Int. J. Plant Sci. 155(5):606–616. 1994.

1058-5893/94/5505-0013$02.00

VEGETATIVE GROWTH OF EORHIZA ARNOLDII ROBISON AND PERSON FROM THE MIDDLE EOCENE PRINCETON CHERT LOCALITY OF BRITISH COLUMBIA

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Anatomical studies of several thousand specimens of *Eorhiza arnoldii* Robison and Person rhizomes and their attached organs have added significantly to our knowledge of these Middle Eocene, semiaquatic dicotyledonous plants from the Princeton chert. Anatomical structure of *Eorhiza* was studied through serial sections on cellulose acetate peels. In order to establish the growth habit for these plants, individual axes were mapped as to their three-dimensional positions in the chert matrix. Plants grew from an extensive sympodial rhizome system similar to many living monocots and exhibited subopposite branching. Branches gave rise to rhizome sympodia or to branches bearing small scale-leaves. The architecture of *Eorhiza* conforms to the Tomlinson Model proposed by Halle, Oldeman, and Tomlinson. Leaves are ensiform, equitant, unifacial (isobilateral), and monocot-like with a large central lacuna. Rhizomes show typical dicot stelar anatomy. The presence of an aerenchymatous cortex and the plants' association with freshwater animal remains and representatives of known aquatic plant families, such as Nymphaeaceae, support an aquatic habitat for *Eorhiza.* The presence of rhizomes that produce roots bearing secondary and tertiary roots indicates in situ preservation of extensive rhizome systems at least 41 cm in length. A reconstruction of the vegetative body of *Eorhiza* is presented and a hypothesis offered concerning the attachment of reproductive structures to these plants.

Introduction

Eorhiza arnoldii Robison and Person was first described in 1973 as a silicified semiaquatic dicotyledon of unknown affinities from the Eocene Allenby Formation of British Columbia. The original fossil material from the Princeton chert locality consisted of short axes up to 5 cm in length that were interpreted as rhizomes. In addition to reexamining the type specimens, several thousand new specimens (Stockey and Cevallos-Ferriz 1987) allow us to expand our knowledge of the morphology and growth habit of this unusual plant, including an analysis of branching patterns, root production and distribution, leaf morphology, and growth habit.

Robison and Person (1973) originally suggested that *Eorhiza* was a rhizomatous plant from a semiaquatic habitat based on the production of roots from one side of the stem and the presence of an aerenchymatous cortex. Recent research on the Princeton chert plants (Cevallos-Ferriz 1987; Cevallos-Ferriz et al. 1991; Erwin and Stockey 1991; Stockey and Pigg 1991) has revealed that a large number of the plants found in association with *Eorhiza* are representative of known aquatic genera or families. In this article we reexamine the anatomy of *E. arnoldii* rhizomes and provide a detailed description of the vegetative morphology of the plant. We reevaluate the hypothesis that these plants are semiaquatic dicotyledonous rhizomes and present a hypothesis concerning the growth habit of *E. arnoldii.*

Material and methods

Several thousand new axes of *Eorhiza arnoldii* have been identified in the chert. In addition, type specimens were obtained from the University of Michigan Museum of Paleontology (UMMP). All specimens come from the east bank of the Similkameen River, approximately 8.4 km south of the town of Princeton, British Columbia. The locality has been referred to as locality "I" (Boneham 1968) and the "Princeton chert" (Basinger and Rothwell 1977; Stockey 1984, 1987). Chert deposits are part of the Princeton Group, Allenby Formation, and are located 630 m above the Princeton-Black coal seam (Boneham 1968). The Princeton Group has been dated as middle Eocene based on studies of freshwater fishes (Wilson 1977, 1982) and mammals (Russell 1935; Gazin 1953) and by K-Ar dates (Hills and Baadsgaard 1967). Chert blocks were cut into slabs and studied using a modified cellulose acetate peel technique and concentrated (48%) hydrofluoric acid (Basinger and Rothwell 1977; Basinger 1981). Peel sections were mounted in Coverbond xylene soluble mounting medium for microscopic examination.

Because of the large size of *Eorhiza* plants, we also mapped the course of rhizomes within large chert blocks and recorded changes in morphology from face to face in the chert slabs. Our understanding of the plant's growth habit is constrained by the limits of slabbing saw size and our ability to collect, lift, and etch pieces of chert large enough to reconstruct entire plants. Some specimens were mapped with the IBM PC-based Three-Dimensional Reconstruction System (HVEM-3D), version 1.2 (Royer 1988).

Type specimens are housed in the University

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Manuscript received December 1993; revised manuscript received May 1994.

of Michigan Museum of Paleontology (UMMP). All new specimens studied here are housed in the University of Alberta Paleobotanical Collections (UAPC-ALTA).

Results

From the relatively small collection initially studied by Robison and Person (1973) the detailed anatomy of *Eorhiza* axes was described. Since only short sections of the plant (≤5 cm) were available to them, the general morphology and growth habit were not well understood. We will confine our remarks on anatomy in this article to observations that amplify or disagree with those of Robison and Person (1973) and we refer the reader to their original paper for further anatomical details.

