a peripheral loop, although not well documented in any of these plants, was considered of prime importance in assessing their affinities. *Reimannia* was proposed as an intermediate between *Arachnoxylon* and *Iridopteris* in a morphological series linking primitive Devonian psilophytes with the coenopterid ferns of the Upper Devonian and Carboniferous (Arnold 1947).

In 1939 Read and Campbell named a second species of *Reimannia*, *R. indianensis*, for a small axis collected from the lower Mississippian (Tournasian) Falling Run Member of the Sanderson



TEXT-FIG. 1. Type specimen of *Reimannia aldenense* Arnold. *Camera lucida* drawings showing organic connection of the three axis orders, the positions of traces in the specimen, and the changes in the configuration of the primary xylem at different levels of the second-order axis. Section numbers are located beside each drawing. Sections 1-3 include portions of the first-order axis and sections 7-5A include only the second-order axis and associated traces to the third order.

Formation of the New Albany Shale in Indiana. This assignment was based upon only a superficial similarity with the smaller axis of *Reimannia*, as described by Arnold, particularly the presence of a three-ribbed or T-shaped primary xylem column with mesarch order of maturation. Hoskins and Cross (1951) rightly segregated *R. indianensis* into its own genus, *Reimanniopsis*, citing differences in the configuration of the stele and in the amount of cortex, as well as the absence of traces in *Reimanniopsis*. Subsequently, Beck (1960a) suggested a possible relationship between *Reimanniopsis* and *Stenokoleos*.

Using evidence from the type specimen and photographs supplied by Arnold, Hoskins and Cross (1951) also redescribed certain aspects of the smaller axis of *R. aldenense*. They pointed out the presence of a fourth protoxylem strand near the centre of the xylem column, and suggested a helical order of trace departure. In addition, these authors expressed the belief that the peripheral loop in this specimen represented an incipient trace near the level of its departure from the primary xylem of the axis. Leclercq (1970), in de-emphasizing the importance of the peripheral loop as a taxonomic character in the face of a suite of other diagnostic features circumscribing the Cladoxylopsida, carried the idea even further. Pointing to *Reimannia* as a plant containing both a peripheral loop and normal protoxylem strands, she suggested that the peripheral loop may have had its evolutionary origin as a discontinuous column or strand of protoxylem parenchyma intimately associated with trace departure.

In 1974 Scheckler noted that since Arnold's original description of *R. aldenense*, several apparently unrelated plants had been discovered in Middle and Upper Devonian sediments containing three-ribbed protosteles including aneurophytalan progymnosperms, and a Devonian *Stenokoleos*.

Without consulting the type material, Mustafa (1975) included *R. aldenense* in a sweeping synonymy of Devonian taxa including *Rellimia* (*Protopteridium*) (Leclercq and Bonamo 1973), *Aneurophyton*, *Reimanniopsis*, and *Triloboxylon* (*Aneurophyton hallii*) *arnoldii* (Arnold 1940; Matten 1974). The resultant taxon, called *Protopteridium thomsonii*, was assigned to the Aneurophytales of the Progymnospermopsida. However, the characters used in support of this synonymy (helical arrangement of branches and three-ribbed steles) have been viewed by other workers (Bonamo 1977; Serlin and Banks 1978) as insufficiently diagnostic in light of known differences between the taxa in other aspects of their morphology.

I became interested in *Reimannia* while comparing the type specimen with other members of Arnold's Iridopteridineae and with possible new representatives of this group. In a view through the plastic in which the specimen had been embedded, I noticed that one axis bore a preserved lateral branch. Thus, a reinvestigation of this specimen promised to provide additional information on the three-dimensional architecture of this plant plus some direct evidence, perhaps, on the relationship between peripheral loop and incipient traces.

LOCALITY

According to Arnold (1935), *Reimannia aldenense* was collected from the well-known locality at Spring Creek, half mile north-east of Alden, Erie County, New York (Fisher 1951; Buehler and Tesmer 1963; Brett 1974). Plants occur in pyrite nodules of various sizes, along with a distinctive invertebrate fauna, in a narrow stratigraphic horizon of the Ledyard Shale Member, Ludlowville Formation, Hamilton Group. The horizon is upper Middle Devonian (Givetian). Besides *Reimannia*, plants recorded from this locality and horizon include *Triloboxylon* (*Aneurophyton hallii*) *arnoldii* (Arnold 1940; Matten 1974), *Xenocladia medulllosina* (Arnold 1952), isolated fragments, occasionally very large, of secondary xylem referred to *Dadoxylon* Dawson (Arnold 1935, 1940), and a doubtful report of *Lepidodendron* (Fisher 1951).

MATERIALS AND METHODS

The single specimen consists of plant axes permineralized with iron sulphide, forming the nucleus of what was probably a nearly spherical pyrite concretion. When obtained for this study, the concretion had already been cut into two parts and both were embedded in plastic, thus maintaining the specimen in excellent condition. A total of three surfaces, all views of axes in transverse section, were prepared by Arnold (1935) and these alone formed

the basis of his report. To the best of my knowledge, based upon personal communication with Dr. Arnold in 1977, and a thorough search of the collections of the Museum of Paleontology, University of Michigan, there are no additional fragments of the specimen. For this study, the individual nodule pieces were trimmed of excess plastic and accretionary pyrite. A total of twenty-one transverse sections were cut at 1 mm intervals except for one 1.5 mm thick section (no. 4), and a 2 mm thick end block (no. 11). All original surfaces prepared by Arnold have been conserved.

From two 1 mm thick transverse sections (no. 7A, no. 10), a total of nineteen longitudinal sections were cut at 1 mm intervals. One section (no. 4) was broken lengthwise several times and observed with scanning electron microscopy for details of pitting in tracheid walls preserved as pyrite casts. For discussions on the interpretation of these structures, see Grierson (1976), Stein (1981), and Beck, Coy and Schmid (1981). All cut sections were individually re-embedded in 'Bioplastic' (Ward's Scientific Establishment, Rochester, New York, U.S.A.). Most surfaces were prepared by grinding with no. 600 silicon carbide grit followed by fine-polishing with 0.05 mm aluminium oxide powder. A few were subjected to a concentrated nitric acid etch for 15 seconds, followed by neutralization with concentrated ammonium hydroxide, and a two step re-acidification of the specimen using hydrochloric acid following a technique similar to that described by Jennings (1972). For more specific information on this method, see Stein, Wight and Beck (1982).

