CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

THE UNIVERSITY OF MICHIGAN

VOL. 26, NO. 12, p. 257-288 December 31, 1983

TRILOBOXYLON ARNOLDII FROM THE MIDDLE DEVONIAN OF WESTERN NEW YORK

BY

WILLIAM E. STEIN JR. and CHARLES B. BECK
Museum of Paleontology
and
Division of Biological Sciences
University of Michigan
Ann Arbor, MI 48109

MUSEUM OF PALEONTOLOGY
THE UNIVERSITY OF MICHIGAN
ANN ARBOR

CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

Philip D. Gingerich, Director

Gerald R. Smith, Editor

This series of contributions from the Museum of Paleontology is a medium for the publication of papers based chiefly upon the collection in the Museum. When the number of pages issued is sufficient to make a volume, a title page and a table of contents will be sent to libraries on the mailing list, and to individuals upon request. A list of the separate papers may also be obtained. Correspondence should be directed to the Museum of Paleontology, The University of Michigan, Ann Arbor, Michigan, 48109.

VOLS. II-XXVI. Parts of volumes may be obtained if available. Price lists available upon inquiry.

TRILOBOXYLON ARNOLDII FROM THE MIDDLE DEVONIAN OF WESTERN NEW YORK

By

William E. Stein Jr. and Charles B. Beck

Abstract—Specimens of *Triloboxylon arnoldii* (*Aneurophyton hallii*) originally described by Arnold have been reinvestigated, and a lectotype selected. Our study confirms the view that this taxon belongs to the Aneurophytales of the Progymnospermopsida, and we suggest that it is most closely related to either *Triloboxylon ashlandicum* or *Aneurophyton germanicum*. However, a combination of features separate *T. arnoldii* from other members of the Aneurophytales including: (1) a three-ribbed primary xylem system with protoxylem strands near the tips and along midplanes of the ribs, (2) small transversely elliptical traces produced in pairs from successive primary xylem ribs, (3) extensive secondary tissues, (4) a heterogeneous inner cortex containing solitary fibers and clusters of sclereids, (5) an outer cortex, with peripheral bundles consisting of fibers and sclereids separated by thin-walled parenchyma cells in ordered arrays, and (6) a simple but extensively developed periderm. Features 3-6 are probably related to the large size of *T. arnoldii* specimens. In an attempt to evaluate these features in relation to the systematics of members of the Aneurophytales with three-ribbed steles, two models of secondary growth in *T. arnoldii* are suggested. In each model, a specific proposal is made, based on known examples in the fossil record, for what the original primary body of *T. arnoldii* might have been like. The essential differences between the models revolve around: (1) initial size of the primary body, largely a function of the volume of the inner primary cortex, and (2) whether the fiber-sclereid bundles of the outer cortex result from primary or secondary growth. Although we cannot firmly reject either model, some evidence suggests that *T. arnoldii*, in an earlier stage of development, might have been similar to *T. ashlandicum*. If this model of development is correct, then it would seem likely that at least some specimens in *T. ashlandicum* were indeterminate in their potential for growth.

INTRODUCTION

The first useful descriptions of structurally preserved Middle Devonian plants from New York were those of Arnold (1935, 1940) and Read (1938) based on material from marine sediments in the western part of the state. Among the forms described by Arnold (1935), from the Leicester (Tully) Pyrite horizon (upper Givetian) in Erie County, were fragments of gymnospermous secondary xylem. Arnold compared this material to *Dadoxylon hallii* Dawson (1862, 1871), although conceding that the latter might be applied to any paleozoic wood showing multiseriate pitting and tall narrow rays. He suggested, however, that his material could be distinguished

from other kinds of paleozoic woods by: (a) the presence of transversely elongate pit-pairs on both tangential and radial walls of the tracheids, and (b) the "extent of seriation" of the pits (Arnold 1935, p. 3). Subsequently, Arnold (1940) described what he believed to be additional evidence of this plant in Erie County from sediments ranging from the Marcellus shale (upper Eifelian—lower Givetian) to the Leicester Pyrite horizon. Two specimens from the Ledyard Shale Member of the Ludlowville Formation (middle Givetian) were figured (1940, figs. 2, 3). Each provided evidence of a three-ribbed primary xylem system interpreted by Arnold to be closely similar to *Aneurophyton germanicum* (Kräusel and Weyland 1923, 1926, 1929). To accomodate this view, the combination *Aneurophyton hallii* (Dawson) Arnold was proposed.

The term Aneurophytales was first introduced by Kräusel and Weyland (1941, p. 68) for a group of primitive Devonian plants consisting of *Aneurophyton* plus the genus *Rhacophyton* (Crepin 1875; see also Leclercq 1951; Andrews and Phillips 1968), known in both Europe and North America. Although not explicitly defined, the concept of this group seems to have revolved around evidence of leaflessness (in contrast to the leafy condition, e.g., in *Archaeopteris*) and the assessment that the anatomy of the included genera was also similar.

In 1957, Beck established the genus *Tetraxylopteris*, based on material from the Upper Devonian (lower Frasnian) of west central New York, and provided the first detailed information on both secondary xylem and secondary phloem in a Devonian plant of this type. Although *Tetraxylopteris* could be distinguished by its four-ribbed primary xylem and decussate arrangement of lateral appendages, Beck recognized the striking similarity between *Tetraxylopteris* and *Aneurophyton* in both internal anatomy and external morphology. He proposed using the term Aneurophytales to encompass these genera and provided a diagnosis for the group in this sense (Beck 1957, pp. 364-365). Following establishment of the Progymnospermopsida (Beck 1960), the Aneurophytales, sensu Beck, has come to be regarded as the earliest and most primitive order of this group (Beck 1960, 1976; Bonamo 1975).

In 1966, Matten and Banks established the genus *Triloboxylon* for Upper Devonian (lower Frasnian) material from Green County, New York, and assigned it to the Aneurophytales. This plant, the second genus in the order with a three-ribbed primary xylem system, was considered to differ from *Aneurophyton* by: (a) a continuous band of protoxylem along midplanes of xylem ribs rather than discrete strands, (b) a homogeneous, parenchymatous cortex in contrast to the heterogeneous cortex of *A. hallii* containing "sclerotic bodies", (c) vascular tissue in ultimate appendages as opposed to its apparent absence in *A. germanicum*, and (d) the absence of secondary xylem in small branch orders in contrast to its abundant development in all known orders of both species of *Aneurophyton*.

In the most comprehensive survey of the anatomy of members of the Aneurophytales undertaken to date, Scheckler and Banks (1971a) presented additional information on both *Triloboxylon* and *A. hallii*. Evidence about the latter was derived not only from Arnold's figured material, but also from a new specimen, loaned to them by Prof. Arnold, from the Leicester Pyrite horizon in Erie County. As a result of their detailed anatomical comparisons, they concluded that these two taxa share several features not observed in Krausel and Weyland's *Aneurophyton* including: (a) more highly ribbed primary xylem systems containing more protoxylem strands at equivalent levels in an axis, and (b) flattened tracheids along midplanes of the xylem ribs (although re-interpreted by them as representing metaxylem elements connecting discrete protoxylem strands). They concluded, as a result, that *Triloboxylon* and *A. hallii* represent a single genus. They believed, however, that the presence of sclerenchyma in the inner cortex, and the apparent absence of primary xylem parenchyma in Arnold's material, was a sufficient basis for specific distinction. Treating Arnold's (1940) material, instead of Dawson's (1862), as the type, they made the incorrect combination *Triloboxylon hallii* (Arnold) Scheckler

and Banks. This nomenclatural problem was subsequently rectified by Matten (1974) in his proposal of a new name, *Triloboxylon arnoldii*, for Arnold's (1940) material.

Since Scheckler and Banks' (1971a) contribution, descriptions of new taxa, and revisions of previously existing ones, have greatly expanded our concept of several members of the Aneurophytales (Scheckler and Banks 1971b; Leclercq and Bonamo 1971; Matten 1973, 1974, 1975; Bonamo 1977; Serlin and Banks 1978; Schweitzer and Matten 1982; Stein 1982). However, to some extent they have also tended to blur what orginally may have been clear cut distinctions between individual taxa. This problem seems particularly acute among the forms with three-ribbed steles, probably the oldest and most primitive members of the group. One reaction to this state of affairs, exemplified by Mustafa (1975), has been to unite all three-ribbed forms into a single taxon (Mustafa used *Protopteridium*, but see Bonamo 1977; Serlin and Banks 1978; Matten and Schweitzer 1982 on synonomies and the use of this name). We think that such an approach is too extreme because it greatly undervalues observed differences in both external and internal features. However, it underscores the necessity of re-considering what, in fact, defining characters of already established taxa should be. Many of us have assumed that differences in specialized fertile axes (Bonamo and Banks 1967; Bonamo 1975; 1977; Leclercq and Bonomo 1971; Scheckler 1975), may provide the key to understanding this group. There is no defensible reason, however, why characters from one organ system in these forms, or one aspect of the life cycle, should be accorded *a priori* more significance than any others. A determined search should be undertaken, therefore, for other potentially useful characters.

The primary vascular architecture of the group seems particularly promising in this connection because there appears to be greater variability in this feature than in most others. Much remains to be done, however, before this variability can be integrated fully into a systematic treatment that is biologically meaningful. It is now clear that taxonomic distinctions based on one or a small number of transverse sections are largely inadequate because anatomical variations in the axis over some distance, characteristic of all biological species, are not taken into account. Several studies have attempted to deal with this problem to the extent possible, but more work is needed. In the meantime, it is critically important to indicate clearly which specimens have described features, and not to over-generalize in the circumscription of taxa.

With these ideas in mind, we have assembled, and are in the process of studying, a large suite of specimens which Arnold almost certainly would have placed in the taxon we now term *Triloboxylon arnoldii.* All are characterized by unusually large size and extensive secondary xylem. Significantly, however, they show variations in nearly every other feature including some previously considered diagnostic of the taxon. This paper presents a re-investigation of Arnold's (1940) material. Our objective has been to document as many aspects of structure and development in the type material as possible since, in this case, there can be no doubt that observed features belong with the name. The results, we believe, significantly increase our understanding of *T. arnoldii.* In a subsequent report, we shall present descriptions of our new material, and attempt to treat observed variability in light of existing taxonomy.

MATERIALS AND METHODS

When obtained for study, the two specimens figured by Arnold (1940, Figs. 2, 3), were mounted together in a plastic block and listed under catalog number 23848 in the collections of the Museum of Paleontology, University of Michigan. Each specimen consists of a single axis fragment permineralized with iron disulfide (pyrite). There is no evidence of organic connection. From this material, Arnold prepared three transverse surfaces. We have separated the specimens

and have assigned a new catalog number to one of them (see Diagnosis). Arnold's figured surfaces have been conserved, and we have prepared an additional 37 transverse and 42 longitudinal sections. Most of our sections were cut at 1 mm intervals. Detailed information on all of our preparations, including relative positions and spacing of all cuts, is deposited with the specimens. Pyrite surfaces were prepared following the procedure described in Stein, Wight and Beck (1982). Some surfaces were fine-polished with 0.05 mm aluminum oxide and then mounted on slides with no further treatment. Most, however, were subjected to etches with concentrated nitric acid (for periods ranging from 10 to 30 seconds) before being mounted. For scanning electron microscopy (SEM), axes were split along different planes, etched for several minutes with concentrated hydrochloric acid (to remove calcite), rinsed, dehydrated, and then sputter-coated with gold using standard techniques.

Figures 18 and 19 are derived from computer images of a series of *camera lucida* diagrams similar to those in Figure 17. The plotting program is part of a package of related fortran programs written by F. L. Bookstein (Center for Human Growth and Development, University of Michigan). Some aspects of this program have been modified by J. Kilgore (Department of Anatomy and Cell Biology of the Medical School, University of Michigan).

DESCRIPTION

The main axis of each specimen (Figs. 1, 20) contains a three-ribbed primary xylem column surrounded by extensive secondary xylem and secondary phloem. To the outside, there is a heterogeneous cortex consisting of thin-walled parenchyma, fibers, and clusters of sclereids. In one specimen (Figs. 1, 2, 5, 6), peripheral regions of the cortex contain fibers, short cells containing dark contents, and thin-walled parenchyma cells in regular arrays. This specimen also provides evidence of a tissue previously interpreted as epidermis (Fig. 9), and a relatively unspecialized periderm (Fig. 2). Both specimens display a single type of vascular trace (Figs. 17, 24), and in one, traces are observed to vascularize bases of lateral appendages (Figs. 16-19).

Cortical Region

All tissues peripheral to the secondary phloem (as indicated by cells in radial files), including regions showing evidence of secondary cell proliferation, are considered here to be part of the cortex. The boundary between these tissues, however, is often indistinct. In the more completely preserved specimen (Fig. 1), cortex varies from 1.7 to 3.3 mm in thickness. Near the vascular tissue in both axes, most cells are thin-walled, varying from 23 to 78 μm in transverse diameter, and are usually isodiametric to no more than twice their transverse diameter in length (Figs. 2, 22, 35). Scattered among these cells, singly or in small clusters, are morphologically similar cells with dark lumina. In addition, the inner cortex contains spherical or longitudinally elongate clusters of cells that we interpret to be sclereids (Figs. 22, arrow). The latter, however, are incompletely permineralized, and the presence of pyrite in the peripheral parts of cell lumina only, may give the appearance of thicker cell walls than originally may have been present. Most of these cells now contain dark materials and/or calcite in their lumina. They measure from 45 to 115 μm in transverse diameter, and range from isodiametric to about half as tall longitudinally as they are wide. Occasional solitary fibers are also observed in the inner cortex often associated with sclereids (Fig. 3).