RHIZOME ANATOMY AND MORPHOLOGY

Rhizome axes were originally reported as 2.0–3.0 cm in diameter (Robison and Person 1973). We now know that axes can vary from 0.3 to nearly 6.0 cm in diameter. They are characterized by a large parenchymatous pith that is surrounded by a narrow ring of vascular tissues and a broad aerenchymatous cortex (figs. 1, 3–5). The pith of rhizome axes is now known to vary from 0.2 to 3.2 cm in diameter and is composed of parenchymatous cells with simple pits (Robison and Person 1973). Lysigenous cavities are observed throughout the pith and other tissues of the axes (figs. 1, 3, 16, 17). These cavities, probably fungal in origin, are always associated with the presence of hyphae.

The vascular cylinder is narrow, 0.2–2.0 mm thick (figs. 1, 3). Xylem maturation is endarch with helical to reticulate thickenings on the narrow tracheary elements of the primary xylem (Robison and Person 1973). Secondary xylem consists of narrow-diametered vessel elements (50–70 μm) with opposite biseriate and triseriate circular-bordered pits on radial walls. Vessels have scalariform perforation plates with 25–30 bars per end plate (Robison and Person 1973). Fiber tracheids, 16–20 μm in diameter with uniseriate circular-bordered pits, are also present (Robison and Person 1973). Secondary xylem parenchyma is diffuse-scattered. Medullary rays are broad and five to seven cells wide (fig. 7), while vascular rays are from two to many cells high and fit Kribs's (1935) type II-A heterogeneous ray classification. The phloem zone is about 0.4 mm thick (Robison and Person 1973). Primary phloem is associated with groups of thick-walled phloem fibers (fig. 7).

The rhizome cortex varies from 2 to 6 mm wide (figs. 1, 3–5). It is characterized by a distinct zone of aerenchyma 3–5 mm wide (figs. 5, 6) and an outer zone of sometimes radially aligned cells, 0.3–2.5 mm wide, that Robison and Person (1973) interpreted as a rudimentary periderm. This zone varies from four to 20 cells in thickness and shows no evidence of a phellogen. This type of radial arrangement of cells in the outer cortex of stems with an aerenchymatous cortex has been reported by Esau (1965) in aquatic plants. When extensive aerenchyma is present, in *Eorhiza* stems with large air spaces, the area of radially aligned cells can be very small. The smallest rhizomes present show very little aerenchyma (fig. 20).

Robison and Person (1973) report a single layer of epidermal cells with conspicuously thickened outer walls. This layer on close examination is translucent suggesting that it is not cell wall material. We have observed this translucent layer on outer and radial walls and occasionally on the inner walls of the epidermal cells. Cells of the epidermis are often filled with dark brown contents and contrast considerably with the underlying cortical cells.

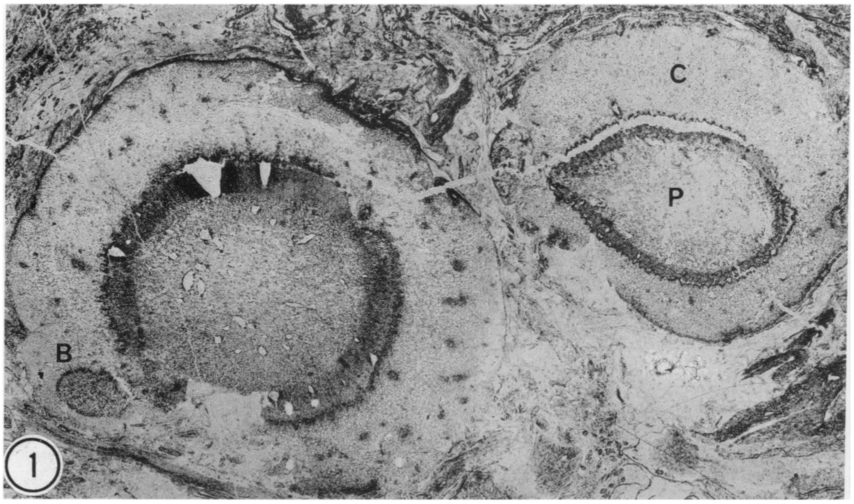
ROOTS

The presence of roots on one side of the stem of *Eorhiza* prompted Robison and Person (1973) to describe it as a horizontal rhizome. In our observations, most stem sections show this type of rooting. However, other stems show roots arising completely around the axis, suggesting that these rhizomes were at least partially recumbent or orthotropic (fig. 3). Stems of this type are usually located at the top of the chert layer (fig. 3). Robison and Person (1973) report as many as seven roots arising at one point on the rhizome axis; we have observed up to nine roots in a single section. Attached roots have also been observed puncturing through the scale leaves that ensheathe the rhizome (fig. 3).

In addition to the roots that are produced at right angles on rhizome axes, both secondary and tertiary roots have been observed in attachment (fig. 2). The presence of these delicate rooting systems strongly suggests that *Eorhiza* plants were preserved in situ.