DESCRIPTION

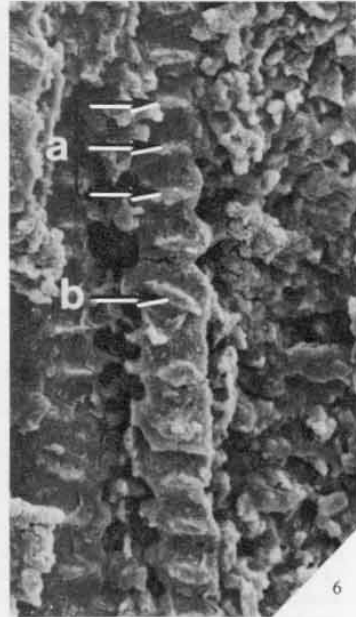
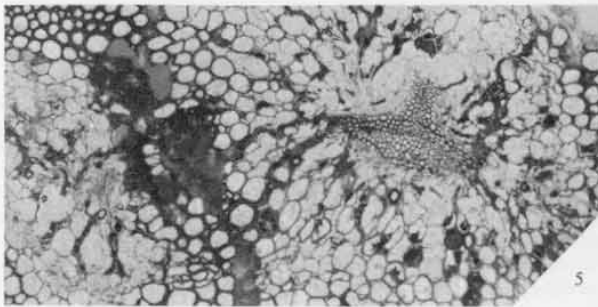
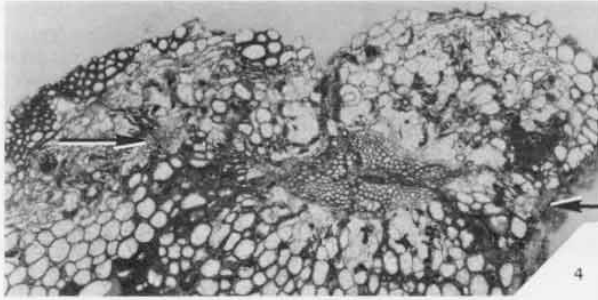
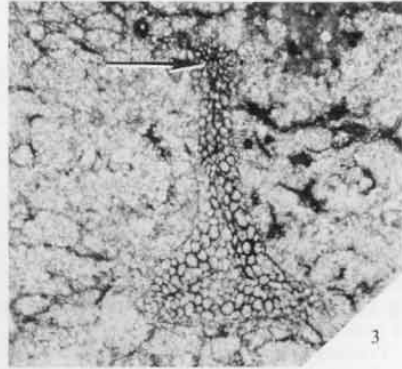
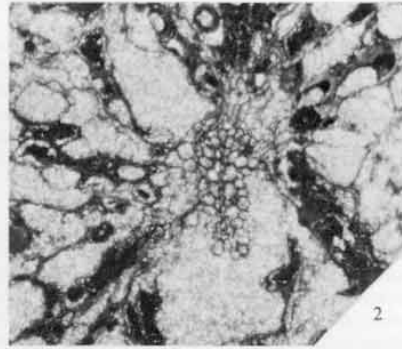
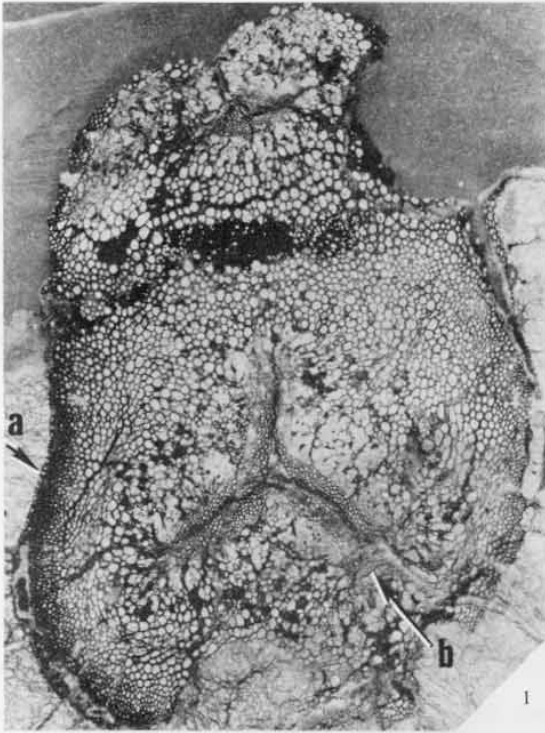
The type specimen provides evidence of three axis orders in organic connection (Pl. 60, fig. 1; Pl. 61, fig. 1; text-fig. 1). In transverse section, the first-order axis measures approximately 9.5 mm in diameter at its greatest extent and bears a second-order axis which is approximately 6.5 mm in diameter. The second-order axis, by far the most extensively preserved of the three orders, was observed over a distance exceeding 2 cm compared to a maximum length of 7 mm for the first-order axis fragment. Axes of the third order are preserved only at their bases and traces to this order have less than 1 mm preserved length. All orders are comprised of primary tissues only. Vascular tissues are protostelic with the primary xylem of first and second orders forming ribbed columns of tracheids. The primary xylem of traces to third-order axes is elliptical as seen in transverse section. External to the primary xylem at all levels is a poorly preserved region which probably represents primary phloem at least in part. Beyond this occurs an extensive and more or less homogeneous cortex. In some parts of the specimen, remnants of cells interpreted as epidermis are also present (see below).

Cortex

Cortex of the first-order axis (Pl. 1, fig. 1) measures from 1 to 3 mm in thickness with an average thickness of about 2 mm. The second-order axis (Pl. 61, fig. 1) has cortex only a little less extensive, ranging from 1.5 to 2.5 mm in thickness. There is no distinct zonation of cortical tissues although cells decrease in size and increase in apparent cell wall thickness toward the periphery of the axes (Pl. 61, fig. 3). Cellular specializations such as sclerotic nests, cortical secretory canals, or discrete fibrous hypodermal strands are not a feature of the specimen.

EXPLANATION OF PLATE 60

Figs. 1-6. *Reimannia aldenense* Arnold—type specimen from Erie County, New York. UMMP No. 16231.
 1, transverse section of the first-order axis with attached proximal portion of the second-order axis. Note the three-ribbed configuration of the primary xylem in the first-order axis, and the four-angled shape of the primary xylem of the second-order axis. Compare with figs. 4, 5, and Pl. 61, fig. 1. Arrow **a** points to a bounding tissue interpreted as epidermis. Arrow **b** indicates the expanded tip of a primary xylem rib which represents an incipient trace at this level, $\times 10$.
 2, transverse section of a trace to the third axis order proximal to the level of its division into two traces, $\times 65$.
 3, transverse section showing three-ribbed configuration of second-order axis at about the level of Pl. 61, fig. 1. Arrow points to a protoxylem cavity probably associated with an incipient trace at this level, $\times 40$.
 4, transverse section, higher magnification of vascular tissues in second-order axis shown in fig. 1. Arrows indicate the sub-opposite pair of traces to third-order axes, $\times 20$.
 5, transverse section of second-order axis distal to the level in fig. 4. Note the increased prominence of the abaxial rib of the primary xylem and one of two traces to third-order axes, $\times 20$.
 6, split-longitudinal section observed by scanning electron microscopy showing the pyrite cast of a metaxylem tracheid with a column of discrete, elliptical aperture casts, arrows **a**. In one instance, an aperture cast leading into a cell lumen above the plane of the specimen surface can be recognized by the different orientation of its long axis, arrow **b**, $\times 1200$.



Toward the centre of the axes, cortical cells range from 35 to 200 μm in diameter and are approximately isodiametric. At the periphery, they usually measure between 30 and 80 μm in transverse diameter but occasionally reach 100 μm . In longitudinal section, these cells appear sclerenchymatous and generally elongate. This outermost cortical layer has previously been interpreted as a fibrous hypodermis (Arnold 1935). Occasional cortical cells with dark materials in their lumina occur throughout most parts of the specimen, but are more common toward the centre of the axes (Pl. 60, figs. 1, 2, 5; Pl. 61, figs. 2, 3). They are generally lacking, however, in the outermost cortical regions (Pl. 61, fig. 3). On the basis of histological features other than the presence of the dark materials, these cells are not distinctive.