The most conspicuous feature of the outer cortex (observed in one specimen only; Figs. 1, 2, 5, 6), is a system of fiber bundles at the periphery of the axis consisting of a few to over a dozen cells

each. Individual bundles have been followed through a series of adjacent transverse sections for as much as 1.5 cm, suggesting little anastomosis longitudinally. Associated with the fibers in most bundles are short cells similar in appearance and preservation to sclereids as described above. In most cases these sclereids appear to partially or completely envelop the fibers of each bundle (Fig. 5, arrows *s*). In transverse section, fibers and adjacent sclereids are often difficult to distinguish. In the best preserved instances (Fig. 5, arrows *f*), fibers appear generally rounder and may be more completely permineralized with pyrite. In longitudinal section (Fig. 6, arrows *f* and *s*), the distinction is clear. The fibers measure between 50 and 115 μm in transverse diameter, with cell walls up to 40 μm thick, and they appear to be quite long although exact measurements could not be made. The sclereids are isodiametric and vary from 45 to 65 μm in diameter. Between the bundles of fibers and associated sclereids, in most instances, is a conspicuous highly ordered parenchyma (Figs. 2, 5, 6, 9). Individual cells are thin-walled, rounded to cuboidal in shape, and most belong to fairly regular radial, tangential and, to a lesser extent, longitudinal files. These cells vary from 20 to 80 μm radially, 30 to 60 μm tangentially, and average about 45 μm in length. In some instances, sclereids associated with the fibers belong to the same regular radial and tangential rows as cells of the intervening parenchyma (Figs. 5, 6).

A tissue, previously interpreted as epidermis (Scheckler and Banks 1971a), is observed at the outer surface of one specimen (Figs. 1, 9). It is comprised of radially flattened cells with dark contents, and varies from one to three cell layers thick. Stomata, or other definitive features of epidermis, however, have not been identified. Individual cells are approximately 40 μm radially, 95 μm tangentially, and 90 μm in length.

Whereas the tissues of the outer cortex, described above, probably comprised the entire outermost region of the axis at one time, they are no longer physically continuous around the periphery of the specimen. Instead, the outer cortex is divided into at least six plates by longitudinal fissures bounded by cells of an apparently unspecialized periderm (Figs. 1, 2). We interpret this condition to be a normal feature of development in this plant. Physical disruption of the cortex by the fissures seems in most, but not all, cases to have occurred between bundles of fibers.

Periderm, unequally developed but quite extensive in some regions (e.g., Fig. 2), is comprised of thin-walled cells arranged in definite radial and longitudinal files. The cells are variable in size, ranging between 30 and 80 μm tangentially, 10 and 35 μm radially, and 25 and 60 μm in length. Variation in the radial dimension of cells throughout the periderm suggests that cell division in this tissue was probably not restricted to a distinct phellogen. Also, the innermost cells of the periderm are not greatly different from more peripheral cells of the same tissue. Thus, there appears to be no basis for recognizing distinct phellem or phelloderm layers. In addition to bounding the fissures, periderm occurs also in many places beneath fiber-sclereid bundles of the outer cortex, and appears to intergrade with the highly ordered parenchyma in this region (Fig. 2).

The cortex in the bases of attached lateral appendages (observed in one specimen; Figs. 1, 16, 33, 34) appears to be more homogeneous than the equivalent region of the main axis (compare with Figs. 2, 35). The cells are generally larger, ranging from 60 to 160 μm in transverse diameter, and some are elongate near the periphery (Fig. 33). Cells have relatively thickened cell walls, and the tissue as a whole shows no evidence of secondary modification.

Vascular Tissues

The primary xylem in both specimens is mesarch and three-ribbed (Figs. 1, 10, 20). Although preservation is incomplete, there is no evidence of xylem parenchyma. Primary xylem ribs are about 0.2 mm wide in one specimen (Fig. 1), 0.3 mm in the other (Fig. 20), and vary between 1.0

and 1.9 mm in radial extent. Discrete protoxylem strands occur near the tips of xylem ribs (associated with incipient traces), along midplanes of the xylem ribs, and near the center of the system (Figs. 1; 10, arrows; 13). Due to poor preservation, however, it has been impossible to determine their number and exact arrangement. Protoxylem or early metaxylem elements measure from 10 to about 30 μm in transverse diameter. Metaxylem tracheids vary from about 30 to 65 μm in transverse diameter. Large metaxylem tracheids have bordered pit-pairs of nearly equal size on all walls.

Secondary xylem is extensively developed with up to about 60 tracheids in a radial file (3.0 mm) in one specimen (Fig. 1), and 90 tracheids (4.0 mm) in the other (Fig. 20). There is no evidence of growth layers. The tissue consists of tracheids and narrow rays (Figs. 4, 10, 23). Tracheids usually appear rectangular in transverse section, vary between 30 and 78 μm in diameter, and most exceed 1.6 mm in length (the height of our tallest longitudinal sections). In tangential section, many tracheids show evidence of intrusive growth at their tips and some branch. Vascular rays are apparently homocellular, lacking evidence of ray tracheids (fig. 4). They are usually one, but occasionally two cells wide, and most are very tall. Some, however, are considerably shorter, consisting of six or fewer cell rows each. Individual ray cells vary from 15 to 30 μm tangentially, and from 30 to 50 um longitudinally. Because of poor preservation, radial dimension of ray cells could not be determined.

Secondary xylem tracheids are characterized by multiseriate circular bordered pit-pairs, with oblique elliptical apertures, on both tangential and radial walls (Figs. 4, 8, 11, 12). The tracheids have pit-pairs in continuous and closely packed arrays on entire wall faces. In only one instance have we observed what *might* be interpreted as grouped pitting (Fig. 8). However, there is evidence of pits between the groups (Fig 8, arrows) similar to those bordering vascular rays in other parts of the same tissue. Since the tracheids are also sinuous in this region, we interpret this as evidence of a short vascular ray.

Primary phloem has not been recognized in the main axis of either specimen, having probably been crushed by the development of extensive secondary tissues. Secondary phloem, indicated by the presence of radially aligned cells outside the secondary xylem, ranges from 0.4 to 0.8 mm thick. The best perserved cells are phloem fibers, and associated sclereids similar in size and structure to those in the cortex, arranged together in radial files (Figs. 1, 7, 15). Phloem fibers measure approximately 35 μm in diameter, and are very long. Other kinds of cells in the secondary phloem region include longitudinal columns of short, thin-walled parenchyma cells with transverse end walls, and scattered, nearly spherical bodies interpreted as isolated cells with dark contents. The parenchyma cells measure from 30 to 40 μm in diameter, and are approximately 80 μm in length. The spherical bodies measure approximately 30 μm in diameter.

Traces

Incipient traces are recognized by an increased prominence of a primary xylem rib associated with a tangentially aligned pair of protoxylem strands near the tip. Due to poor preservation, it is unclear how the protoxylem strands relate to each other or to other protoxylem strands within the primary xylem system. Near the level of trace departure, primary xylem ribs have a two pronged appearance in transverse section (Figs. 17, level 6C; 19; 21, arrows; 24, level 10A). At a slightly higher level the traces are observed to depart in subopposite pairs, with one trace slightly preceding the other (Figs. 17, levels 3C & 2C; 20, arrows; 23, arrows; 24, level 10B). The distance between equivalent levels of each trace in the pair is very small, however, compared to the total distance between successive trace pairs (Figs. 17, 18, 24), estimated to exceed 1 cm in both specimens. At the level of separation, the primary xylem of each trace is circular or elliptical in transverse section, with a radial dimension of about 0.2 mm, and contains one, or occasionally

two, protoxylem strands. Secondary xylem is usually associated with the traces at this level (Figs. 13, 20, 23), but this tissue is lost as the traces traverse the cortex (figs. 15, 16). Distally, each trace becomes elliptical, as observed in transverse section, and contains two protoxylem strands. The long axis of the ellipse is at an oblique angle to the plane of departure (Figs. 1; 17, level 8C; 18; 19).

Near the periphery of the axis, the primary xylem of each trace is surrounded by small, thin-walled cells interpreted to be primary phloem (Figs. 14; 17, level 8C). Individual xylem elements are as much as 30 μm in transverse diameter, and the surrounding cells range from 10 to 40 μm in transverse diameter. Beyond this level, the two traces diverge from each other, and each enters the base of what appears, based on the structure of surrounding cortical tissues, to be a separate lateral appendage (Figs. 1; 16; 17, level 7C). At a slightly higher level, each trace divides (Figs. 1, arrows; 14; 16; 17, level 6C; 18; 19), indicating that each lateral appendage may also divide at or near its base. Evidence of traces from both specimens suggests that lateral appendage pairs are borne helically on the main axis in three ranks.

DISCUSSION

This work, utilizing the syntype material of *Triloboxylon arnoldii* (Matten 1974), supplements previous descriptions by Arnold (1935, 1940), and Scheckler and Banks (1971a). Our present understanding is that this plant had anatomy typical of members of the Aneurophytales, and that it was probably most closely related to *Aneurophyton germanicum* (Kräusel and Weyland 1929; Leclercq 1940; Schweitzer and Matten 1982), or *Triloboxylon ashlandicum* (Matten and Banks 1966; Scheckler and Banks 1971a). New interpretations of significant anatomical features are discussed here.

Most important, perhaps, is the discovery that although traces in this taxon are much like the smallest, or "ultimate" order traces in other members of the Aneurophytales (Scheckler and Banks 1971a, 1971b; Bonamo 1977), they are unusual in being produced in coordinate pairs from the tips of primary xylem ribs. One of the two specimens described here shows this pattern clearly (Fig. 24). Trace departure in the other specimen is more problematical, but we think the bulk of the evidence supports our interpretation (Figs. 17, especially levels 3C & 2C; 18). In a previous analysis of this taxon, Scheckler and Banks (1971a, Fig. 23) described a single trace near the level of its separation from the primary xylem of the main axis and, because it contained two protoxylem strands, they suggested that it probably would divide over a short distance distally. Their evidence came from the distal end of the specimen shown in Figure 24 (level 1B). Based on our study of the entire specimen, however, we suggest that this trace is most likely one of an original pair of traces, with the second trace incipient and poorly preserved at this level. We have no evidence for the division of traces in this specimen. In the other specimen, traces are observed to divide only in the bases of lateral appendages, approximately 0.6 mm distal to the level of their departure from the primary xylem of the main axis (Figs. 17, 19).

It has been suggested that terete traces produced in pairs from the primary xylem of the main axis might be the unique anatomical manifestation of ultimate fertile appendages in some or all members of the Aneurophytales (Scheckler 1975, 1976; Wight and Beck 1982). Demonstration of such a relationship would be quite useful since it is rare to find preservation of both external morphology and internal anatomy in the same specimen. However, proof of this relationship, which requires evidence of one-for-one correspondence, will be extremely difficult. It is interesting to note that if *T. arnoldii* does, in fact, represent the fertile region of some aneurophytalean plant, then its large size and extensive secondary growth might argue more for

an overall reconstruction like that suggested for *Triloboxylon ashlandicum* (Scheckler 1975) than for those proposed for other taxa [see, for instance, *Aneurophyton* (Serlin and Banks 1978; Schweitzer and Matten 1982), *Tetraxylopteris* (Bonamo and Banks 1967), and *Protopteridium* (*Rellimia*) (Leclercq and Bonamo 1971; Bonamo 1977; Schweitzer and Matten 1982)]. The former, however, is based only on a single, relatively poorly preserved specimen and its validity has been questioned (Bonamo 1977).

The outermost cortex of *T. arnoldii* has been interpreted variously as bundles of hypodermal sclerenchyma (Arnold 1940), or fibers (Scheckler and Banks 1971a), alternating with thin-walled parenchyma. In this work we present evidence of three types of cells in this region: fibers, short cells with dark lumina interpreted as sclereids, and short, thin-walled parenchyma. As far as we are aware, only two other specimens of aneurophytaleans with three-ribbed steles approach this level of complexity in the outer cortex (Figs. 26, 30). Both were assigned to *Triloboxylon ashlandicum* by Scheckler and Banks (1971a), but the type of *T. ashlandicum* is not extensively enough preserved to show these tissues (Matten and Banks 1966), and differences in other features (Wight, personal communication) indicate that this assignment may not be secure. Scheckler and Banks originally described only two kinds of cells, fibers and parenchyma, in the outer cortex of these specimens. We suggest, however, that like *T. arnoldii*, this region probably contained three distinct types of cells. We agree on the presence of fibers (Figs. 27, arrow *f*; 28, arrow *f*). Short cells, described as parenchyma by Scheckler and Banks, we believe to be sclereids similar to those in *T. arnoldii* (Figs. 27, arrow *s*; 28 arrow *s*; see also Scheckler and Banks 1971a, fig. 19). Thin-walled parenchyma cells have not been observed but, as in *T. arnoldii*, they probably occurred in regions separating the bundles of fibers and sclereids (Figs. 27, arrow *p*; 28; 29). It is significant to note, however, that although it is possible to interpret the outer cortex of these *T. ashlandicum* specimens as being equivalent to that in *T. arnoldii*, the relative quantity of different cell types must vary. Sclereids are far less abundant in the *T. ashlandicum* specimens (compare Figs. 2, 6, 27, 28), and parenchyma cells between the fiber-sclereid bundles are probably also fewer since the fiber-sclereid bundles are closer together. These differences are consistent with the hypothesis that the outer cortex of *T. arnoldii* expands considerably as a result of secondary development (see below).