VEGETATIVE BUDS AND FOLIAGE

Robison and Person (1973) originally reported scalelike leaves that ensheathed the rhizome axes and that covered up to one-third the circumference (figs. 3, 4, 21). The aerenchyma in these ensheathing leaves has larger air spaces than that in rhizomes. Large numbers of leaf traces can be seen in the rhizome cortex (fig. 1). Traces make an arc within the cortex before entering leaf bases (fig. 4). Robison and Person (1973) note the "oblique" orientation of leaf traces in the cortex and their trifurcation to form a large median trace and two small lateral traces near the outer edge of the cortex. From five to six large wedge-shaped vascular bundles and from 10 to 12 small nearly circular bundles are present in each leaf base.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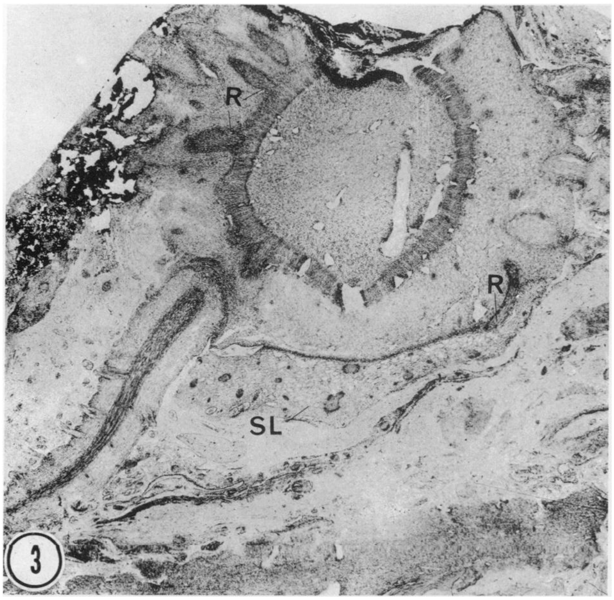
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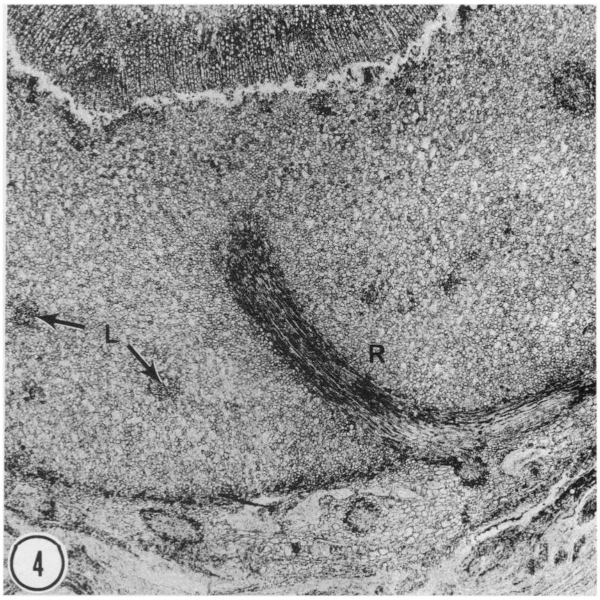
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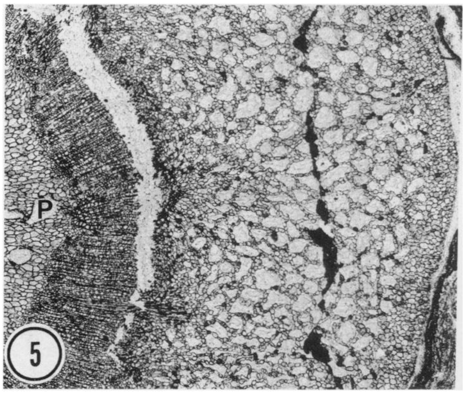
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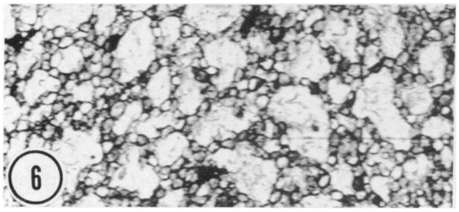
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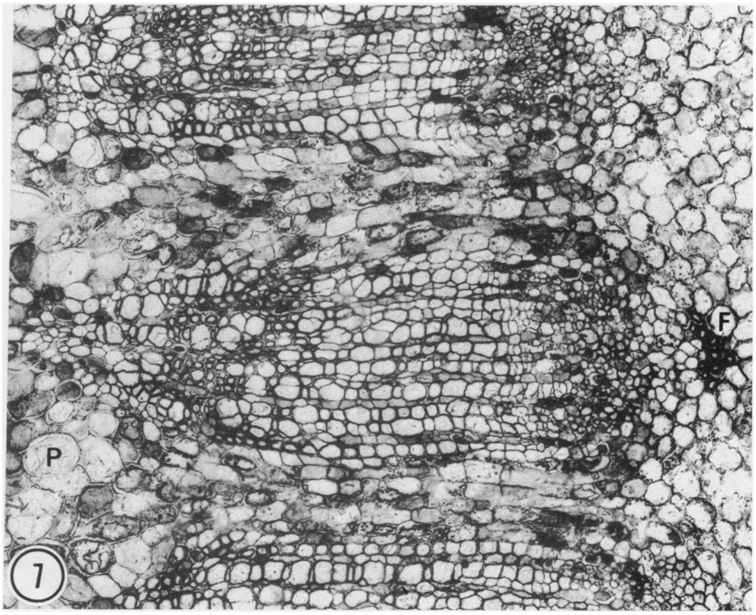
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In addition to these scale leaves we have also identified vegetative buds along the rhizome surface in a large number of specimens (figs. 8, 19). These vegetative buds commonly have from three to four immature leaves attached (figs. 9–11, 15, 21). Leaf bases entirely ensheathe the bud and lack extensive aerenchyma at this stage of development (fig. 9). From their point of origin in the bud, leaves have an abaxial lacuna and an adaxial notch (figs. 9, 10, 15). Leaves are ensiform with an equitant base and unifacial (isobilateral) and medianly flattened lamina like those reported in the Iridaceae (Arber 1925; Dahlgren and Clifford 1982; Rudall 1994). They are, thus, very monocot-like, including the possession of alternating major and minor vascular bundles (fig. 10). The presence of secondary xylem in the major bundles in these leaves, however, differentiates them from monocot foliage in the chert.