At the periphery of the preserved axes in some regions is a tissue apparently one, or at most two or three cell layers thick, which previously has been interpreted as an epidermis (Arnold 1935). Cell preservation is not sufficient, however, to enable one to recognize cuticle or to define the cells clearly on a histological basis. In transverse section, most of the cells appear isodiametric to slightly radially flattened. All are characterized by the presence of a large amount of a dark substance filling cell lumina (Pl. 60, fig. 1, arrow a; Pl. 61, fig. 3, arrow). These cells vary from 80 to 130 μm in transverse diameter, and are probably no more than twice the greater measurement in length.

Vascular tissues

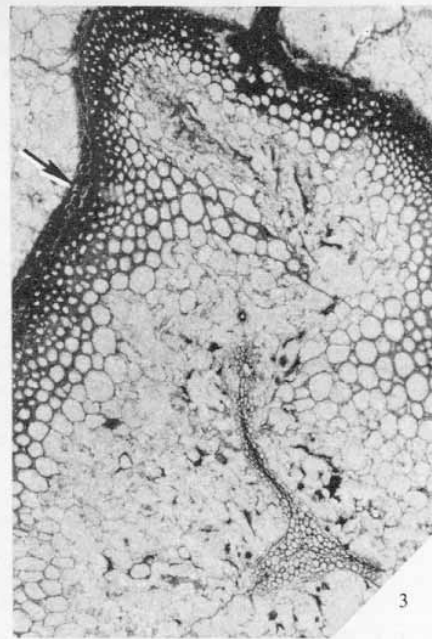
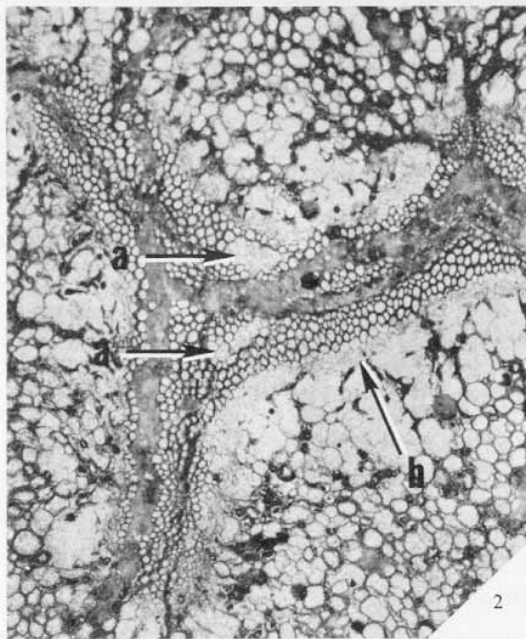
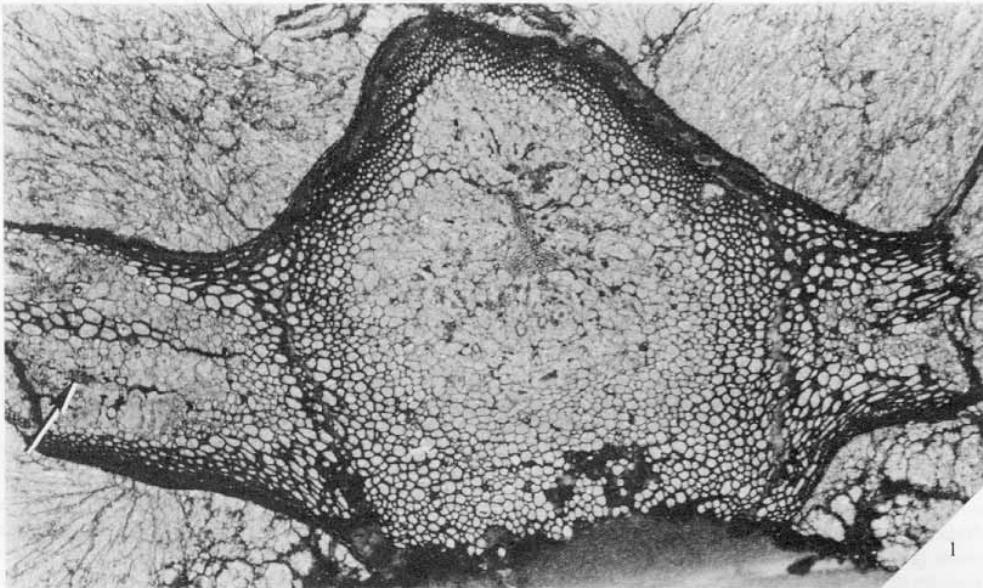
Elements of the primary xylem form a deeply three-ribbed column in the first-order axis (Pl. 60, fig. 1; Pl. 61, fig. 2). Primary xylem in the second-order axis is shallowly four-ribbed or diamond shaped proximally near the level of its departure from the first-order axis (Pl. 60, figs. 1, 4; Pl. 62, fig. 2), but becomes progressively more three-ribbed (Pl. 60, figs. 3, 5; Pl. 61, fig. 3; Pl. 62, figs. 1, 3). The maximum diameter of the primary xylem of the first order is approximately 3 mm with individual xylem ribs averaging 1.8 mm in radial extent, and 0.6 mm in width. In a distal portion of the second-order axis, the maximum primary xylem diameter varies from 0.8 to over 1.5 mm with primary xylem ribs varying in width from 0.1 to 0.3 mm, and in radial extent from 0.3 mm to as much as 1.3 mm in one case probably associated with the departure of a trace (Pl. 61, fig. 3; text-fig. 1).

Where well preserved, the primary xylem is apparently comprised only of conducting elements. At certain levels in the specimen, it is possible that isolated patches of xylem parenchyma were originally present (Pl. 61, fig. 2, arrow a). However, in most of these cases I have been unable to distinguish this possibility from the effects of poor preservation.

Primary xylem maturation was clearly mesarch. Although poorly preserved in the first-order axis, several probable examples of protoxylem strands were observed in the expanded tips of primary xylem ribs and also in a few positions internally along the median planes of some of the xylem ribs (Pl. 61, fig. 2). The peripheral protoxylem strands were probably associated with incipient traces but proof of this is lacking in the specimen. The positions of protoxylem strands in the primary xylem of the second-order axis have been determined with much greater precision. Proximally (Pl. 60, fig. 4; text-fig. 1, section 3), protoxylem strands occur near the tips of the lateral and abaxial ribs of the primary xylem. The adaxial rib of the primary xylem at this level is not associated with a protoxylem strand, and distally, it becomes indistinct. A fourth protoxylem strand is located at the centre of the primary xylem system in this axis. Although not obvious proximally, it is clearly present in distal sections (Pl. 60, fig. 5; Pl. 61, fig. 3; Pl. 62, figs. 1, 3). Between protoxylem strands along the median-radial planes, of xylem ribs, several very small and tangentially flattened or irregularly shaped tracheids can be seen in some transverse sections. These are interpreted as flattened elements of the metaxylem, and appear to be variable in expression but more prevalent in distal portions of the second-order axis (Pl. 61, fig. 3; Pl. 62, fig. 1). A single

EXPLANATION OF PLATE 61

Figs. 1-3. *Reimannia aldenense* Arnold—type specimen from Erie County, New York. UMMP No. 16231. 1, transverse section of the second-order axis distal to the level in Pl. 60, fig. 5, showing the bases of a sub-opposite pair of third-order axes. In the third-order axis base to the left, one of a pair of traces can be seen, arrow. Compare with text-fig. 1, $\times 10$. 2, transverse section, higher magnification of primary xylem of first-order axis at a level near that of Pl. 60, fig. 1. Poorly preserved regions in the xylem, arrows a, suggest possible presence of xylem parenchyma. Arrow b indicates a partially preserved tissue immediately adjacent to the primary xylem interpreted as probable primary phloem, $\times 23$. 3, transverse section of second-order axis distal to the level of fig. 1. The abaxial rib of the primary xylem is highly elongate at this level and probably associated with an incipient trace. Arrow points to the bounding tissue interpreted as epidermis in this specimen, $\times 20$.