Scheckler and Banks (1974, fig. 7) have suggested that the periderm in *T. arnoldii* consists of a phellogen plus discrete phellem and phelloderm layers. In addition, they have suggested morphological equivalence between these tissues and the periderm of living seed plants. Our observations of the same material, however, suggest that *T. arnoldii* had a simple periderm derived from cell divisions occuring throughout the tissue. The idea that aneurophytaleans, or progymnosperms as a whole, share with seed plants a unique type of secondary cortical development (in addition to sharing a unique kind of secondary vascular development) is intriguing but, at present, without support.

Scheckler and Banks (1971a) have suggested that *Callixylon*-like grouped pitting should be considered a diagnostic feature of *T. arnoldii*. Their observations were based on a specimen from a different locality and age (see below) sharing few significant features with the specimens described here. Moreover, all of their characterizations were made from split surfaces studied only with light microscopy. In our opinion, they provided insufficient detail to establish any pitting character with certainty. Under SEM, the vast majority of secondary xylem tracheids in *T. arnoldii*, and all other aneurophytaleans from western New York studied so far, show only evidence of closely packed circular bordered pits on both radial and tangential walls. Some preparations, however, do provide a very localized and, we believe, false appearance of grouped pits as described above.

Several features, listed below, have previously been ascribed to *T. arnoldii*, but are poorly documented. In our opinion, these should not serve as defining features of the taxon.

Epidermis—A tissue consisting of radially flattened cells with dark contents at the periphery of one specimen (Figs. 1, 9) has been interpreted previously as epidermis (Scheckler and Banks 1971a). Although the tissue apparently forms a discrete boundary one to several cell layers thick, definitive histological evidence of function is lacking.

Lack of parenchyma in the primary xylem—Primary xylem parenchyma, like that observed in some specimens of *T. ashlandicum* (especially in association with incipient traces), is considered to be absent in *T. arnoldii* (Scheckler and Banks 1971a, 1971b). The primary xylem in *T. arnoldii*, however, is poorly preserved in most regions, and we caution that this difference may be more apparent than real.

Radial bands in the primary xylem—Tangentially flattened tracheids along the midplanes of xylem ribs, variously interpreted as protoxylem or metaxylem (Matten and Banks 1966; Scheckler and Banks 1971a; Bonamo 1977; Stein 1982), was one of the features cited by Scheckler and Banks (1971a) in assigning this taxon to the genus *Triloboxylon*. We believe, however, that this assessment was based mostly or entirely on their new specimen. In the specimens described here, we have not observed this feature.

SYSTEMATICS

We have referred above to the fact that the material figured by Arnold (1940), subsequently cited as the type of *T. arnoldii* (Matten 1974), consists of two specimens. Although both come from the same locality and appear to belong to the same species based on all available evidence, it is nevertheless essential to designate a lectotype (Stafleu et al. 1978). We designate the more extensively preserved specimen [illustrated here in Figures 1-3, 5, 6, 9, 10, 13-19, 33-35; by Scheckler and Banks (1971a), Figs. 25-28; and by Arnold (1940), Fig. 3] as the lectotype of *T. arnoldii*. This specimen will retain the original number in the collections of the Museum of Paleontolgy, University of Michigan. The other specimen, [illustrated here in Figs. 4, 7, 8, 11, 12, 20-24; by Scheckler and Banks (1971a), Fig. 23; and Arnold (1940), Fig. 2], will be given a new number (see below).

A combination of features distinguishes *T. arnoldii* from closely related taxa: (1) a three-ribbed, mesarch, primary xylem column with protoxylem strands near the tips and along the midplanes of the ribs, (2) small transversely elliptical traces produced in pairs from the tips of successive primary xylem ribs, (3) extensive secondary xylem, including some associated with traces at proximal levels, (4) a heterogeneous inner cortex with many clusters of sclereids and occasional fibers, (5) an outer cortex with bundles consisting of fibers and short sclereids, separated by ordered arrays of thin-walled parenchyma cells, and (6) a simple but extensively developed periderm. Several of these features (3, 4, 5, 6) are probably size related.

In establishing a clear concept for *T. arnoldii*, we think it is important to include, at present, only those specimens which show a significant fraction of the above features. We consider the evidence of paired small traces (2) to be especially significant. Of specimens previously assigned to this taxon, however, only the two described in this report show this feature. We suggest that other specimens, notably one described by Scheckler and Banks (1971a, Figs. 22, 24), and another by Matten (1974, Plate 3, A-F), should be excluded from *T. arnoldii*, at least until the systematics of aneurophytaleans with three-ribbed steles becomes better understood.

Although *T. arnoldii* and *T. ashlandicum* have been grouped together in the same genus, there is no compelling reason to suggest a close relationship. In particular, the observed differences in trace size and arrangement are well within the range used to separate genera, or even taxa of higher rank, in the Aneurophytales (Matten 1973). On the other hand, it seems unreasonable to

suggest that a plant with a main axis as large as that in *T. arnoldii* bore only lateral "ultimate" order axes (as indicated by small traces), and did not branch or bear larger lateral axis systems (as indicated by large and ribbed traces) of some sort. Since the vascular architecture of major branch systems in all known members of the Aneurophytales appears largely similar, present differences between the species of *Triloboxylon* may mostly reflect our ignorance of these plants as biological entities.

Triloboxylon Matten and Banks 1966
Amer. Jour. Bot., 53:1020-1028.
Emend. Scheckler and Banks 1971. Amer. Jour. Bot.,
58:737-751.

In light of present knowledge, the genus is inadequately defined, and there is considerable disagreement over acceptable criteria for its proper definition (for commentary, see Bonamo 1977; Stein 1982; Wight and Beck 1982). We are aware that several features of the species, diagnosed below (type of vascular traces and their mode of departure, structure of the primary xylem, and histology of the cortex) are at variance with existing definitions of this genus. Since work on this problem is underway (Wight, personal communication), however, we shall not attempt to rediagnose the genus at this time.

Triloboxylon arnoldii Matten 1974.
Bot. Jour. Linn. Soc., 68:303-318.
Aneurophyton hallii (Dawson) Arnold 1940 (in part).
Amer. Jour. Bot. 27:57-63.
Triloboxylon hallii (Arnold 1940, non Dawson 1862)
Scheckler and Banks 1971. Amer. Jour. Bot. 58:737-751.

EMENDED DIAGNOSIS: Plants, represented by permineralized axis fragments, with primary and secondary tissues, bearing lateral appendages containing only primary tissues. Primary xylem of the main axis three-ribbed, ca 2.8 mm in diam at greatest extent, mesarch. Protoxylem strands near the tips and along midplanes of primary xylem ribs. Protoxylem and/or early metaxylem tracheids from 10 to ca 30 μm in diameter. Metaxylem tracheids from 30 to 65 μm in diameter. Large metaxylem tracheids having circular bordered pit pairs with elliptical apertures on all walls. Vascular traces produced in pairs from the tips of successive primary xylem ribs. Each trace circular in transverse section proximally, ca 0.2 mm radially, dividing once in the cortex at an oblique angle. Resultant pairs of traces entering the bases of a separate lateral appendages. Tracheids of the traces up to 30 μm in diam; in the lateral appendages, surrounded by thin-walled cells 10 to 40 μm in transverse diam (possible primary phloem). Secondary xylem consisting of tracheids and narrow vascular rays. Tracheids 30 to 78 μm in transverse diam, exceeding 1.6 mm in length. Secondary xylem tracheids having circular bordered pit pairs, with elongate elliptical apertures, in closely packed arrays over entire wall surfaces. Rays uniseriate or partly biseriate, mostly tall but some less than six cell rows high. Secondary phloem consisting of fibers, sclereids, parenchyma cells, and spheroidal bodies with dark contents. Fibers ca 35 um in diam; parenchyma cells from 30 to 40 μm in diam, ca 80 μm in length; spheroidal bodies ca 30 μm in diam. Inner cortex heterogeneous, consisting of thin-

walled parenchyma, some with dark contents, clusters of sclereids, and occasional fibers. Parenchyma cells from 23 to 78 μm in diam; sclereids from 45 to 115 μm in diam. Outermost cortex consisting of discrete bundles of fibers and sclereids, separated by thin-walled parenchyma cells which occupy regular tangential, radial, and to a lesser extent, longitudinal files. Fibers from 50 to 115 μm in diam, with cell walls up to 40 μm thick; sclereids from 45 to 65 μm in diam; parenchyma cells from 20 to 80 μm radially, 30 to 60 um tangentially, ca 45 μm in length. Simple periderm forming internal to the fiber-sclereid bundles and in association with fissures in the outer cortex. Individual cells not evidently specialized, ranging from 30 to 80 um tangentially, 10 to 35 μm radially, 25 to 60 μm in length. Outer surface of the axis comprised of 1 to 3 layers of cells with dark lumina (possible epidermis). Cell dimensions ca 40 μm radially, 95 μm tangentially, 90 μm in length. Cortex of lateral appendage homogeneous, consisting of thick-walled parenchyma, between 60 and 160 μm in diam, becoming increasingly elongate toward the periphery.

LECTOTYPE: 25 slides and 2 preparations for SEM bearing No. 23848 in the Museum of Paleontology, University of Michigan, Ann Arbor.

ADDITIONAL SPECIMEN: 33 slides and 16 additional peparations, UMMP 65131.

LOCALITY: Spring Creek, 1/2 mile NE of Alden, Erie County, New York, U.S.A. Pyrite horizon in the Ledyard Shale Member, Ludlowville Formation, Hamilton Group (Givetian).

MODELS OF SECONDARY GROWTH IN *Triloboxylon arnoldii*

Large size and extensive secondary vascular tissues are distinctive features of *T. arnoldii.* However, this combination of features also characterizes nearly all of the aneurophytalean axes collected in western New York to date, including some with a strikingly different vascular architecture. It is important, therefore, that we consider carefully the nature of secondary development, especially as it relates to size, in order to get at the question of whether some or all of the features listed above have systematic significance. We shall describe, and compare in detail, our new specimens in a subsequent work; possible modes of development of secondary tissues in *T. arnoldii* will be explored here. Since the lectotype is the only specimen with extensive evidence of extra-xylary tissues, our discussions will be limited mostly to it. In reconstructing what the primary body of this axis might have been like, several features can be considered.

The outermost cortex.—Longitudinal fissures in the surface of the axis, and abundant periderm in the outer cortex (Figs. 1, 2), can be interpreted as evidence of the response of outer cortical tissues to increasing diameter of the axis. We can estimate the overall increase in size due to fissuring by matching the plates of remaining outer cortex end-to-end (Figs. 36, 37). Cross-sectional area of the resultant axis is approximately 57% of the present axis. However, it is still large compared to most aneurophytalean taxa (Figs. 39-42). Highly ordered arrays of parenchyma separating the peripheral fiber-sclereid bundles (Figs. 2, 5, 6), suggest multiple tangential and radial divisions of the cells in this tissue. This activity might also have contributed significantly to increased axis size. The extent of the contribution is difficult to estimate, however, because not all of this tissue is necessarily of secondary origin. If assumed to be entirely secondary, a cross-sectional area of approximately 36% of the present axis can be estimated (Fig. 38).

Histology of the cortex.—As described above, the cortex of the main axis is conspicuously more complex than the cortex observed in the bases of lateral appendages in the same specimen (Figs. 33-35). The lateral appendages contain no secondary vascular tissues and the cells of the cortex appear very similar to the general condition in aneurophytalean axes displaying little or

no secondary growth (Figs. 31, 32). We suggest that the primary cortex of the main axis of *T. arnoldii* was initially quite similar, and that its present state is entirely due to secondary modification. There are several ways in which secondary modification might occur, however, and it is difficult to determine the extent to which such modification, by itself, might have increased the overall size of this axis.

Secondary vascular tissues.—Extensive secondary vascular tissues, especially secondary xylem, suggests fairly sustained secondary development. From studies of living plants, there is little doubt that secondary xylem contributes significantly to increased axis size. However, knowledge of the initial size of the primary body (and therefore changes in size due to secondary growth) is not recoverable from an analysis of the secondary xylem only.

Size of the primary xylem.—The only tissue remaining in *T. arnoldii* beyond doubt of primary origin is the primary xylem. It is possible that some measure of this tissue (such as volume or surface area) might serve as a reliable predictor of the initial primary body size in all, or at least some, aneurophytalean taxa. At present, however, we lack a sufficient number of well-preserved specimens containing only primary tissues from which a correlation could be determined.

Based on the histological evidence listed above, and on the structure of possibly related aneurophytalean taxa, we think there are at least two possible models for what the initial primary body of the lectotype of *T. arnoldii* (at least at levels preserved in the specimen) might have been like. Since the models differ significantly, each imposes unique constraints on how subsequent seondary development could have proceeded in order to yield the axis in its present state.

According to the first model, the primary body of *T. arnoldii* might originally have been quite large, consisting of an extensive primary cortex with cells similar to those presently preserved in the bases of its lateral appendages. An example of such an axis is *Reimannia aldenense* (Arnold 1935; Stein 1982) known from the same locality and horizon (Figs. 25, 32, 42). The cortex in this form is essentially homogeneous, consisting of parenchyma cells which decrease in transverse diameter and become increasingly elongate toward the periphery. Although extensively preserved, there is no evidence of fiber-sclereid bundles in the outermost cortex. In some regions of the axis, however, groups of somewhat thicker-walled cells occur at regular intervals near the periphery (fig. 25, arrows; see also Stein 1982, Pl. 1, fig. 4, and Pl. 2, fig. 3), and it is conceivable that these represent the bundles at an earlier developmental stage.