The ptyxis, or manner in which the leaves are folded in the bud, is, in the terminology of Dahlgren and Clifford (1982), "supervolute-curved" (fig. 10). They are "conduplicate-plicate" (Dahlgren and Clifford 1982) or equitant-conduplicate (D. R. Kaplan, personal communication, 1994) in transverse section after separation from the bud (fig. 13). The vascular bundle system in these leaves is double, with both adaxial and abaxial bundle series (figs. 10, 12, 14). In more distal sections leaves become slightly crenulate, invaginated or "foliated" as in some monocotyledons (Arber 1925). Leaves retain the abaxial lacuna as far as we have been able to trace them distally (at least 7 cm) (figs. 12–14). Larger and more mature leaves were probably strap-shaped in appearance, and we have observed no evidence for broad leaf laminae or floating blades.

Growth habit

In all of the chert blocks studied by us, rhizomes appeared to be short on first examination, since they could not be traced through large numbers of slabs with certainty. While several rhizomes may be observed in any one large block, rarely did they appear to extend beyond two slabs (about 5 cm). After very careful examination using camera lucida drawings and computer three-dimensional reconstructions (Royer 1988) we were able to follow several extensive rhizome systems, discern patterns in their vertical and horizontal distribution in the rock matrix, and reconstruct the growth habit (fig. 23). Some layers of the chert were better suited to this reconstruction since they are almost exclusively composed of *Eorhiza* rhizomes. Other layers of chert have a large conifer component (*Metasequoia* Miki or *Pinus* L.) and several other types of plant remains, making tracing of the rhizomes difficult. We concentrated on layers 12, 15, and 17 (table 1) of the 49 reported chert layers (Stockey 1987), as these gave us the clearest views of *Eorhiza* as the dominant macrophyte. Layer 15, in particular, shows a series of rhizomes that are consistently buried just beneath what we interpret as the peat surface. The usual depth within the peat was probably 1.5–2.3 cm.

Based on our mapping of axes in the matrix, we now know that *Eorhiza* rhizomes have sympodial growth like that reported in many living monocots (Holttum 1955). These rhizomes are perpetuated by the growth and expansion of axillary branches resulting in a branched rhizome system rather than a single stem. Robison and Person (1973) report branch traces in *Eorhiza* and state that lateral branches are smaller than but structurally identical to main axes. This is true for branches that we now know continue the sympodial rhizome system (figs. 16, 17, 20). Branching is axillary, as is typical of seed plants, and subopposite (figs. 16, 17). Prior to branching we observed that rhizomes increase considerably in diameter over a short distance, the largest rhizomes being those sectioned at a point of branch divergence. At the level of branch divergence we have often observed a single root trace associated with each lateral branch trace (fig. 16). Just after branch divergence, the parent rhizome produces a large number of roots, and shortly thereafter this parent rhizome grows upward and disappears off the edge of the block. Roots at this stage are produced all around the rhizome, probably as prop roots (e.g., as in fig. 3). All rhizomes that disappear vertically off the top of the block first branch and produce roots. Rooting of the rhizome in nonbranching zones is as Robison and Person (1973) described, from one (the lower) side of the rhizome. Rhizome orientation, in fact, can be used to distinguish the top and bottom of