STEIN, *Reimannia*

central protoxylem strand occurs in traces to the third-order axes (Pl. 60, figs. 2, 4). These divide once, tangentially with respect to the second-order axis, in association with division of the traces themselves.

All available evidence suggests that protoxylem strands are of a type which is typical of most vascular plants (for example, see Pl. 62, fig. 2, arrow, 3). In some cases (e.g. Pl. 60, fig. 3, arrow; Pl. 62, fig. 1, arrow), there may have been some xylem parenchyma associated with protoxylem strands. However, this by itself does not constitute sufficient evidence for applying the term 'peripheral loop' to this plant.

Individual metaxylem tracheids range between 30 and 95 μm in transverse diameter in the first-order axis, and between 25 and 60 μm in the second-order axis. Some of these were observed with elliptical apertures (Pl. 60, fig. 6), but it is unclear whether the tracheids are characterized by circular bordered pit pairs or scalariform or reticulate secondary wall thickenings. No difference in wall sculpturing has been noted between radial and tangential walls of the elements. Probable protoxylem elements, with diameters between 10 and 30 μm , were observed only in transverse section.

The region of presumed primary phloem is not well preserved in this specimen. In a few cases (Pl. 61, fig. 2, arrow b), small cells, approximately 30 μm in diameter, occupy positions immediately adjacent to xylem elements. It is possible that these cells were phloem conducting elements, but no distinct histological evidence, except their position, supports this interpretation. Immediately exterior to the small cells is a poorly preserved region, probably innermost cortex in part but also, perhaps, outer phloem or pericycle. In transverse section, cells of this region are very large, up to 300 μm in diameter and radially elongate. Many contain dark substances in their lumina. However, most cells are represented by isolated, radially aligned wall fragments and there is little evidence of histological zonation or a distinct boundary between vascular and cortical tissues.

Relationship between axis orders

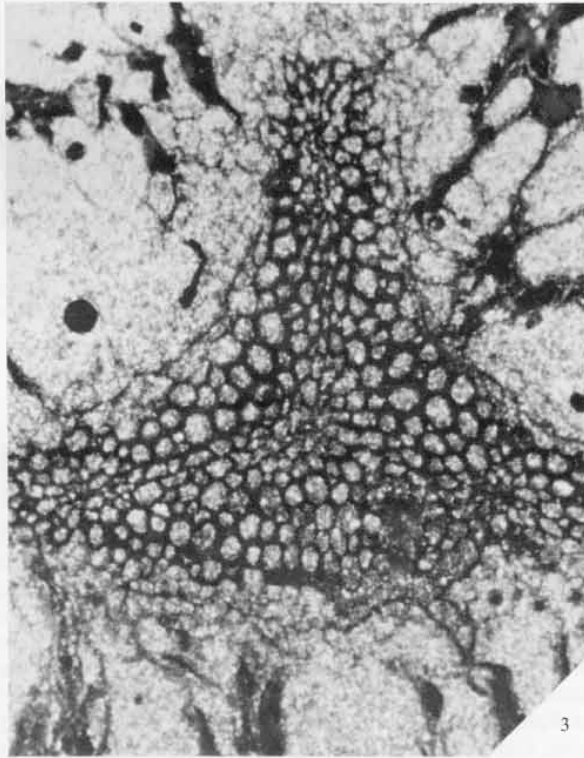
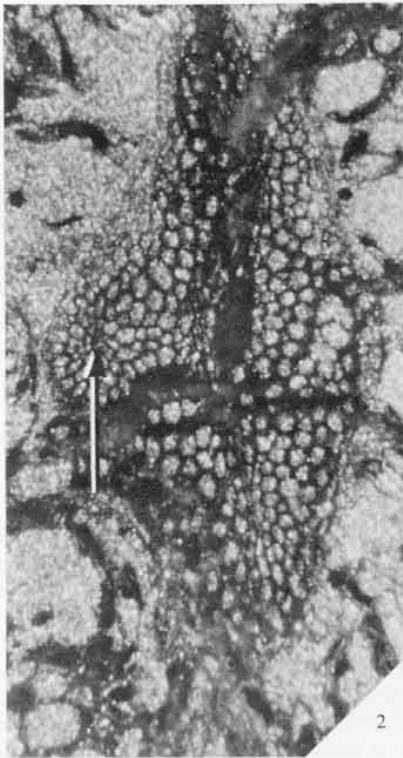
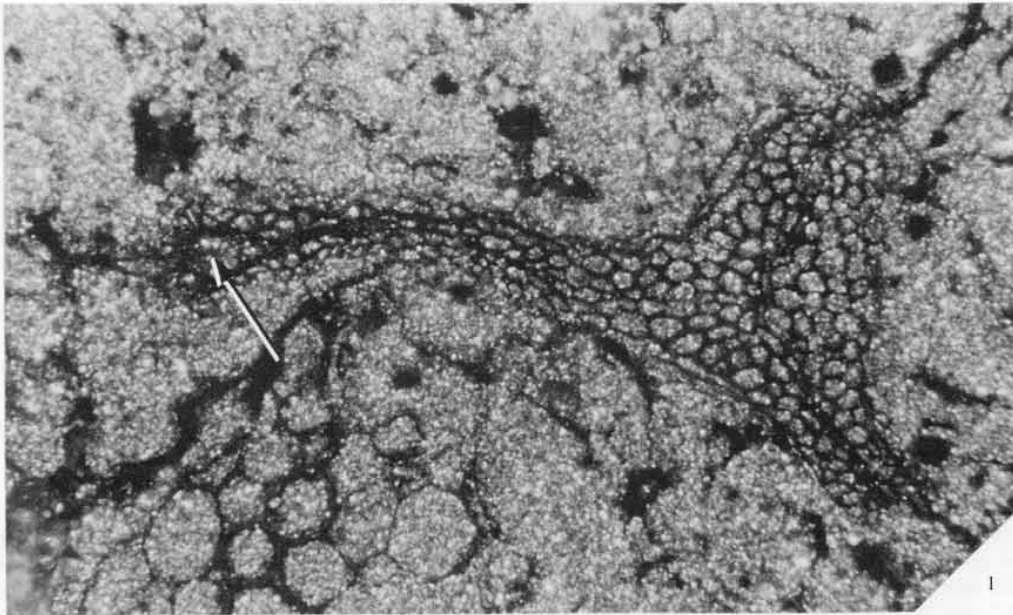
Proof of organic connection of the three axis orders can be seen in Pl. 60, figs. 1 and 4 and Pl. 61, fig. 1, where continuity of cortical tissues is evident. Traces to second-order axes were not observed to depart the primary xylem of the first-order axis. At the most proximal level of its occurrence in the specimen, the primary xylem of the preserved second-order axis is already enveloped by its own cortical tissue (Pl. 60, fig. 1). However, evidence of an additional trace to a second-order axis, incipient in the preserved region of the first-order axis, can be inferred from the marked tangential expansion of the tip of one of the primary xylem ribs (Pl. 60, fig. 1, arrow b). The presence of one trace at a great distance from the primary xylem of the central stele, an incipient trace at an adjacent primary xylem rib, and a third xylem rib with no associated trace suggests a helical but widely spaced $\frac{1}{3}$ 'organotaxy'.