Modification of *Reimannia* to produce the structures observed in the lectotype of *T. arnoldii* would involve: (a) formation of extensive secondary vascular tissues, (b) cell proliferation in the cortex to accomodate growth in vascular tissues, yielding a more heterogeneous tissue comprised of generally smaller and shorter cells, (c) differentiation of fiber-sclereid bundles in the outermost cortex interspaced by a highly ordered secondary parenchyma (the latter probably contributing to some degree to an increase in axis size), and finally (d) fissuring of the outer cortex associated with the development of a simple periderm.

In the second model, we suggest that the primary body of the lectotype of *T. arnoldii* might originally have been very much smaller than *Reimannia*, more like that observed in some specimens assigned to *T. ashlandicum* (Scheckler and Banks 1971a) from the Upper Devonian of eastern New York (Figs. 26, 30, 39-41). In one specimen with primary xylem approximately equal in volume to *Reimannia* and *T. arnoldii* but lacking secondary tissues (Fig. 26), the entire axis is three-angled and contains only a very narrow inner cortex. However, as discussed above, these forms have a well developed system of fiber-sclereid bundles, probably identical in organization to *T. arnoldii*, but differing in the relative quantity of the different cell types.

Development of the lectotype of *T. arnoldii* from this kind of axis would include: (a) formation of extensive secondary vascular tissues, (b) extensive proliferation of cells in the primary cortex, or outermost primary and/or secondary phloem, creating a tissue which contributes significantly to the increase in total volume of the axis, (c) separation of the bundles of fibers in the outer

cortex by proliferation of intervening parenchyma (contributing directly to increased axis size) and finally, (d) fissuring of the axis and formation of a periderm as in the previous model.

The essential differences between the two models are thus: (a) the initial size of the primary body, largely a function of the volume of the inner part of the primary cortex, and (b) whether the fiber-sclereid bundles in the outer cortex are part of the primary body or develop during a period of secondary modification of the axis.

The similarities between *T. arnoldii* and *Reimannia*, especially in the structure of cells in unmodified primary cortex (compare, for instance, Figs. 14, 16, 25, 32-34), might argue in favor of the first model. These similarities, combined with the fact that the taxa co-occur at the only locality where either has been collected, suggest that they might even represent the same biological entity. However, this model, and the constraints on secondary development that it implies, has several problems. The major problem, in our opinion, lies with whether the fiber-sclereid bundles of *T. arnoldii* can reasonably be expected to have developed from the simple, if slightly heterogeneous, primary cortex of *Reimannia*. Since we lack any developmental or comparative evidence among aneurophytaleans with three-ribbed steles of an intermediate condition, the model is generally without support.

In contrast, the second model, with its proposed pattern of secondary development, can be considered to be supported by at least two distinct lines of evidence: (a) Equivalence of the outer cortical tissues in *T. arnoldii* and at least some specimens assigned to *T. ashlandicum* has been suggested on the basis of evidence presented above. The major difference between *T. arnoldii* and the other specimens seems to be in the relative number of fibers versus sclereids within peripheral bundles, and especially, in the amount of parenchyma between the bundles. The model proposes that fibers in *T. arnoldii* orginally developed as part of the primary body. Evidence from living plants suggests that fibers, once mature, are the least capable among all cortical cells of further cell divisions (although they may become segmented longitudinally). This would imply that growth in these regions would have to be accomplished by other cells, namely the parenchyma plus, perhaps, some sclereids (or their precursors) in the primary body. The greater abundance of these cells in *T. arnoldii*, the presumably more completely developed axis, can be viewed as the expected result of the model. (b) If the specimens described above are arranged in a sequence according to the amount of secondary xylem each possesses (i.e., using the additive growth of this tissue as an estimate of the relative developmental age of each specimen), then it is significant to note that variation between the specimens in other, potentially independent, features is also consistent with the developmental proposals of this model. Possible examples include the amount of parenchyma separating fiber-sclereid bundles of the outer cortex, the number of sclereids associated with fibers in each peripheral fiber-sclereid bundle, and the total amount of cortex present in the axis (compare Figs. 1, 26, 30). The two specimens of *T. ashlandicum* are far more similar to each other than either is to the lectotype of *T. arnoldii*, however, and we have been unable to quantify these observations.

If *T. arnoldii* developed along the lines proposed by our second model, then this suggests that at least some specimens we call *T. ashlandicum* (i.e., those which represent *T. arnoldii* in the primary state) might have had the potential to grow for a relatively long time. This appears to be inconsistent, however, with the hypothesis that all specimens of *T. ashlandicum* are part of determinate branch systems as suggested by Scheckler (1976). Scheckler based his proposal on observed changes in the primary xylem of a few axis fragments, plus general comparisons between groups of specimens assigned *a priori* to specific axis "orders". In our opinion, this rigid system constrains to an unwaranted degree the range of morphologies in *T. ashlandicum* which might be considered likely or possible.

Although we have a long way to go before the existence of different developmental patterns in the Aneurophytales can be considered to be established, we nevertheless suspect that such

patterns may provide an important key to the understanding of the morphology and systematics of this group. To be more useful, a concerted effort will have to be made to extend our analysis into three-dimensions. A particularly difficult problem needing careful attention is whether distinct developmental patterns observed in different specimens must necessarily represent distinct taxa, or whether development in at least some aneurophytaleans might have been more variable and more complex than previously supposed. The converse is also a problem; demonstration of equivalence in development is not necessarily a guarantee of morphological or taxonomic equivalence.

ACKNOWLEDGEMENTS

We wish to thank D. C. Wight and S. E. Scheckler for helpful discussions, H. P. Banks and P. G. Gensel for reviews of the manuscript, and K. J. Niklas for the loan of several specimens from the paleobotanical collections at Cornell University. This work was supported by NSF grants DEB-78-11165 and DEB-81-13542 to C. B. Beck. Support for development of the computer programs used came from NSF grant PCM-04643 to T. Connelly, Department of Anatomy and Cell Biology of the Medical School, and NIH grant DE-05410 to F. L. Bookstein, Center for Human Growth and Development, both at the University of Michigan. We wish to thank Drs. Connelly and Bookstein for allowing access to the programs, and we are especially grateful to Jim Kilgore for facilitating our use of them.

LITERATURE CITED

ANDREWS, H. N., and T. L. PHILLIPS. 1968. *Rhacophyton* from the Upper Devonian of West Virginia. Bot. Jour. Linn. Soc. 61:37-64.

ARNOLD, C. A. 1935. Some new forms and new occurrences of fossil plants from the Middle and Upper Devonian of New York State. Buffalo Soc. Nat. Sci. Bull. 17:1-12.

_____. 1940. Structure and relationships of some Middle Devonian plants from western New York. Amer. Jour. Bot. 27:57-63.

BECK, C. B. 1957. *Tetraxylopteris schmidtii* gen. et sp. nov., a probable pteridosperm precursor from the Devonian of New York. Amer. Jour. Bot. 44:350-367.

_____. 1960. The identity of *Archaeopteris* and *Callixylon.* Brittonia 12:351-368.

_____. 1976. Current status of the Progymnospermopsida. Rev. Palaeobot. Palynol. 21:5-23.

BONAMO, P. M. 1975. The Progymnospermopsida: building a concept. Taxon 24:569-579.

_____. 1977. *Rellimia thomsonii* (Progymnospermopsida) from the Middle Devonian of New York State. Amer. Jour. Bot. 64:1272-1285.

_____, and H. P. BANKS. 1967. *Tetraxylopteris schmidtii*: its fertile parts and its relationships within the Aneurophytales. Amer. Jour. Bot. 54:755-768.

CREPIN, F. 1875. Observations sur quelques plantes fossiles des dépots dévoniens rapportés par Dumont à l'étage quartzo-schisteux inférieur de son système eifélien. Bull. Soc. Roy. Belg. 14:214-230.

DAWSON, J. W. 1862. On the flora of the Devonian period in north-eastern America. Proc. Geol. Soc. (London) 18:296-330.

_____. 1871. The fossil plants of the Devonian and upper Silurian formations of Canada. Publ. Geol. Surv. Canada, Montreal.

KRÄUSEL, R., and H. WEYLAND. 1923. Beiträge zur Kenntnis der Devonflora I. Senckenbergiana 5:154-184.

_____, and _____. 1926. Beiträge zur Kenntnis der Devonflora II. Abh. Senckenb. Naturforsch. Ges. 40:114-155.

_____, and _____. 1929. Beiträge zur Kenntnis der Devonflora III. Abh. Senckenb. Naturforsch. Ges. 41:315-360.

_____, and _____. 1941. Pflanzenreste aus dem Devon von Nord-Amerika. Palaeontogr., Abt. B, 86:1-78.

LECLERCQ, S. 1940. Contribution à l'étude de la flore du Dévonien de Belgique. Acad. Roy. Belg., Cl. Sci., Mem. 12:1-65.

_____. 1951. Étude morphologique et anatomique d'une fougère du Dévonien Supérieur, le *Rhacophyton zygopteroides* nov. sp. Ann. Soc. Geol. Belg. 9:1-62.

_____, and P. M. BONAMO. 1971. A study of the fructification of *Milleria* (*Protopteridium*) *thomsonii* Lang from the Middle Devonian of Belgium. Palaeontogr., Abt. B, 136:83-114.

MATTEN, L. C. 1973. The Cairo flora (Givetian) from eastern New York. I. *Reimannia*, terete axes, and *Cairoa lamanekii* gen. et sp. n. Amer. Jour. Bot. 60:619-630.

_____. 1974. The Givetian flora from Cairo, New York: *Rhacophyton*, *Triloboxylon* and *Cladoxylon*. Bot. Jour. Linn. Soc. 68:303-318.

_____. 1975. Additions to the Givetian Cairo flora from eastern New York. Bull. Torrey Bot. Club 102:45-52.

_____, and H. P. BANKS. 1966. *Triloboxylon ashlandicum* gen. and sp. n. from the Upper Devonian of New York. Amer. Jour. Bot. 53:1020-1028.

_____, and H.-J. SCHWEITZER. 1982. On the correct name for *Protopteridium* (*Rellimia*) *thomsonii* (fossil). Taxon 31:322-326.

MUSTAFA, H. 1975. Beiträge zur Devonflora I. Argumenta Palaeobotanica 4:101-133.

READ, C. B. 1938. Some psilophytales from the Hamilton Group in western New York. Bull. Torrey Bot. Club 65:599-606.

SCHECKLER, S. E. 1975. A fertile axis of *Triloboxylon ashlandicum*, a progymnosperm from the Upper Devonian of New York. Amer. Jour. Bot. 62:923-934.

_____. 1976. Ontogeny of progymnosperms. I. Shoots of Upper Devonian Aneurophytales. Can. Jour. Bot. 54:202-219.

_____, and H. P. BANKS. 1971a. Anatomy and relationships of some Devonian progymnosperms from New York. Amer. Jour. Bot. 58:737-751.

_____, and _____. 1971b. *Proteokalon* a new genus of progymnosperms from the Devonian of New York State and its bearing on phylogenetic trends in the group. Amer. Jour. Bot. 58:874-884.

_____, and _____. 1974. Periderm in some Devonian plants. In: Y. S. Murty, B. M. Johri, H. Y. Mohan Ram, and T.M. Varghese (eds.). Advances in Plant Morphology. V. Puri Comm. Vol., Sarita Prakashan, Meerut City, India. pp. 58-64.

SCHWIETZER, H.-J., and L. C. MATTEN. 1982. *Aneurophyton germanicum* and *Protopteridium thomsonii* from the Middle Devonian of Germany. Palaeontogr., Abt. B, 184:65-106.

SERLIN, B. S., and H. P. BANKS. 1978. Morphology and anatomy of *Aneurophyton*, a progymnosperm from the late Devonian of New York. Palaeontogr. Amer. 8:343-359.

STAFLEU, F. A., V. DEMOULIN, W. GREUTER, P. L. HIEPKO, I. A. LINCZEVSKI, R. Mc VAUGH, R. D. MEIKLE, R. C. ROLLINS, R. ROSS, J. M. SCHOPF, and E. G. VOSS (eds.). 1978. International Code of Botanical Nomenclature. Bohn, Scheltema & Holkema, Utrecht.

STEIN, W. E. 1982. The Devonian plant *Reimannia*, with a discussion of the class Progymnospermopsida. Palaeontology 25:605-622.

_____, D. C. WIGHT, and C. B. BECK. 1982. Techniques for preparation of pyrite and limonite permineralizations. Rev. Palaeobot. Palynol. 36:185-194.

WIGHT, D. C., and C. B. BECK. 1982. A distinctive aneurophytalean progymnosperm from the Middle Devonian of southwestern Virginia. (abstr.) Bot. Soc. Amer. Misc. Publ. 162:67.

FIG. 1— *Triloboxylon arnoldii.* Lectotype. Transverse section of main axis with attached lateral appendages. Traces are indicated by arrows, section number 6C. UMMP 23848. X 13.