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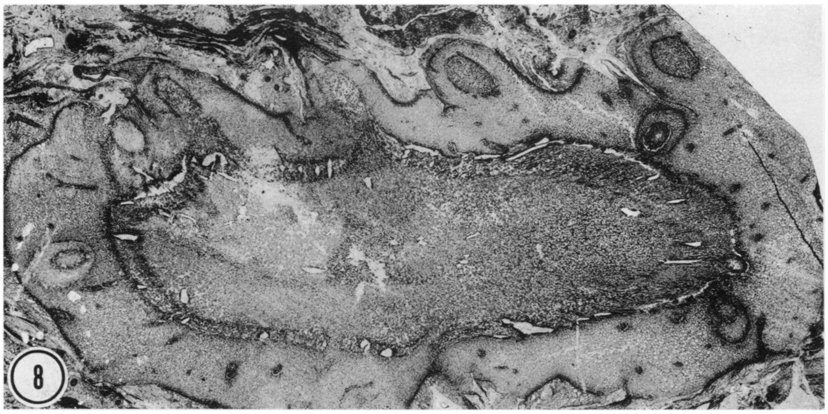
Figs. 1–7 *Eorhiza arnoldii* Robison and Person rhizomes and roots. Fig. 1, Transverse section of rhizomes; one showing a branch trace (*B*). P2610 H top #4; × 2.6. Fig. 2, Transverse section of root giving rise to secondary roots. P2467 F top #60; × 9. Fig. 3, Transverse section of rhizome near top of chert layer showing numerous roots, two of which pierce an aerenchymatous scale-leaf (*SL*). P1777 B bot #2; × 3.2. Fig. 4, Transverse section of rhizome showing vascular cylinder (at top) and broad cortex with leaf and root traces, scale leaf at bottom. P2097 G bot #3; × 10. Fig. 5, Transverse section of rhizome showing aerenchymatous cortex. P 4268 A1 #0; × 10. Fig. 6, Transverse section of rhizome cortex aerenchyma. P4268 A1 #0; × 16. Fig. 7, Transverse section of vascular tissues showing two broad medullary rays and fiber cap of primary phloem. P2097 G bot #3; × 70. *B* = branch, *C* = cortex, *F* = fiber bundle cap, *L* = leaf trace, *P* = pith, *R* = root trace.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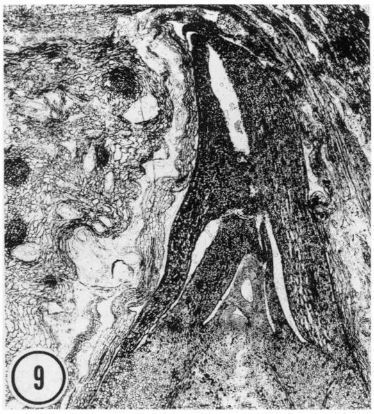
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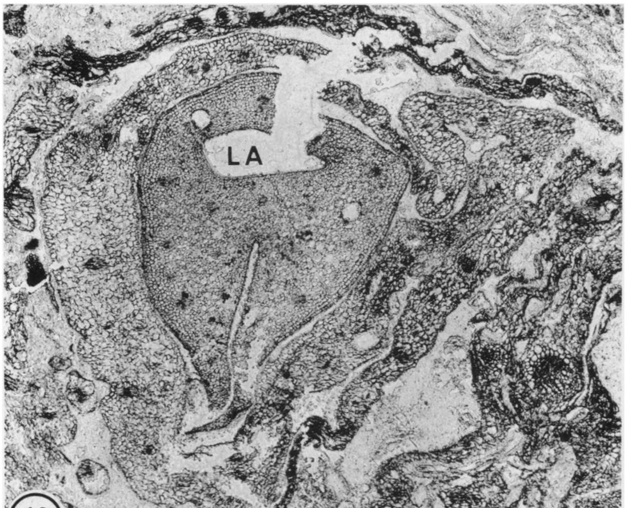
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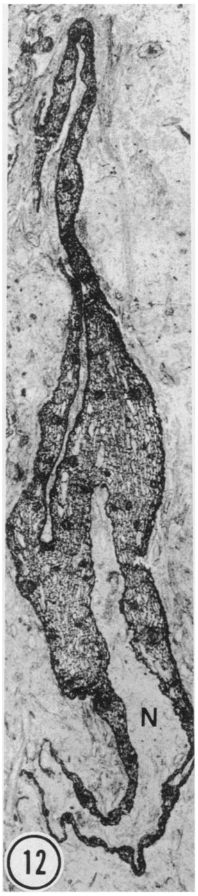
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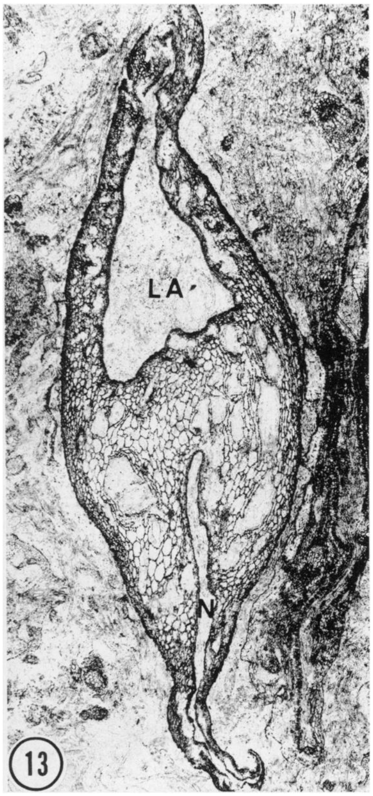
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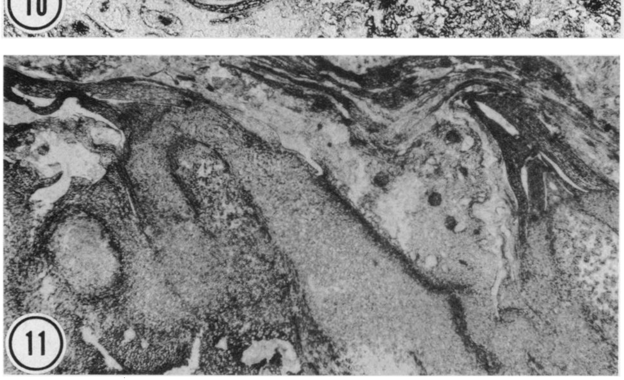
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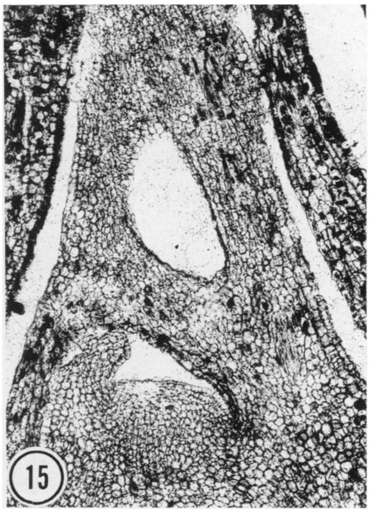
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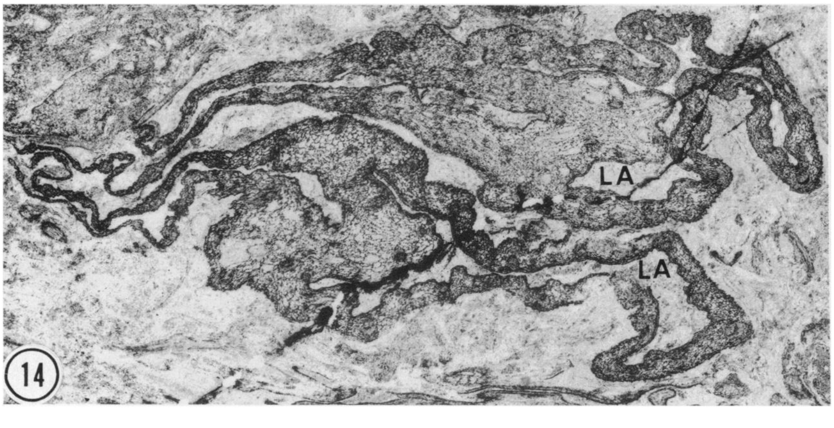
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Table 1