Departure of traces from the primary xylem of the second-order axis also was not directly observed. At the most proximal level of their occurrence in the specimen, traces to the third order are found in the cortex of the second-order axis (Pl. 60, fig. 4). Distally, they occupy the central portions of independent axes (Pl. 60, fig. 5). The second-order axis produces laterally (i.e. tangentially with respect to the first-order axis) the first two traces in a sub-opposite pair. Through the course of departure, these traces divide once equally in a plane at right angles to the plane of their departure (i.e. tangentially with respect to the second-order axis). Distally, pairs of traces vascularize third-order axes which appear to be bifurcate at or near their bases (Pl. 61, fig. 1, arrow).

Successive transverse sections through more distal portions of the preserved second-order axis shows increased elongation of the abaxial primary xylem rib (Pl. 61, fig. 3). This feature is probably associated with the departure of an additional trace. It is unclear, however, whether the trace actually departs the primary xylem in the region of the preserved specimen. It may be reasonable to assume that trace departure here is associated with a division of the protoxylem strand near the tip of the elongated rib, but preservation is insufficient to determine if this really happens or not. The configuration of cortical tissues immediately adjacent to the elongated xylem rib suggests that distally this trace divides, but this also was not actually observed.

EXPLANATION OF PLATE 62

Figs. 1-3. *Reimannia aldenense* Arnold—type specimen from Erie County, New York. UMMP No. 16231. Second-order axis, transverse sections. 1, detail of primary xylem between the levels shown in Pl. 60, fig. 3 and Pl. 61, fig. 3. Arrow indicates a protoxylem strand with a poorly preserved centre (previously interpreted as a peripheral loop) probably associated with an incipient trace, $\times 80$. 2, detail of primary xylem near the base. Arrow indicates the same protoxylem strand marked with an arrow in fig. 1, $\times 80$. 3, detail of primary xylem near the level of Pl. 60, fig. 5, $\times 80$.



STEIN, *Reimannia*

Genus REIMANNIA Arnold, 1935

Amplified diagnosis. Plants, represented by permineralized axes with three orders of branching, containing primary tissues only. Vascular tissues protostelic. Primary xylem three-ribbed in first- and second-order axes, circular in transverse section in traces to the third order. Primary xylem maturation mesarch. Protoxylem strands simple, occurring near the tips or along the median planes of primary xylem ribs in the first- and second-order axes, occurring singly in the centre of the primary xylem of third-order traces. Order of trace departure in the first-order axis probably helical ($\frac{1}{3}$ 'organotaxy'). Primary xylem of second-order axis four-angled proximally, producing a sub-opposite pair of traces, becoming three-ribbed distally and probably producing a single abaxial trace. Traces to third-order axes dividing once equally in a tangential plane with respect to the parent second-order axis. Some cells surrounding the primary xylem with dark materials in their lumina. Cortex consisting of cells decreasing in size and increasing in cell wall thickness toward the periphery of axes; outermost cortex comprised of a semi-discrete tissue of hypodermal sclerenchyma. Epidermis consisting of isodiametric to radially flattened cells as seen in transverse section, containing dark materials in their lumina.

Reimannia aldenense Arnold

Amplified diagnosis. Plants as described in the generic diagnosis. First-order axis 9.5 mm in diameter at greatest extent containing primary xylem with 3 mm maximum diameter and rib width of 0.6 mm. Second-order axis 6.5 mm in diameter containing primary xylem approximately 1.3 by 0.7 mm proximally, attaining dimensions of 0.8 by 1.5 mm distally. Bases of third-order axes approximately 3 mm in diameter containing primary xylem strands 0.1 mm in diameter. Primary xylem of second-order axis often containing tangentially flattened tracheids, as observed in transverse section, along median planes of the primary xylem connecting four discrete protoxylem strands, one near the tip of each rib and one located at the centre of the xylem column. Protoxylem tracheids measuring 10 to 30 μm in diameter possibly disintegrating in incipient traces. Metaxylem tracheids outside median band from 30 to 95 μm in diameter. Cells of the inner cortex between 35 and 200 μm in diameter, isodiametric to twice or three times longer than wide. Cells of the outermost cortex elongate, usually between 30 and 80 μm in diameter. Epidermal cells ranging between 80 and 130 μm in diameter, probably isodiametric to slightly flattened, probably no more than twice longer than wide.

Holotype. Twenty-two slides and fourteen unmounted sections bearing number 16231 in the Museum of Paleontology of the University of Michigan, Ann Arbor, Michigan, U.S.A.

Locality. Spring Creek near Alden, Erie County, New York, U.S.A. Pyrite horizon in the Ledyard Shale Member, Ludlowville Formation, Hamilton Group (Givetian).

DISCUSSION

Concept of the genus

The genus *Reimannia* is monotypic, and at present, only the type specimen can be assigned without doubt to the type species, *Reimannia aldenense*. The reinvestigation of this specimen provides a much clearer concept of this taxon than has been held heretofore (for example, see Scheckler and Banks 1971b; Scheckler 1974; Beck 1960b). Significant new information includes: (1) three orders of branching in organic connection, (2) changes in configuration of the primary xylem in the second-order axis, and (3) positions of protoxylem strands in the primary xylem of first- and second-order axes. In light of the new information, the doubt expressed by Scheckler (1974) about the 'naturalness' of *Reimannia*, although not removed is at least somewhat lessened. Although clearly not one of the most completely understood of Middle Devonian plants, it is known to an extent comparable to many other stem fragment genera.

From time to time, other specimens have been assigned to *R. aldenense* based primarily upon general similarities with the three-ribbed primary xylem of the second-order axis, and the presence of an ill-defined 'peripheral loop' type of protoxylem strand (Matten 1973; Banks 1966; Wilcox 1967). To the extent I can tell from the published descriptions, none of these specimens share a sufficient number of characters with what is now known in *Reimannia* to be confidently assigned to the genus. In one case, an axis placed in *Reimannia* by Matten (1973, see his figs. 6 and 7, p. 622) is clearly not assignable to this genus. It is characterized by the presence of a pair of tangentially aligned protoxylem strands near the tip of one of the three primary xylem ribs, and is thus clearly different from the condition in the second-order axis of the type specimen. In the future, possible new specimens should be assigned to *R. aldenense* only on the basis of the new combination of characters reported here. I agree with the reasons for the establishment of *Reimanniopsis* (to include the former *Reimannia indianensis* Read and Campbell 1939) by Hoskins and Cross (1951) for the material from the New Albany Shale, and like several recent workers (Matten and Banks 1969; Beck 1960a), I see no compelling reason to consider *Reimannia* and *Reimanniopsis* closely related.

Systematic affinities

The combination of characters now available for *Reimannia* no longer supports a close relationship for this plant with *Iridopteris* or *Arachnoxylon* (Read 1938; Arnold 1940, 1947; Stein 1981). Instead, I suggest that *Reimannia* is clearly more similar to the permineralized axis fragment members of the Aneurophytales (Progymnospermopsida) (see Bonamo 1975, 1977; Beck 1976). Features which support this relationship include: (1) ribbed columns of primary xylem with mesarch order of maturation, (2) simple protoxylem strands located near the tip of each primary xylem rib or along the median planes of the ribs, (3) a helical order of trace departure, and (4) a general equivalence between the taxa in the organization of successive axis orders. In view of these similarities, lack of secondary tissues in *Reimannia* is not judged to be of systematic significance since variation in these tissues occurs at single levels in most plants during normal development. Additional aspects of the morphology of *Reimannia*, relevant to the proposed change in the systematic placement of this genus, merit brief consideration below.