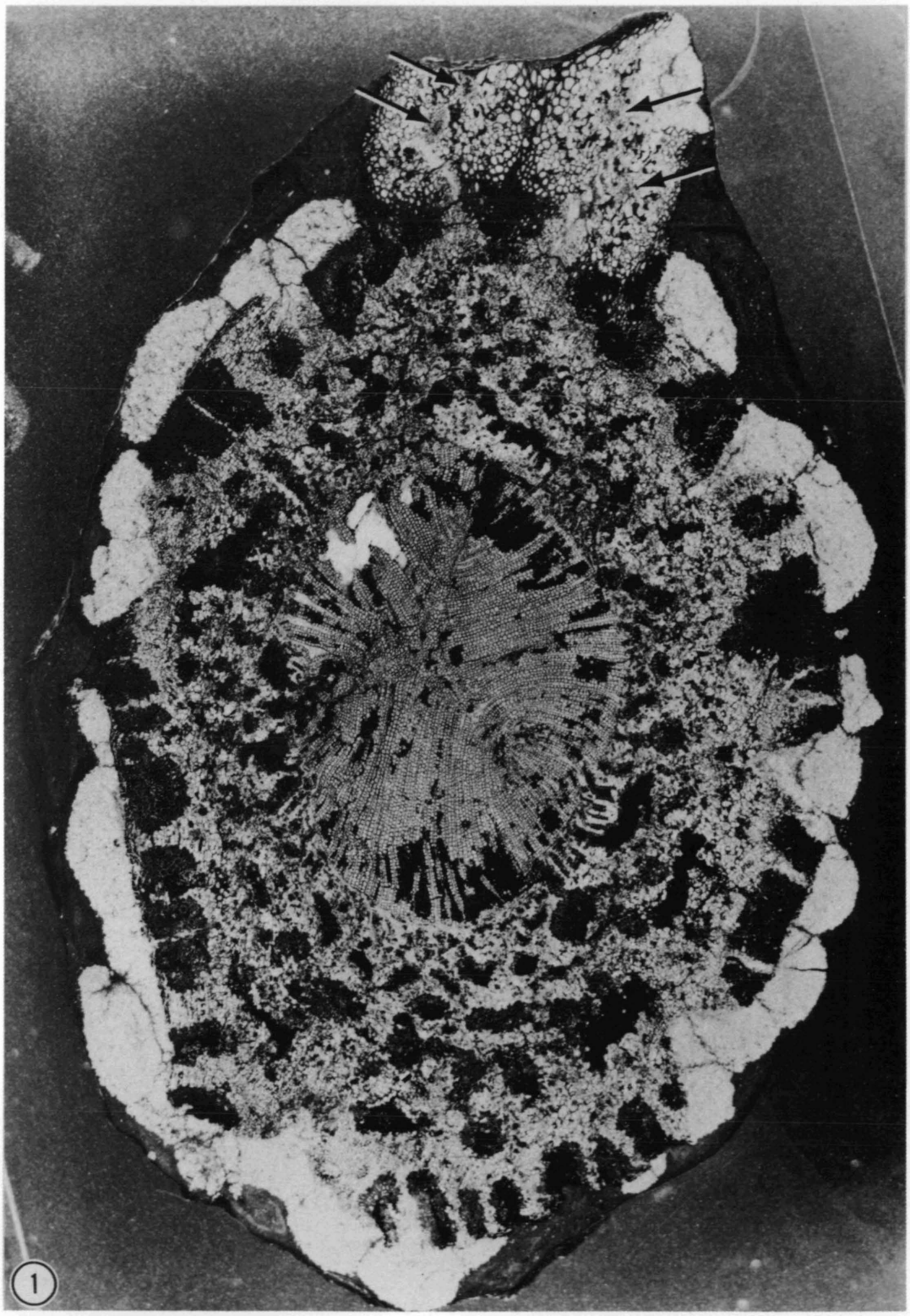

1

FIG. 2-7— *Triloboxylon arnoldii* (section numbers in parentheses). FIG. 2. Transverse section of the outer cortex of the main axis showing peripheral fiber-sclereid bundles separated by parenchyma cells in regular arrays, and at the right a fissure in the cortex bounded by simple periderm. UMMP 23848 (2C). X 24. FIG. 3. Longitudinal section showing a cortical fiber, associated sclereids, and other cells of the inner cortex. UMMP 23848 (3L). X 81. FIG. 4. Tangential section of the secondary xylem showing tracheids and tall uniseriate rays. UMMP 65131 (11L). X 100. FIG. 5. Transverse section at the periphery of the cortex showing a fiber-sclereid bundle and surrounding thin-walled parenchyma cells in regular files. Arrows *s* indicate sclereids, most of which belong to the same files as adjacent parenchyma cells. Arrows *f* indicate thick-walled fibers. UMMP 23848 (13C). X 110. FIG. 6. Longitudinal section of a fiber-sclereid bundle, similar to the one shown in Figure 5, displaying the arrangement of fibers (arrow *f*), sclereids (arrow *s*), and parenchyma cells. UMMP 23848 (13-9CL). X100. FIG. 7. Longitudinal section of a region of secondary phloem showing fibers and associated sclereids. UMMP 65131 (5-3AL). X 100.

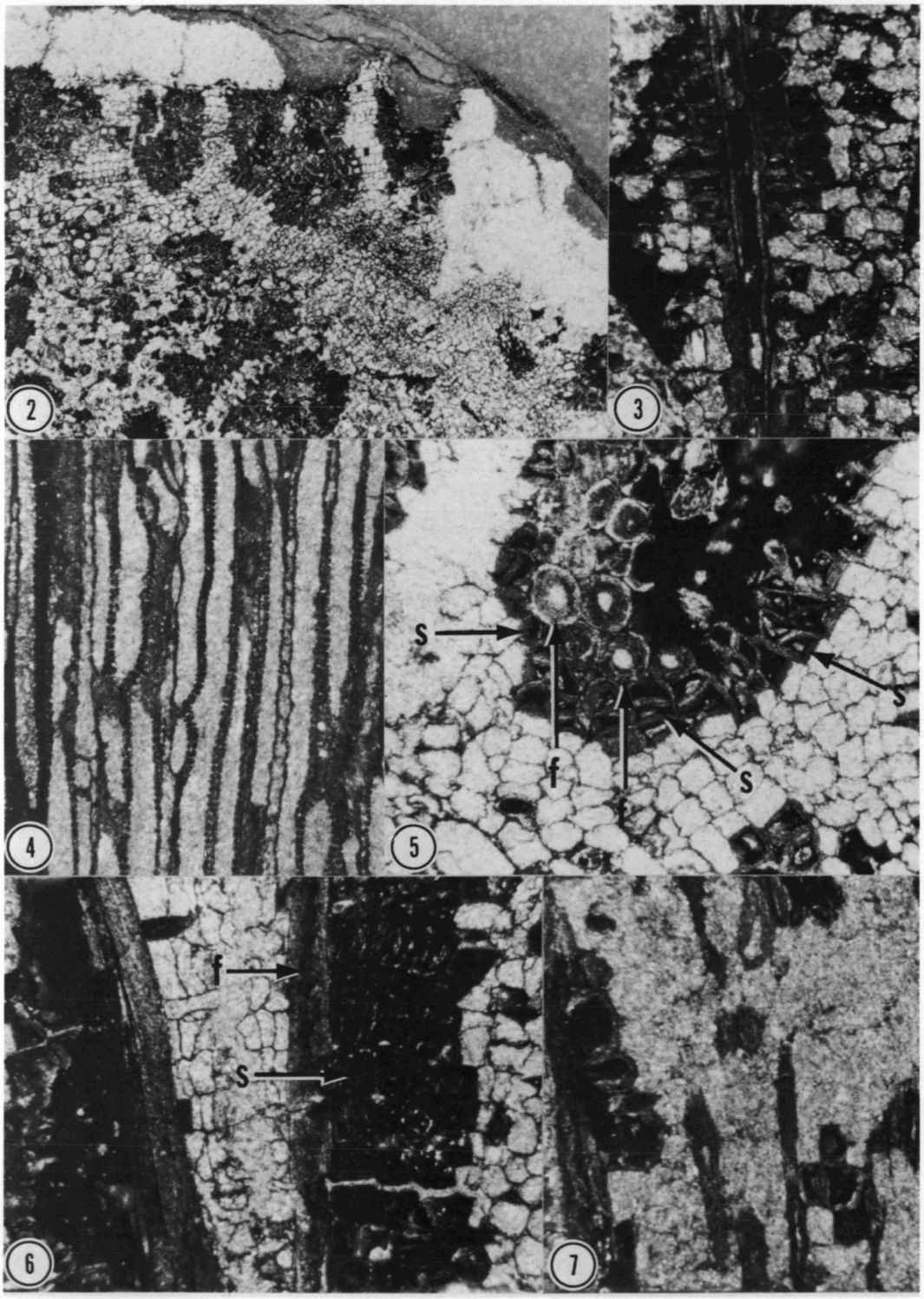

2
3
4
S
f
S
S
5
f
S
6
7

FIG. 8-12— *Triloboxylon arnoldii* (section numbers in parentheses). FIG. 8. SEM of radial surface of secondary xylem tracheids. Closely packed circular bordered pits are interrupted by a poorly preserved ray, probably only a few cells high, creating a false appearance of grouped pits. Some of the pits in the region of the ray are indicated by arrows. UMMP 65131 (6A). X 220. FIG. 9. Longitudinal section showing cells of the outermost cortex, right, and a boundary tissue (possible epidermis), left, consisting of several layers of cells with dark lumina. UMMP 23848 (10-9CL). X 130. FIG. 10. Transverse section of the primary xylem and the inner part of the secondary xylem. Arrows indicate at least some of the protoxylem strands in the three-ribbed primary xylem system. UMMP 23848 (10C). X 37. FIG. 11. SEM of tangential surface of secondary xylem tracheids showing the casts of bordered pit pairs in edge view, left, and casts of single pits in surface view mostly at the level of the pit membrane, right. UMMP 65131 (6A). X 640. FIG. 12. SEM of radial surface of tracheids in the region of late metaxylem or early secondary xylem. Casts of bordered pit pairs are seen in surface view at the level of the aperture. UMMP 65131 (6A). X 1300.