MEASURED AXES OF EORHIZA

Specimen number	Chert layer	Entire rhizome length (cm)	Individual sympodium length (cm)
P 1901	15	Linkage unknown	20.8
			14.0
			17.0
			13.0
P 1903	15	41.0 with 2 branches	28.6 (branch)
			20.0 (branch)
P 1904	15	7.9	
		7.5	
		5.1	
			8.8
			8.4
			7.5
P 2610	17	15.9	
		15.4	
		9.7	
			20.7
P 2489	17	21.2	11.3 (major axis)
			8.7 (branch)
		15.9	13.3 (major axis)
P 6043	12	28.8	15.1 (major axis)
			10.1 (branch)
			13.0 (branch)
		17.7	7.2 (branch)
			7.2 (branch)

Note. Entire rhizome lengths include major axes and any branches. Individual sympodia related to a particular rhizome are designated as to their relationship (major axis or branch).

the chert layer after blocks are brought back to the laboratory.

Lateral branches that extend the sympodial rhizome system are initially small and increase in diameter as they depart at a fairly narrow angle from the parent rhizome (fig. 20). Their overall shape is conical. These sympodia also increase in diameter to the size of the original parent axis and then produce axillary branches. The largest rhizome system that we have been able to trace through one rock is at least 41 cm long and produces two branches (table 1). Another reaches at least 28.8 cm and has two zones of branching resulting in four sympodia (table 1). Sympodia reach lengths of up to 28.6 cm (table 1). Preservation is sometimes a limiting factor in tracing complete rhizome systems, with fungi often associated with poor preservation. In other cases, rhizome systems were cut in the longitudinal plane, i.e., nearly parallel to the long axis of growth. Blocks that were originally sectioned in this manner are very difficult to use for reconstruction but lengths of some sympodia can be calculated from this material.

In addition to branches of the rhizome that continue the sympodial system, we have observed a few lateral branches that also produce small axillary branches (subopposite\-ly) that bear scalelike leaves (figs. 18, 22). The ultimate fate of these lateral branches is unknown.

Discussion

Eorhiza stems show a dicotyledonous anatomy with a broad pith, endarch primary xylem maturation, collateral vascular bundles, a vascular cambium, and a zone of secondary tissue production even in the smallest specimens. They have axillary, subopposite branches that are produced shortly after a considerable increase in stem diameter of the parent axis. The stems also bear