Like other members of Arnold's Iridopteridinae, the attribution of a 'peripheral loop' to *Reimannia* was based upon very little direct evidence (for a discussion of this problem in more detail, see Stein 1981). In transverse section, I have been unable to find any evidence of a distinct parenchymatous tissue in the region of the 'loop'. Thus, Arnold's original description of this region (1935, p. 6) as 'an open area' (now filled with pyrite) is clearly a more objective representation of what is actually present (see Pl. 62, fig. 1, arrow). The unusual association of a supposed 'peripheral loop' in *Reimannia* with normal protoxylem strands at single levels in the plant, and the association of the peripheral loop with an incipient trace, has been appreciated by most authors who have considered the genus in any detail (Arnold 1935, 1940; Hoskins and Cross 1951; Leclercq 1970). Surprisingly, however, in most cases this has not lessened convictions about the applicability or the usefulness of the term as applied to this or other Devonian genera. Because there is no direct histological evidence for a specialized structure of the protoxylem in *Reimannia*, I suggest discontinuance of the term as applied to this taxon. I suggest, furthermore, that the 'open area' probably represents a developmental feature of the plant associated with trace departure, perhaps a protoxylem lacuna. These suggestions, although made independently of any taxonomic relationship for *Reimannia*, are nevertheless clearly in line with interpretations made by others of apparently identical structures observed in members of the Aneurophytales. For example, compare *Reimannia* with *Proteokalon* at an equivalent level (Scheckler and Banks 1971b, p. 876, fig. 8) in which a similar 'open area' is not interpreted as a peripheral loop.

A distinct band of tangentially flattened tracheids, usually one or two cells wide, as observed in transverse section, occurs at several levels in the primary xylem of the second-order axis of *Reimannia* (Pl. 62, fig. 1). This feature has been variously interpreted in *Rellimia* and *Triloboxylon*, where it also occurs, as a continuous or discontinuous median band of protoxylem (Matten and Banks 1966; Bonamo 1977) or a median band of metaxylem linking discrete protoxylem strands (Scheckler and

Banks 1971*b*). I prefer the latter interpretation not only because of the scalariform to reticulate wall sculpture of these cells reported by Scheckler and Banks, but also because in *Reimannia* (Pl. 60, fig. 3; Pl. 62, figs. 1–3) as well as in *Triloboxylon* (Scheckler and Banks 1971*b*, fig. 5) and *Rellimia* (Bonamo 1977, fig. 20), protoxylem strands appear to be clearly recognizable discrete entities. Scheckler and Banks note the intermittent occurrence of the median band of metaxylem in *Triloboxylon* but stress its possible usefulness as a taxonomic character. At present, however, I am unsure of the morphological significance or systematic importance of this feature.

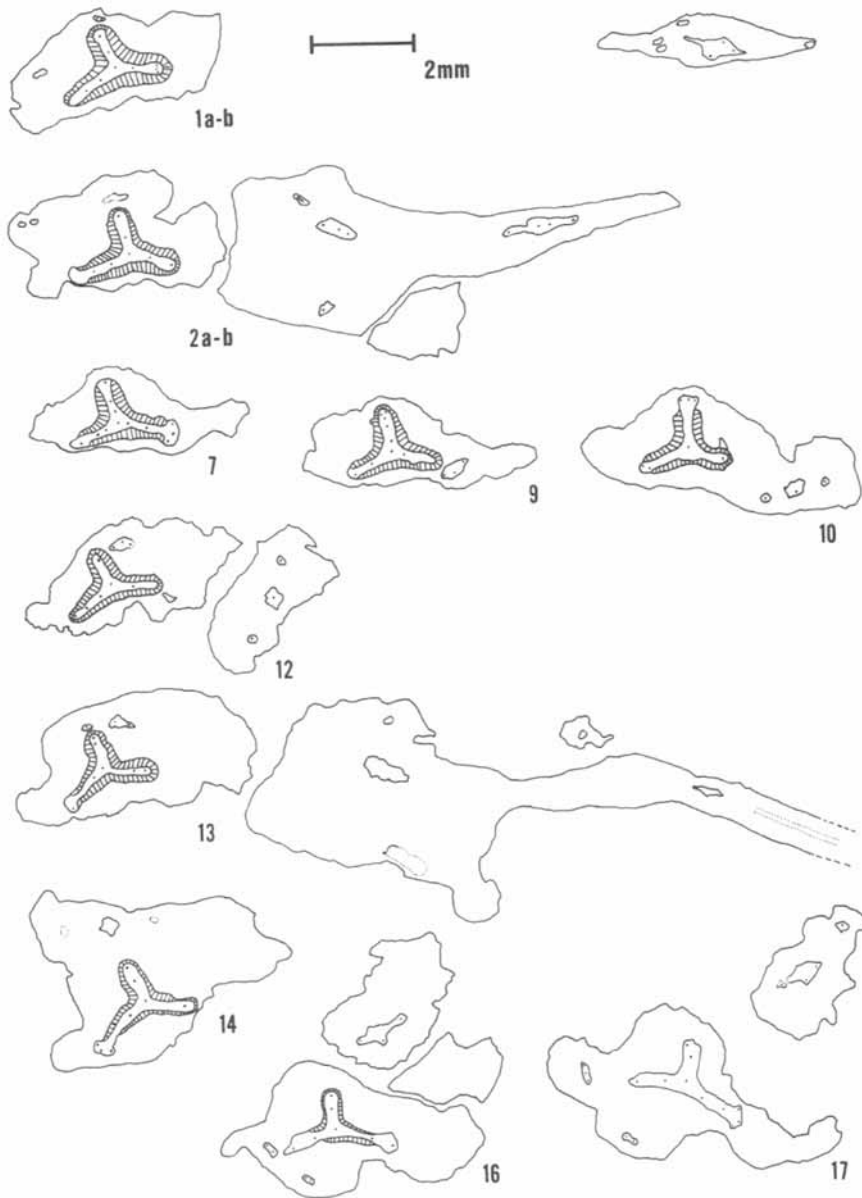
Related taxa

Reimannia aldenense resembles the published description of *Cairoa lamanekii* (Matten 1973, 1975) more than that of any other known aneurophytalan taxon. Similar features include: (1) a first-order axis ('penultimate axis' of Matten) containing a deeply three-ribbed aneurophytalan stele, (2) a trace to a second-order axis (the 'ultimate axis' of Matten) which is proximally broadly elliptical or diamond-shaped in transverse section containing protoxylem strands near the single abaxial and two lateral angles of the trace, (3) a sub-opposite pair of traces to third-order axes (the 'ultimate appendages' of Matten) at the base of the second-order axis, each elliptical in transverse section containing a single protoxylem strand, bifurcating at least once distally, and (4) similar histological features of phloem or inner cortex (including cells filled with dark materials), outer cortex, and epidermis. However, *Reimannia* differs from *Cairoa* by being larger at nearly all equivalent levels. It also lacks secondary xylem (a feature not necessarily viewed as significant), and lacks the alternating bands of parenchyma and sclerenchyma observed in *Cairoa*. Furthermore, the primary xylem of *Reimannia* becomes distinctly three-ribbed in distal portions of the second-order axis whereas in *Cairoa*, according to Matten's description, the primary xylem remains elliptical or becomes increasingly four-angled as seen in transverse section, thus *not* repeating the primary xylem configuration of the previous order. If Matten's interpretation is correct, then this feature alone could serve to distinguish the two genera. I have had the opportunity to study the type specimen of *C. lamanekii* (text-fig. 2). I am not convinced that the observed pattern of trace departure from the primary xylem of the first-order axis and the orientation of second-order axes, in organic connection with the first (text-fig. 2, sections 1*a*, *b* and 7 to 13), are necessarily explained by simple right angle bends in some second-order ('ultimate') axes as proposed by Matten (1975). Particularly disturbing is the fact that some of the laterals, those with the most clearly defined rhomboidal primary xylem (text-fig. 2, sections 1*a*, *b* and 2*a*, *b*), were observed to be reflexed (i.e. borne backwards at an angle from the first-order axis greater than 90°). Furthermore, the primary xylem of these laterals has not yet been proven to be the distal continuation of the primary xylem of the observed second-order traces. It is possible that the reflexed axes are in fact additional appendages, perhaps roots or root-like stems, attached to the base of at least some second-order axes.