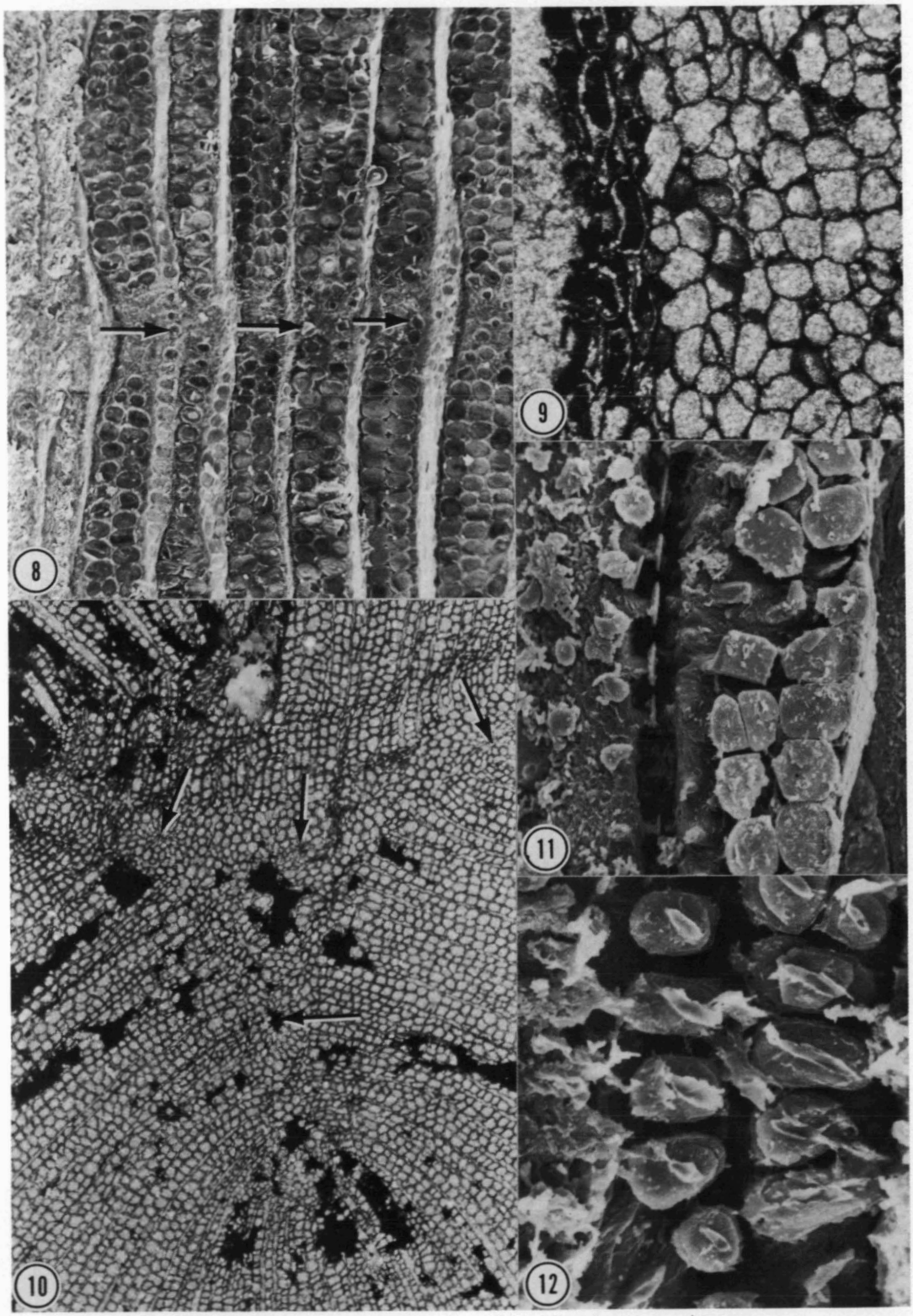
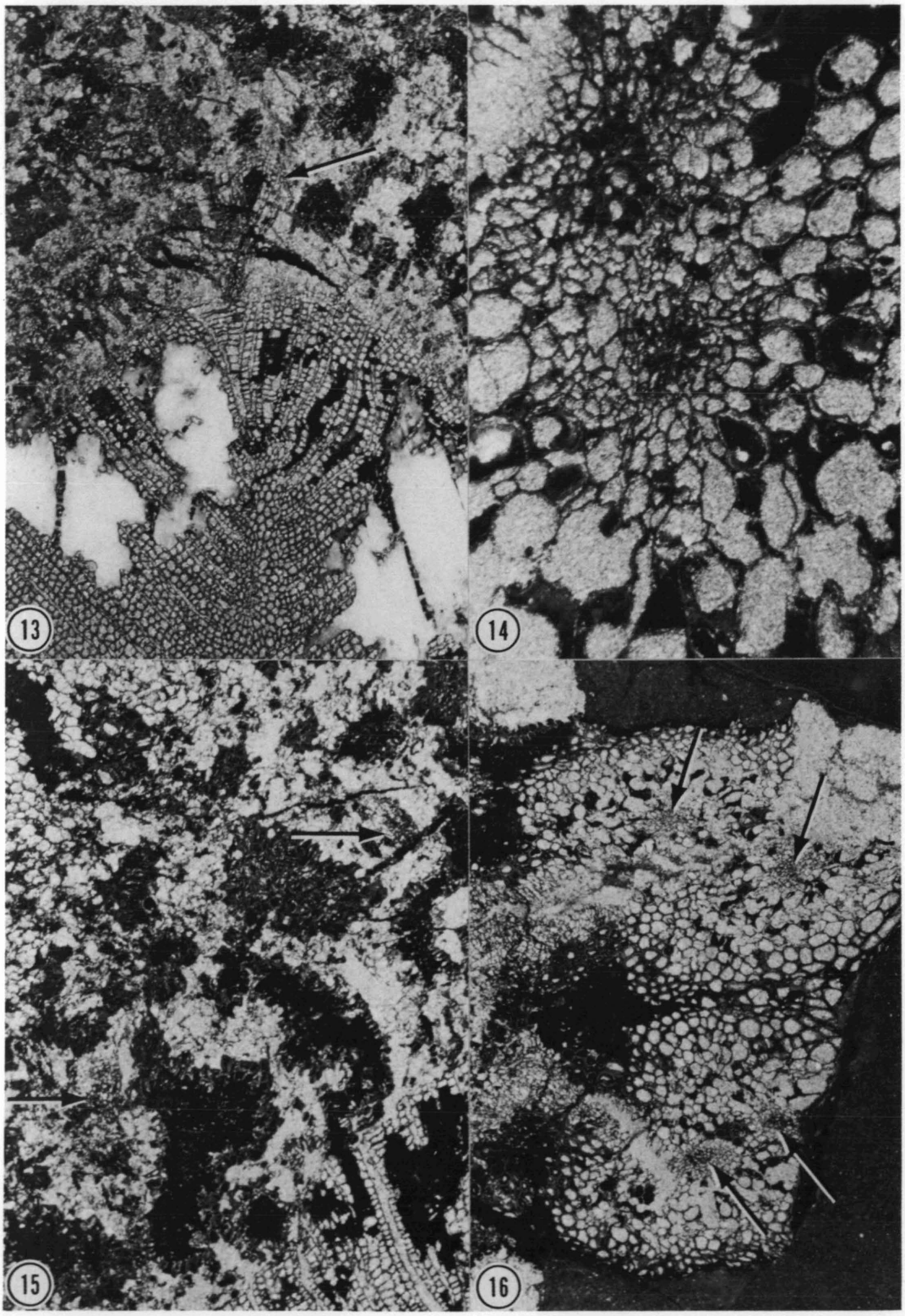

8
9
10
11
12

FIG. 13-16— *Triloboxylon arnoldii* (section numbers in parentheses). UMMP 23848. FIG. 13. Transverse section showing the separation of a small vascular trace, arrow, from the secondary xylem of the main axis (13C). Compare with Figure 17. X 29. FIG. 14. Transverse section of a pair of traces showing small primary xylem tracheids surrounded by thin-walled cells which may represent primary phloem (7C). Compare with Figures 1 and 16. X 110. FIG. 15. Transverse section showing secondary xylem, lower right, secondary phloem, center, and inner cortex, upper left. Arrows indicate a pair of traces derived from a single primary xylem rib of the main axis (2C). Compare with Figure 17. X 35. FIG. 16. Transverse section of two lateral appendages bases, each containing a pair of traces, arrows. Histological evidence for the independence of the lateral appendages is provided, among other things, by the presence of small cells with thick walls along their common boundary, center (6C). X 22.


13
14
15
16

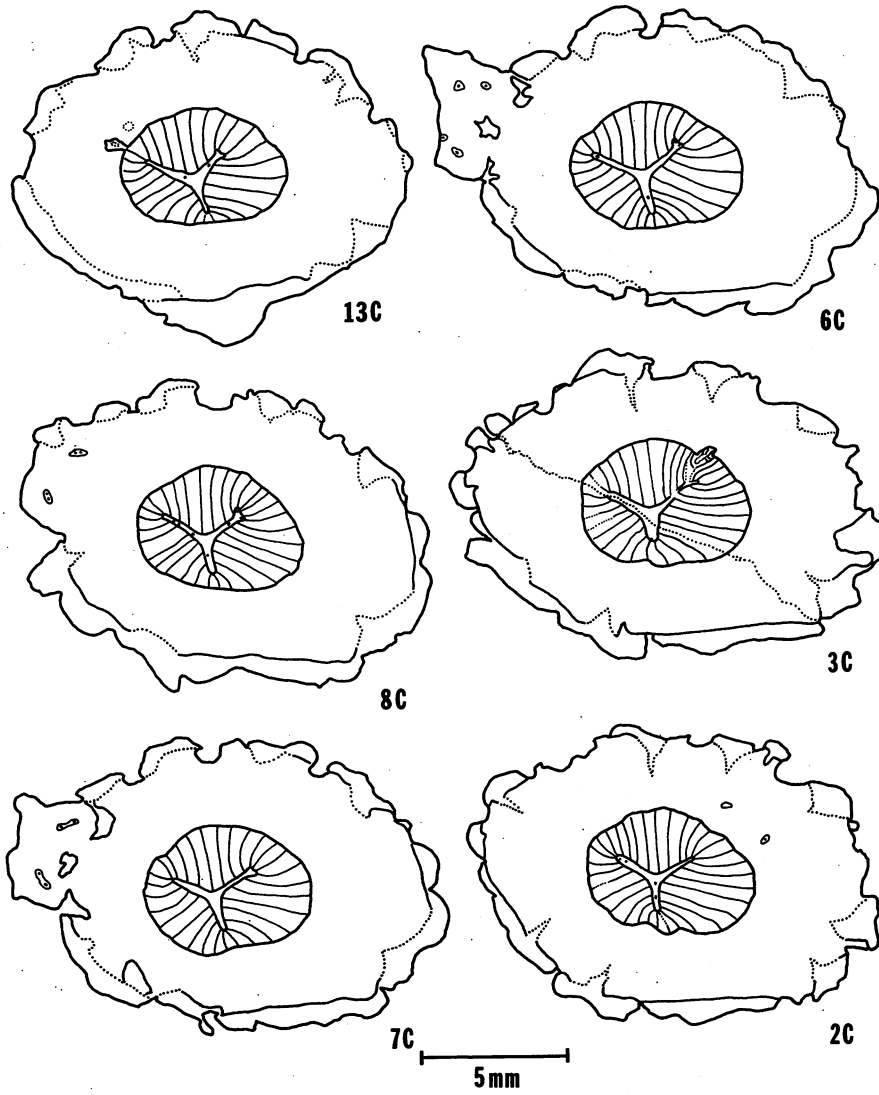


FIG. 17— *Triloboxylon arnoldii.* Lectotype. Serial camera lucida drawings showing changes in the configuration of the primary xylem, and trace departure through the length of the specimen as seen in transverse section. Proximal section (13C), upper left, and distal section (2C), lower right. Read series from top to bottom starting at the left. UMMP 23848.

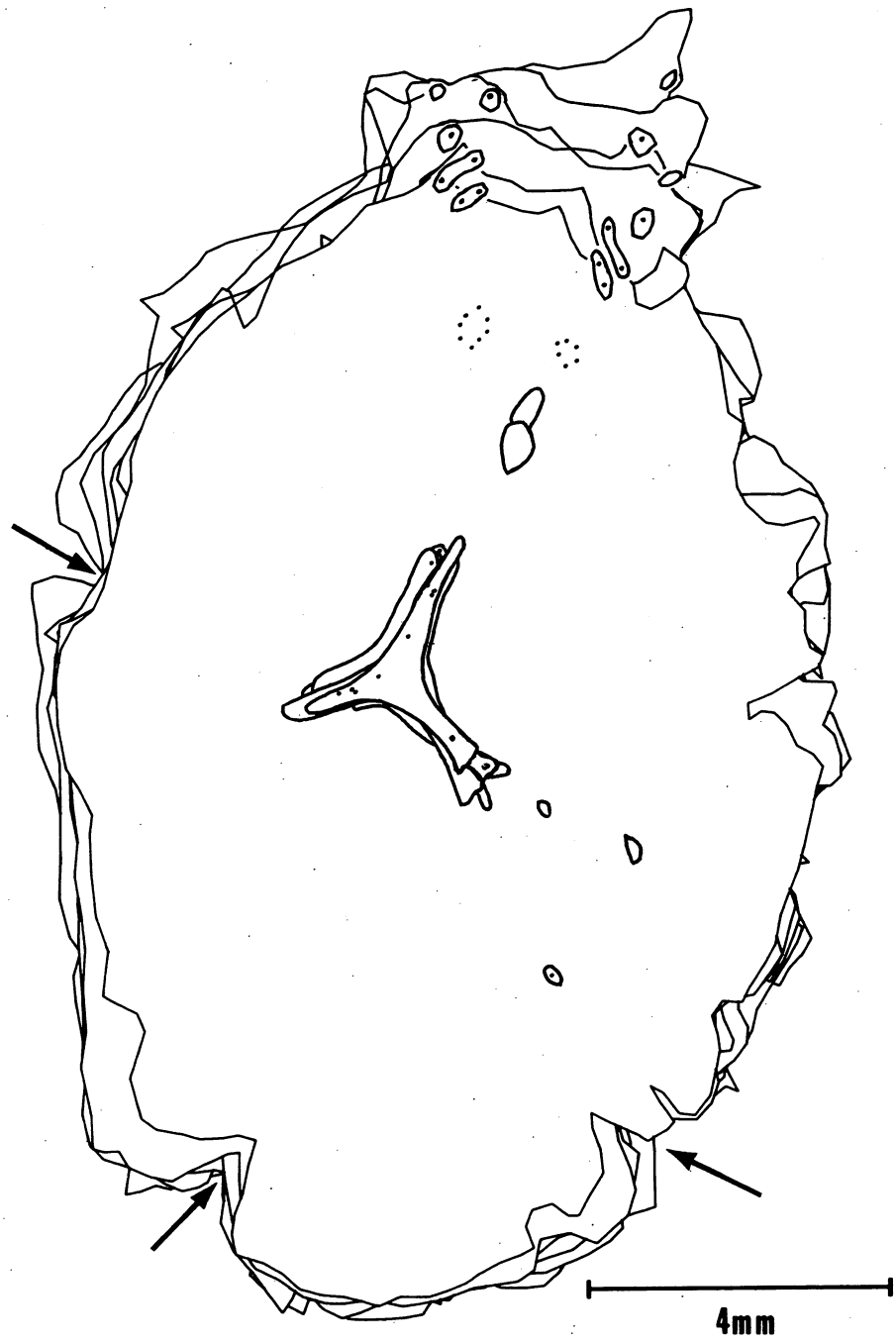


FIG. 18— *Triloboxylon arnoldii.* Lectotype. View of a series of camera lucida drawings, like those in Figure 17, stacked one on top of another with the most proximal section above, and progressively more distal sections behind. The series provides evidence on the departure and division of traces in the specimen. Arrows indicate some of the longitudinally persistent fissures in the outer cortex of the axis.