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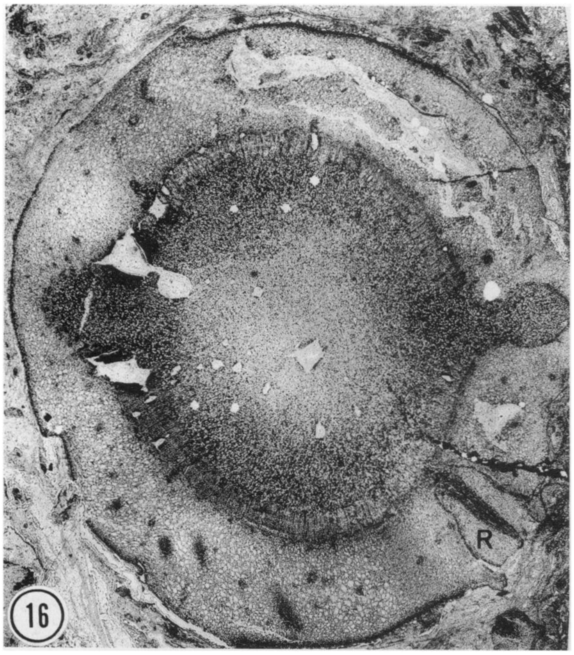
Figs. 8–15 *Eorhiza arnoldii* Robison and Person buds and foliage. Fig. 8, Oblique longitudinal section of rhizome showing several buds on upper surface. P1399 A2 #8; × 2.1. Fig. 9, Longitudinal section of bud on rhizome in fig. 8, showing three ensheathing leaves. P1399 A2 #7; × 12. Fig. 10, Transverse section of ensheathing leaves. P3305 B top #5; × 15. Fig. 11, Longitudinal section of two buds on rhizome in fig. 8. P1399 A #7; × 5. Fig. 12, Transverse section of a broken leaf blade showing notch (*N*) at bottom and lacuna at top. P4117 C #2; × 8. Fig. 13, Transverse section of leaf showing notch (*N*), lacuna (*LA*), and aerenchymatous tissues. P4268 A1 #0; × 11. Fig. 14, Transverse section of two leaves showing notches and lacunae (LA). P2352 B bot #9; × 9. Fig. 15, Longitudinal section of bud showing cells of the shoot apex region, one leaf primordium, and one ensheathing leaf with its lacuna. P1399 A #7; × 70. *LA* = lacuna, *N* = notch.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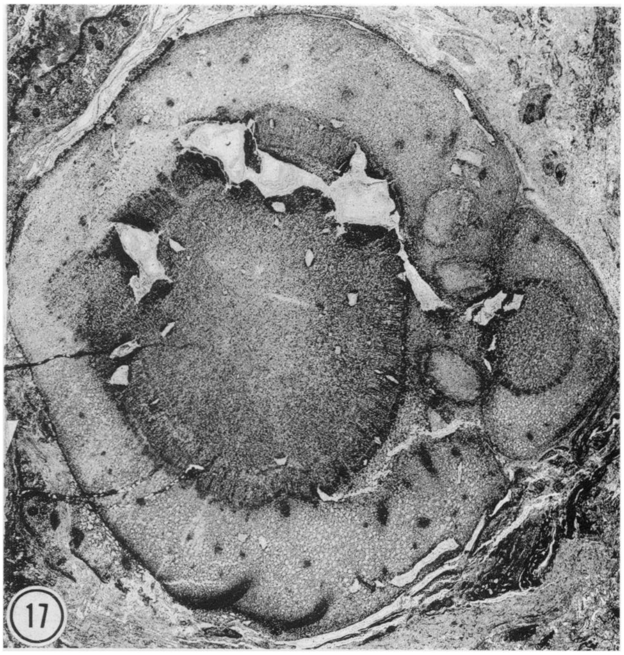
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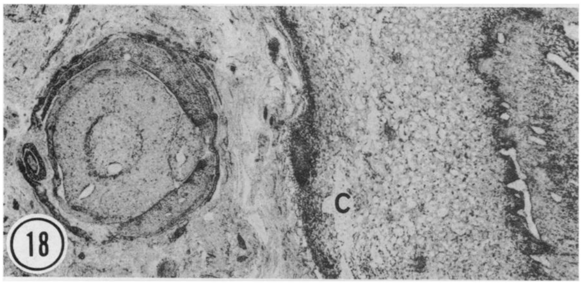
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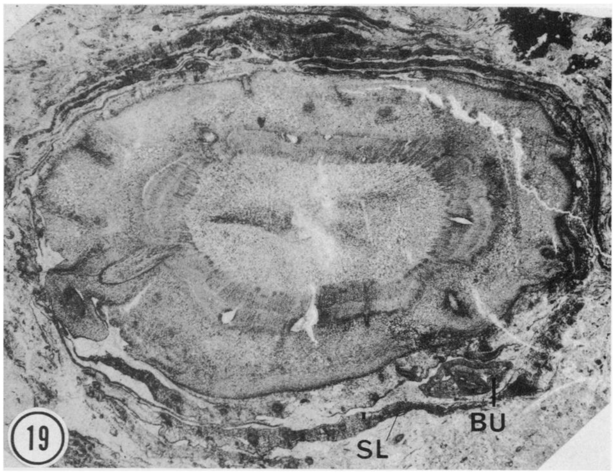
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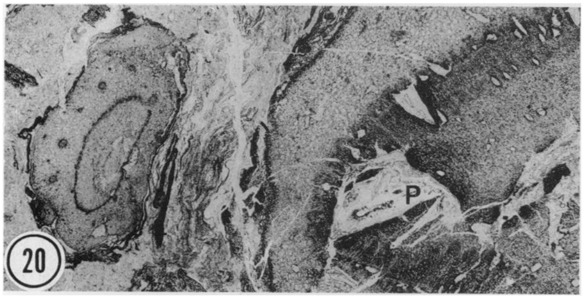
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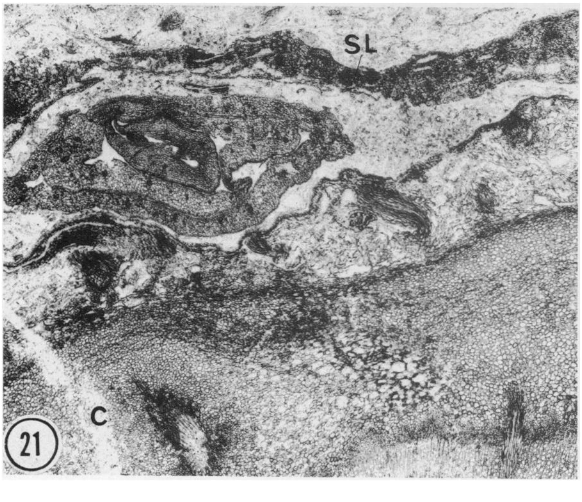
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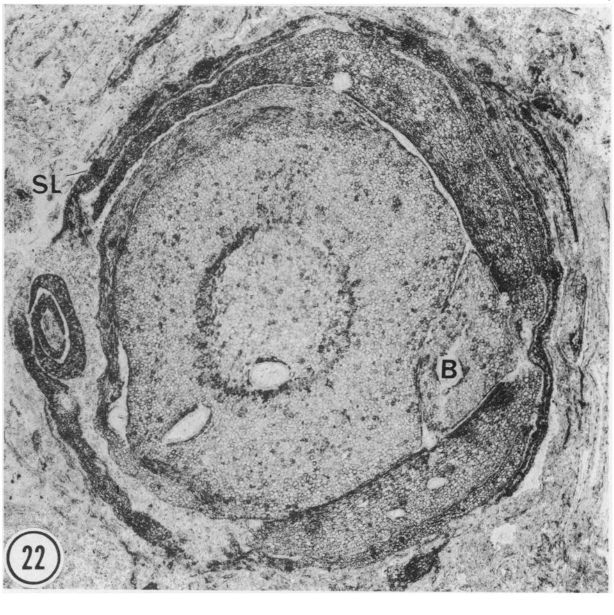
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numerous roots with secondary and tertiary roots and many-veined ensiform leaves that appear foliated in distal sections. These axes were originally interpreted as rhizomes because of their lateral orientation in the chert blocks and their production of roots on one side of the axis (Robison and Person 1973).