Reimannia is similar in most major respects to the genus *Triloboxylon* (Matten and Banks 1966; Scheckler and Banks 1971*a*). The only differences between the two genera, at present, seem to be the four-angled configuration of primary xylem and the presence of a sub-opposite pair of traces in the basal second-order axis of *Reimannia* as opposed to a basal three-ribbed configuration in *Triloboxylon* with an apparent helical order of trace departure from the start. These differences may be insufficient to distinguish taxa, however, since considerable variation can be observed in aneurophytes under study in this laboratory.

A striking resemblance is noted between the second-order axis of *Reimannia* and the second-order 'branch' of the lower Upper Devonian genus *Proteokalon* (Scheckler and Banks 1971*b*) in the configuration of the primary xylem, the location of protoxylem strands, and in the overall size relationships of vascular tissue to cortex. The primary xylem of the first-order axis in *Proteokalon* is four-ribbed, however, and contains conspicuous metaxylem parenchyma whereas in *Reimannia*, to the extent known, metaxylem is composed of tracheids only and the vascular system is three-ribbed.

In 1973 Matten suggested that within the Aneurophytales, *Proteokalon* and *Cairoa* should be placed in a separate family since successive orders in these plants show changes in the number of primary xylem ribs. This system may not be workable, however, because variability in the



TEXT-FIG. 2. Type specimen of *Cairoa lamanekii* Matten from Greene County, New York. *Camera lucida* diagrams showing some aspects of trace departure in this specimen. Section numbers are indicated beside each drawing. The most proximal level of the specimen presented here is section 1a, b, and the most distal is section 17.

configuration of the primary xylem within single axis orders of aneurophytes is becoming evident. For example, a change in the primary xylem column from four-angled to three-ribbed has been noted in the second-order axis of *Reimannia*, and in one second-order axis of *Proteokalon*, the primary xylem has been observed to change from three-ribbed proximally to distinctly four-ribbed distally (Scheckler and Banks 1971*b*; Scheckler, pers. comm. 1978).

CONCEPT OF THE PROGYMNOSPERMOPSIDA

As presently conceived, the class Progymnospermopsida is comprised of three orders and between fifteen and twenty genera depending upon the acceptability of some assignments (Barnard and Long 1975; Bonamo 1975; Beck 1976). From the start (Beck 1960*b*), members of this group have been considered phylogenetic intermediates between the primitive vascular plants of the Lower Devonian, now placed within the Rhyniophytina and Trimerophytina of Banks (1968), and early seed plants, the oldest of which occur in sediments of late Upper Devonian age. More specifically, the Progymnospermopsida have been considered to comprise the basal portions of a single clade of vascular plants, the members sharing some, but not all, of the derived features of seed plants. To accommodate this idea, evidence for membership in the Progymnospermopsida has often been spelled out in a combination of primitive (free-sporing habit), and derived ('typically gymnospermous' secondary vascular tissues) characters (Beck 1960*b*, 1976; Bonamo 1975). In my opinion, it is permissible to define a group in this manner so long as one accepts the initial postulate that one or several members of this group were actually the *direct ancestors* of the later forms. To be sure, a postulate of direct ancestry is only one of several possible phylogenetic trees included in a 'sister group' hypothesis proposed by strict adherence to cladistic methodology (see Hennig 1979; Eldredge 1979; Eldredge and Cracraft 1980) and, as opposed to the later, not arrived at solely by analysis of characters. However, it is clearly falsifiable.* Furthermore, when repeated testing fails to falsify either postulate, the fact that direct ancestry is only one hypothesis about what actually happened, as opposed to several, is more impressive to me.

In the case of the Progymnospermopsida, I am inclined to accept as a working hypothesis the position of the group as direct ancestors of seed plants even though the present understanding of characters is insufficiently detailed to enable one to recognize natural species, or to determine which of the known taxa actually gave rise to descendent groups, or even to know how many descendent groups actually evolved from this plexus of forms. This acceptance is based primarily upon stratigraphic evidence that recognizable members of the Progymnospermopsida significantly predate the earliest occurrences of seeds, and upon the confidence that the combination of potentially independent characters comprising 'typically gymnospermous' secondary vascular tissues (as opposed to other possible or actual types of secondary tissues) was unique in occurrence in the history of vascular land plants. However, in accepting the definition of the Progymnospermopsida given above, it is important to realize that the two kinds of characters used to circumscribe the group, primitive and derived, contain distinctly different information about phylogenetic history. Thus, when considering possible phylogenetic patterns within the Progymnospermopsida, or even membership in the group, the two types of characters should not be treated as equivalent information.

In 1975 Bonamo suggested that taxa within the Progymnospermopsida should be segregated into categories in order to minimize confusion of those which represent isolated permineralized axis fragments or fragmentary compressions, with others representing 'whole' organisms more or less completely understood. I feel this approach is helpful since it emphasizes the degree to which taxa are known, and underscores the importance of evaluating the extent of morphological comparability between named entities. However, one must recognize that although some taxa are incompletely known at present, the discovery in the future of additional information about these forms may

* One can disprove the hypothesis that one taxon is ancestral to another by discovering clear advancements in the proposed ancestor which are not shared by the proposed descendent (i.e. 'autapomorphous characters' in the terminology of Hennig 1979).

necessitate significant changes in our view about their systematic importance. Thus, I would not agree with Bonamo (1977) if she concluded that the concept of a taxon-like *Triloboxylon ashlandicum*, formerly known from details of internal anatomy and, to a limited extent, branching patterns, should not be extended to encompass structures found in organic connection, such as the sporangial complexes proposed by Scheckler (1975). This would be a fundamental contradiction of the general application of botanical scientific nomenclature (see Schopf 1978). If, on the other hand, Bonamo meant to say that proof of organic connection in a single case should not be considered as proof of a similar connection in all other cases within the genus *Triloboxylon*, then I would certainly agree.