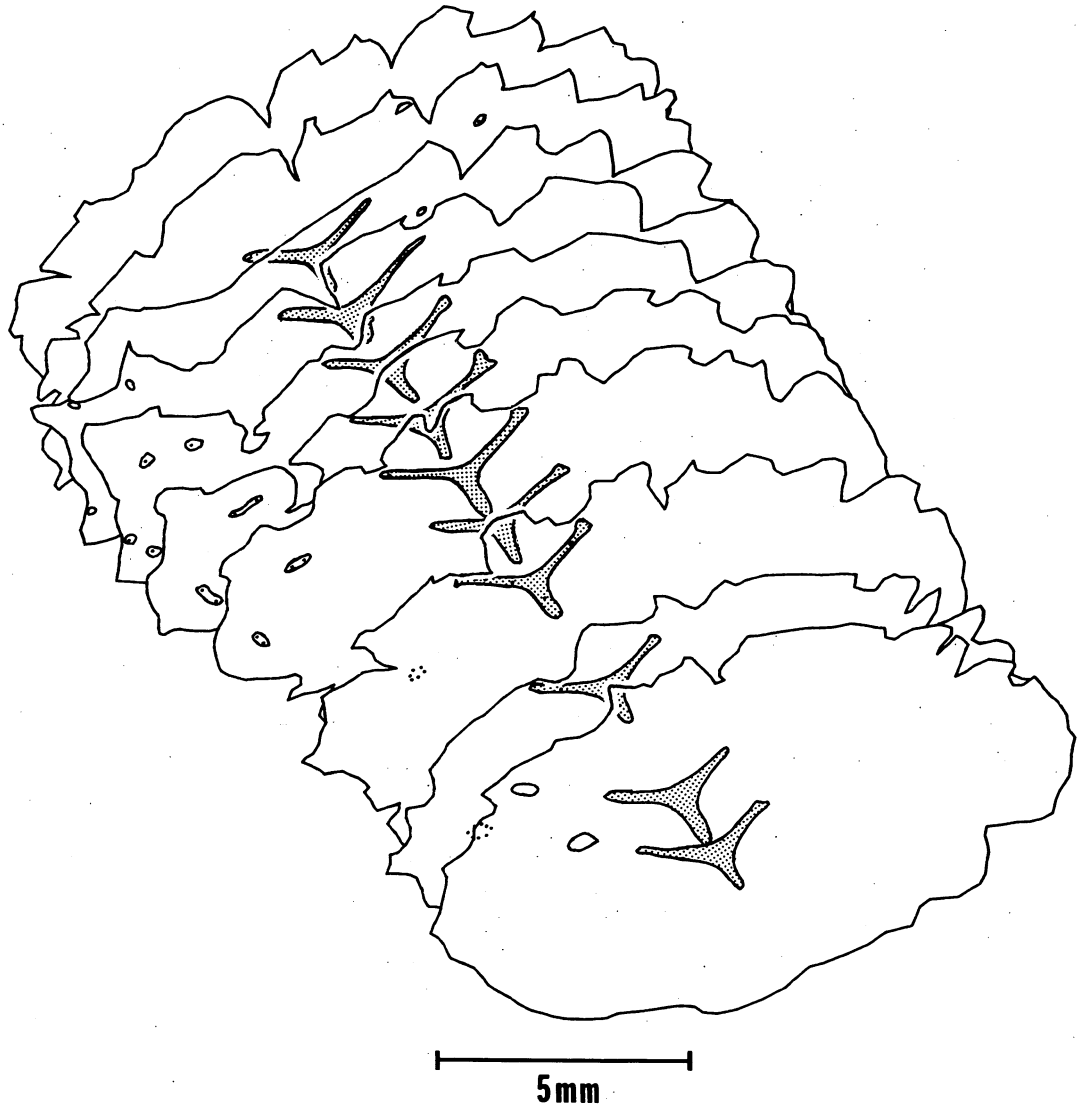
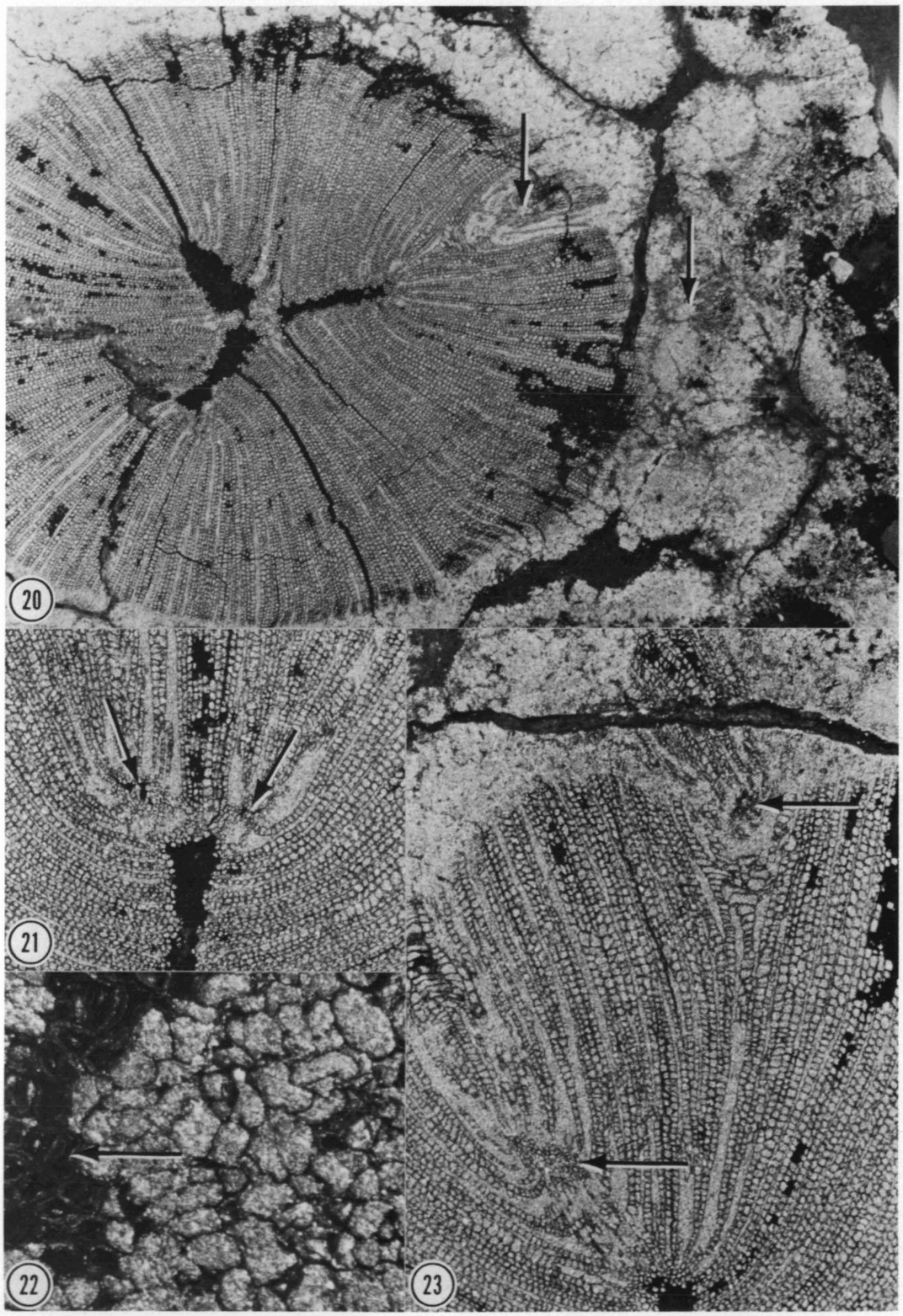


FIG. 19— *Triloboxylon arnoldii.* Lectotype. Adjacent camera lucida diagrams of transverse sections shown in perspective 45° from a line normal to the plane of the sections. Sections are depicted at twice their actual spacing. Shading indicates primary xylem of the main axis. UMMP 23848.

FIG. 20-23— *Triloboxylon arnoldii* (section numbers in parentheses). UMMP 65131. FIG. 20. Transverse section of main axis showing primary and secondary xylem, and a pair of traces at arrows (9B). Compare with Figure 24. X 14. FIG. 21. Transverse section of a pair of traces, arrows, near the level of their separation from a primary xylem rib of the main axis (11A). X 28. FIG. 22. Longitudinal section of the inner cortex consisting of thin-walled parenchyma cells, center and right, and sclereids indicated by arrow at left (3L). X 110. FIG. 23. Transverse section of a pair of traces, arrows, at a level between those shown in Figures 20 and 21 (10B). Compare also with Figure 24. X 28.


20
21
22
23

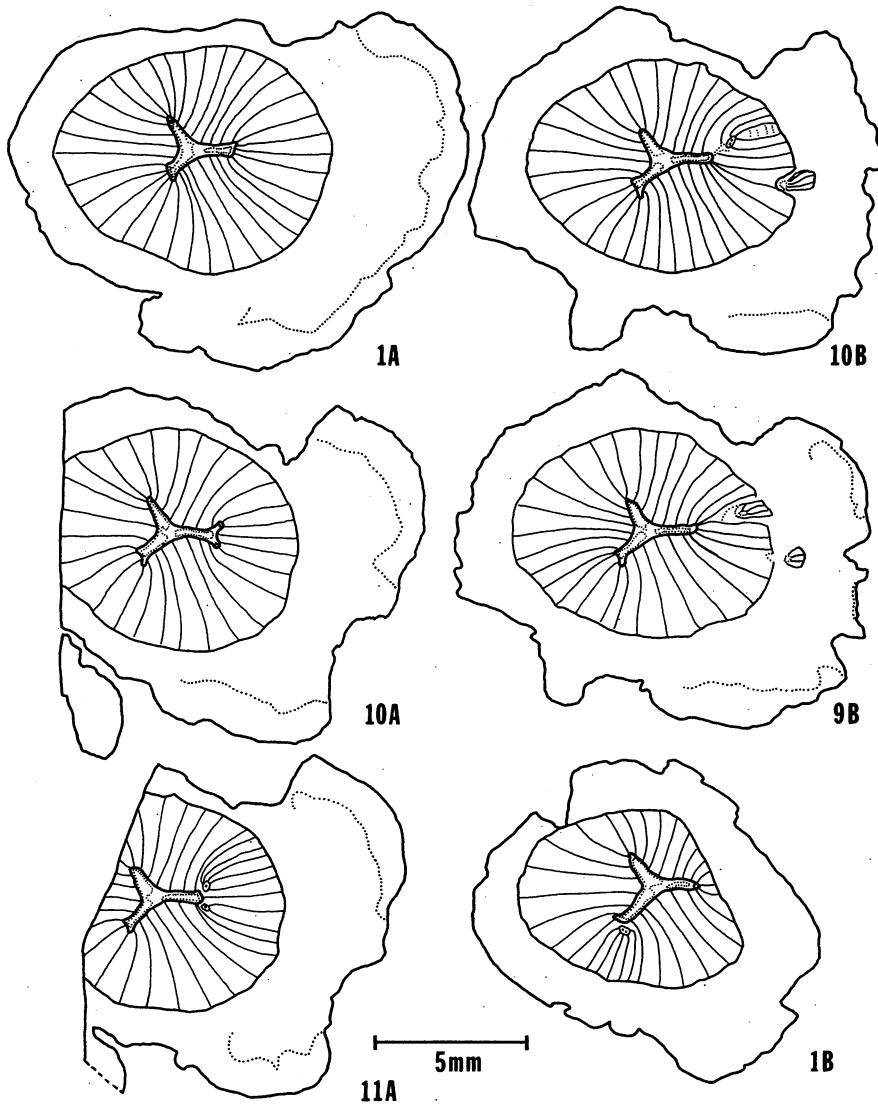
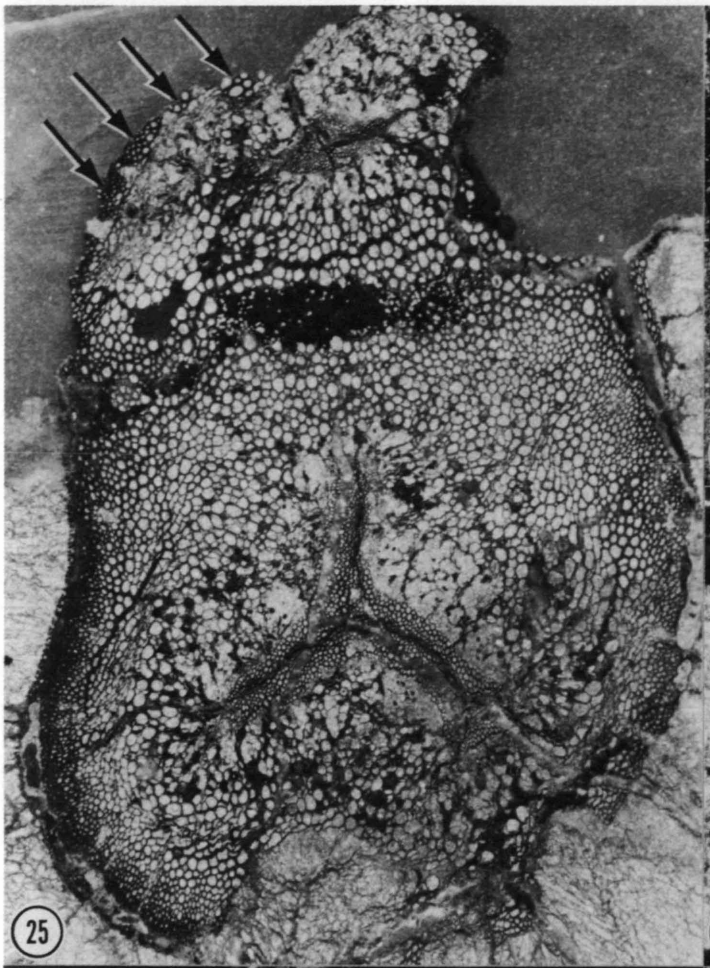
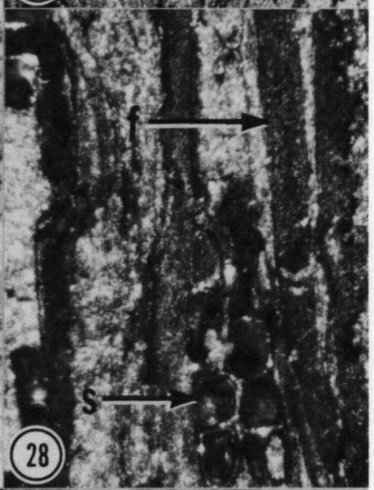


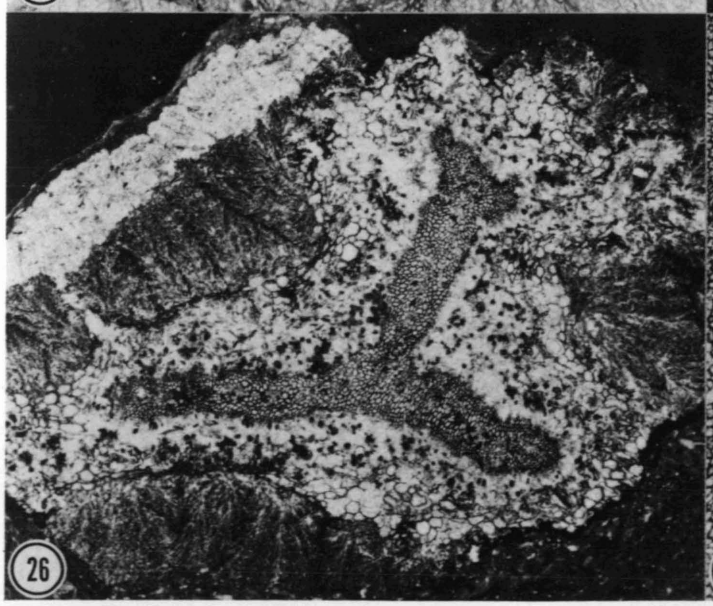
FIG. 24— *Triloboxylon arnoldii.* Serial camera lucida drawings showing trace departure. Proximal section (1A), upper left, and distal section (1B), lower right. Read series from top to bottom starting at the left. UMMP 65131.