In the categorization of taxa within the Progymnospermopsida, Bonamo (1975) suggested that only those taxa showing positive evidence of a free-sporing habit combined with 'typically gymnospermous' secondary vascular tissues, the combination of characters originally cited in the establishment of the group, can be considered bona fide members. She used the categories ('incertae sedis (anatomy)' and 'incertae sedis (morphology)' for less complete, but presumably related, forms known primarily on the basis of internal anatomy alone or external morphology alone respectively. This approach represents an attempt to be as rigorous as possible in the definition of the Progymnospermopsida in order to exclude disparate elements which, on the basis of incomplete evidence, might otherwise be assigned to the group. However, a weakness in this scheme, in my opinion, lies in the fact that primary consideration for membership in the Progymnospermopsida then rests on only two of many potentially useful characters. Much recent work (Bonamo and Banks 1967; Leclercq and Bonamo 1971; Bonamo 1977; Beck 1971, 1979; Serlin and Banks 1978; Scheckler and Banks 1971a, b; Scheckler 1975, to name a few examples) has shown that other features of progymnosperms, such as the architecture of the primary vascular system or the morphology of sporangial complexes, may be equally useful in determining membership in this group. In this report, for example, I have presented what I consider to be good evidence for placement of *Reimannia aldenense* within the Aneurophytales of the Progymnospermopsida even though the type specimen lacks evidence of either original defining character.

Another problem is that, as noted above, the two original diagnostic characters, one primitive and the other derived at this level of analysis, do not contain equivalent phylogenetic information. Therefore, in terms of systematic significance, the failure of certain taxa positively to demonstrate one of the characters should not be interpreted in the same way as the failure of other taxa to demonstrate the presence of the other. Clearly, the derived characters are more important. For example, if one accepts that 'typically gymnospermous' secondary tissues arose only once, then the presence of this derived character in incompletely understood forms such as *Triloboxylon*, *Proteokalon*, and *Cairoa* is sufficient to ally them with the Progymnospermopsida. Furthermore, if one considers the stratigraphic occurrences of these forms, it becomes relatively certain that they do in fact represent members of the Progymnospermopsida even though the specimens fail to demonstrate a free-sporing habit. On the other hand, the primitive character contains far less information. Under no circumstance would one feel justified in placing a taxon within the Progymnospermopsida in the absence of any knowledge of internal structure simply on evidence of 'pteridophytic reproduction'.

For these reasons, I suggest the use of more descriptive categories within the Progymnospermopsida not tied to the demonstratable presence of specific primitive or derived characters, but emphasizing instead only the nature of the evidence collected for each taxon. Requirements for membership in the group, in my opinion, should be treated as an entirely separate issue. For each taxon, this decision should be based on all available evidence and, of course, is subject to close scrutiny and debate. Table 1 presents my view of the Aneurophytales of the Progymnospermopsida, the group to which *R. aldenense* is now assigned. In this list, primary emphasis is placed on the type of information required to recognize taxa from the fossil record.

Perhaps the best-known aneurophytalian taxon, from the standpoint of understanding the whole plant, is *Tetraxylopteris schmidtii* (Beck 1957; Scheckler and Banks 1971a; Bonamo and Banks 1967). Not only are fertile structures known in considerable detail, but they are understood in the context of several orders of decussate branching which in turn is correlated with information on primary

TABLE 1. A list of probable members of the Aneurophytales (Progymnospermopsida) according to the nature of the evidence for each

Genera recognized primarily from internal structure	Genera recognized from either internal anatomy or external morphology	Genera recognized primarily from external morphology
<i>Stauroxylon</i> *	<i>Tetraxylopteris</i> *†	<i>Rellimia</i> *†
<i>Triloboxylon ashlandicum</i> *†		<i>Aneurophyton</i> *†
<i>arnoldii</i> *		(<i>Eospermatopteris</i>)
<i>Proteokalon</i> *		
<i>Cairoa</i> *		
<i>Reimannia</i>		

* Secondary tissues reported.

† Fertile regions reported.

vascular architecture. Although placed in the centre category in Table 1, this does not mean that the plant is completely understood. Serious unresolved questions remain concerning the proposed helical versus decussate organization of the main axis of the plant (Beck 1957; Banks 1970; Bonamo, pers. comm. 1979), as well as the relationship of aerial axes to rooting structures, and the overall stature of the plant. However, the plant may be reliably identified either from internal anatomy or from external morphology.

Rellimia (Kräusel and Weyland 1933; Leclercq and Bonamo 1971, 1973; Bonamo 1977) and *Aneurophyton* (Kräusel and Weyland 1923, 1926, 1929; Leclercq 1940; Serlin and Banks 1978) are genera whose sporangium-bearing complexes are known in detail along with information on branching patterns. In addition, a certain amount of data exists on the anatomy of these genera and suggestions have been made (Scheckler and Banks 1971*a, b*; Bonamo 1977; Serlin and Banks 1978) on how to separate the taxa on this basis (e.g. amount of primary xylem ribbing, location, and number of protoxylem strands). However, the vascular architecture of either plant, particularly trace departure and changes in vascular organization from one axis order to the next, remains at present very incompletely understood. Thus, I maintain that information on the anatomy of these genera is insufficient to enable one to distinguish them from each other or from several other forms known only from permineralizations. It is characteristics of external morphology alone which make the taxa recognizable.

Eospermatopteris (Goldring 1924), large sandstone casts found with compression material thought to resemble *Aneurophyton*, presents a very weak case for its inclusion in the Progymnospermopsida. We are now aware of several kinds of Middle Devonian plants, besides presumed ancestors of seed plants, which attained arborescent stature.

In contrast to above, *Triloboxylon ashlandicum* (Matten and Banks 1966; Scheckler and Banks 1971*a, b*; Scheckler 1975, 1976), *Triloboxylon arnoldii* (Arnold 1940; Scheckler and Banks 1971*a, b*; Matten 1974), *Cairoa lamanekii* (Matten 1973), *Proteokalon petryi* (Scheckler and Banks 1971*b*), *Stauroxylon beckii* (Galtier 1970), and *Reimannia aldenense* are known mostly from fragmentary permineralized specimens showing only evidence of internal anatomy. These should be considered to be axis fragment form genera, not equivalent, and only partially comparable to *Tetraxylopteris*, *Rellimia*, and *Aneurophyton*. When compared among themselves, and with equivalent information from the other forms, there is evidence of considerable variability in the organization of primary vascular tissues which is in turn suggestive of a considerable diversity within this group. However, the magnitude of variation within single taxa has not yet been established and it is therefore difficult to decide on the importance of what has been observed to date.

Thus, with respect to the Aneurophytales as a whole, two lines of evidence have been accumulating which for the most part have offered little in the way of directly comparable evidence. From comparisons, we know something about their overall morphology and are beginning to understand some of the characters which might serve to further delimit the group in a more or less biological way. From the study of internal structure, we are accumulating evidence of diversity but, as yet, the meaning of this kind of evidence is less evident.

Acknowledgements. I wish to express my gratitude to Dr. Charles Beck for encouragement, advice, and support during all phases of this study. Thanks are extended to Dr. Lawrence Matten for the loan of the type specimen of *Cairoa*, to Dr. James Doyle for allowing work on the type specimen of *Reimannia*, and to Dr. Carlton Brett for valuable information on the geology of New York. Thanks are also due to Dr. Stephen Scheckler, Dr. Patricia Bonamo, Dr. Daniel Fisher, Dr. Garland Upchurch, and Mr. David Wight for helpful discussions on various aspects of this work, and to Dr. Robert Lowry and Ms. Constance Stein for valuable technical advice. This work was supported by NSF grant No. DEB-78-11165 to C. B. Beck, and portions of this report were submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Horace H. Rackham School of Graduate Studies at the University of Michigan, Ann Arbor.

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Original typescript received 9 February 1981

Revised typescript received 14 July 1981