FIG. 25-29— *Reimannia aldenense* and *Triloboxylon ashlandicum* (section numbers in parentheses). FIG. 25. *Reimannia aldenense.* Type specimen. Transverse section of first order axis with attached second order axis. Arrows indicate cells with relatively thick cell-walls near the periphery of the second order axis which might be the precursors of fiber-sclereid bundles like those observed in *Triloboxylon arnoldii.* See text for further details. UMMP 16231 (2). X 12. FIG. 26. *Triloboxylon ashlandicum.* Transverse section of main axis showing primary xylem, a narrow inner cortex, and a well developed sclerenchymatous outer cortex. CUPC 151 (1). X 18. FIGS. 27-29. *Triloboxylon ashlandicum.* Sclerenchymatous outer cortex of the specimen shown in Figure 30. CUPC 150. FIG. 27. Longitudinal section. Compare with Scheckler and Banks (1971a, p. 741, figure 19). Arrows indicate the different kinds of cells in this tissue, f = fiber, s = sclereid, p = parenchyma (1L). X 28. FIG. 28. Higher magnification of same region as Figure 27 (with arrows f and s similarly defined). X 110. FIG. 29. Transverse section showing discrete fiber-sclereid bundles separated by regions which probably initially contained thin-walled parenchyma (8). X 28. →


25


f
s
27


f
s
28


26

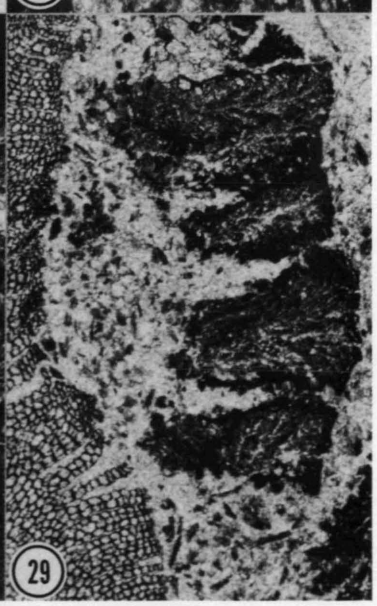
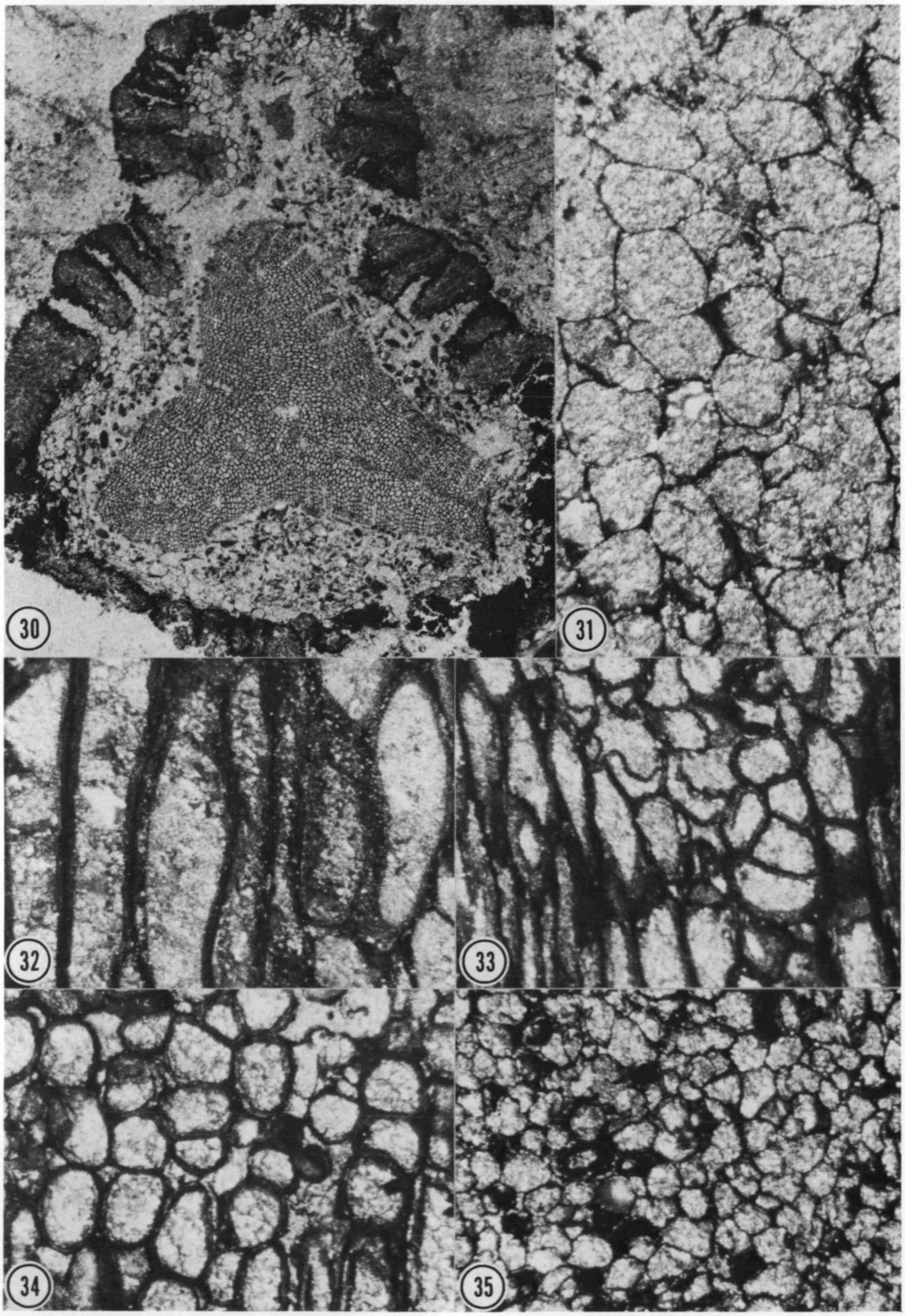

29

FIG. 30-35— *Triloboxylon ashlandicum*, *Reimannia aldenense*, and *Triloboxylon arnoldii* (section numbers in parentheses). FIG. 30. *Triloboxylon ashlandicum*. Transverse section of main axis showing primary and secondary xylem, inner cortex, and fiber-sclereid bundles of the outer cortex separated by poorly preserved regions which probably originally contained thin-walled parenchyma. CUPC 150 (9). X 17. FIGS. 31-35. Comparisons of the cortex in different specimens as observed in longitudinal sections, all X 110. FIG. 31. Inner cortex of *Triloboxylon ashlandicum*, showing short thin-walled parenchyma cells. CUPC 150 (4L). FIG. 32. Cortex of *Reimannia aldenense* showing generally elongate thick-walled cells. UMMP 16231 (10L). FIGS. 33-34. Two views of the cortex in the lateral appendage of *Triloboxylon arnoldii*, showing thick-walled cells, remarkably like those of *Reimannia*, including some which become increasingly elongate toward the periphery. UMMP 23848 (2-9CL, and 1-9CL respectively). FIG. 35. Inner cortex of the main axis of *Triloboxylon arnoldii*, showing a more heterogeneous tissue than in the lateral appendages of the same specimen, comprised of generally smaller cells. UMMP 23848 (11-9CL).


30
31
32
33
34
35

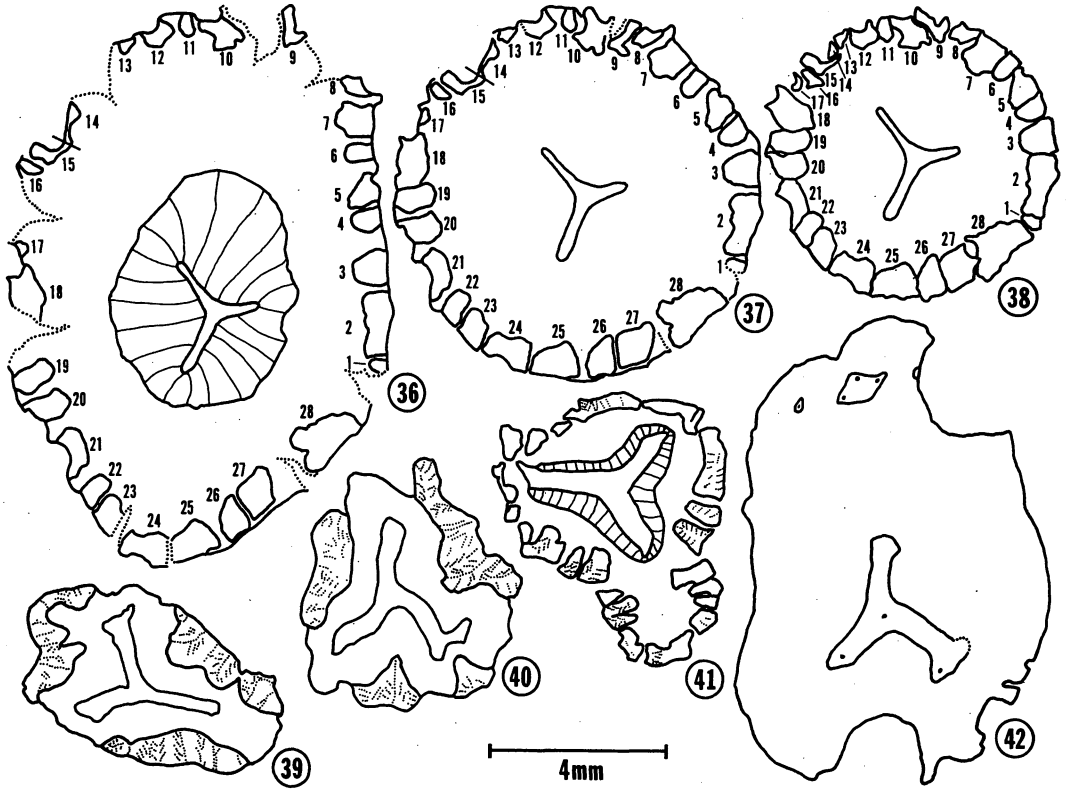


FIG. 36-42 Estimates of secondary growth in *Triloboxylon arnoldii*, and a comparison of sizes of known aneurophytaleans which might serve as a model for the primary body of this taxon. All are camera lucida drawings of transverse sections. See text for details. FIG 36. *Triloboxylon arnoldii* in its present state. The limits of primary and secondary xylem are indicated, and the fiber-sclereid bundles of the outer cortex have been outlined and numbered. Fissures between the plates of more or less intact cortical tissues are indicated by dotted lines. UMMP 23848 (2C). FIG. 37. Estimate of the effect on size of the axis shown in Figure 36 with the cortical fissures removed. Plates of outer cortex have been matched end-to-end and an estimate of diameter derived, assuming a circular cross section, from a measurement of total remaining perimeter. Numbers correspond to those in Figure 36. FIG. 38. Estimate of size of the axis shown in Figure 37 with the ordered parenchyma separating fiber-sclereid bundles removed. The estimate was derived from a measurement of total perimeter of remaining tissues. Numbers correspond to those in Figures 36 and 37. FIGS. 39-40. *Triloboxylon ashlandicum*. Note dense sclerenchymatous outer cortex. CUPC 151 (2, and 18 respectively). See also Figure 26. FIG. 41. *Triloboxylon ashlandicum*. Outer cortex with apparently more discrete fiber-sclereid bundles. Note presence of a small amount of secondary xylem. CUPC 150 (9). See also Figures 27-30. FIG. 42. *Reimannia aldenense*. Type specimen. Axis with an extensive, more or less homogeneous primary cortex, and no secondary xylem. UMMP 16231 (2).