It now seems clear that *Eorhiza* was indeed a rhizomatous, dicotyledonous plant with a sympodial growth architecture similar to many monocots (Holttum 1955). The plant body consisted of a series of grown-out axillary branches that became the main axes, resulting in a rhizomatous branching system rather than a single monopodial stem. This type of growth architecture corresponds to the Tomlinson Model proposed by Halle, Oldeman, and Tomlinson (1978) and occurs in such families of monocots as the Heliconiaceae, Zingiberaceae, Cannaceae, and Arecaceae (Palmae) (Tomlinson 1970; Halle et al. 1978). Within the palms, *Euterpe,* which illustrates this model, is typically found in marshy forested areas of intermittent water stress (Halle et al. 1978). This type of growth is also known to occur in the dicots about which Holttum (1955) states, "The majority of these have some cambium development, which allows greater flexibility in growth-habit; the growth-patterns of most such plants are much less precise than among Monocotyledons" (p. 402).

The sympodial system of *Eorhiza* comprises a combination of lateral-growing rhizomatous axes and some occasional upright stems. We see this orientation of rhizomes from the mapping of blocks that have been cut perpendicular to the bedding plane. In many blocks, we have mapped plants that were growing 1.5–2.3 cm below the top of the block prior to fossilization. We interpret this distribution of rhizomes to be close to their natural growth position. After a branching event, where two lateral sympodia diverge suboppositely from the parent rhizome, the parent rhizome turns upward in the chert and usually disappears off the top of the block.

The interpretation of *Eorhiza* as having partially upright axes is further supported by the presence of fiber tracheids in the secondary xylem and by the pattern of root production on rhizomes. Wood with fiber tracheids is unusual in aquatic plants (S. Carlquist, personal communication, 1987) but would presumably provide strength for an upright axis. Single root traces are consistently associated with branch trace divergence. After branching, the parent axis produces prop roots completely around its perimeter (fig. 23).

In addition to the details of rhizome growth, some new interpretations can be made concerning cortical and epidermal anatomy of *Eorhiza.* Robison and Person (1973) reported what they considered to be evidence of a "vestigial periderm with apparently unsuberized cells" in axes. The radial alignment of cells of the outer cortex is confirmed by us; however, we see no evidence of a phellogen. Instead we find that, while many rhizomes with extensive aerenchyma in the cortex have few cells in this outer cortical zone, others have a broad zone of outer cortex. Within single rhizomes cut in transverse section we find both radially aligned and nonradially aligned cells. Esau (1965) reports that the radial alignment of cortical cells in roots of aquatic plants is often associated with the presence of large intercellular spaces or aerenchyma. We suggest that the same is true in the outer cortex of *Eorhiza* rhizomes and interpret these cells as radially aligned primary cortical tissues.

Epidermal cells of *Eorhiza* have been previously described as rectangular with conspicuously thickened outer walls (Robison and Person 1973). This outer layer appears translucent and can be seen covering outer radial and sometimes inner cell walls of the epidermis. This translucent material may be mucilage, and it is similar to a substance interpreted as mucilage on the large lythraceous seeds found in the Princeton chert (Cevallos-Ferriz and Stockey 1988*b*). It is equally possible that this translucent material is cuticular. The presence of waxy cuticles is noted on floating leaves of some aquatic plants (Sculthorpe 1967). Thicker cuticle on submerged organs of aquatic plants also is an advantage if water levels fluctuate. It is quite possible that *Eorhiza* grew in such a situation. The development of large numbers of adventitious roots in a plant such as this would still permit the efficient absorption of water (Sculthorpe 1967) and prevent water loss at times of low water.

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Figs. 16–22 *Eorhiza arnoldii* Robison and Person branching rhizomes and axillary buds. Fig. 16, Transverse section of rhizome showing subopposite branching and root (*R*). P2733 H top #7; × 3. Fig. 17, Transverse section of rhizome showing subopposite branching. P2733 H bot #5; × 3. Fig. 18, Transverse section of lateral branch with ensheathing scale leaves. Parent rhizome at right. P1804 B top #1; × 5. Fig. 19, Transverse section of rhizome showing axillary bud (*BU*). P2674 E bot #7; × 2.5. Fig. 20, Transverse section of small rhizome with parent rhizome at right. P3294 D #19; × 3.4. Fig. 21, Transverse section of axillary bud and subtending scale leaf with parent rhizome below. P2674 E bot #7; × 9. Fig. 22, Small lateral branch showing subopposite axillary branching and ensheathing scale leaves. P1804 B top #1; × 13. *B* = branch, *BU* = bud, *C* = cortex, *L* = leaf, *R* = root.

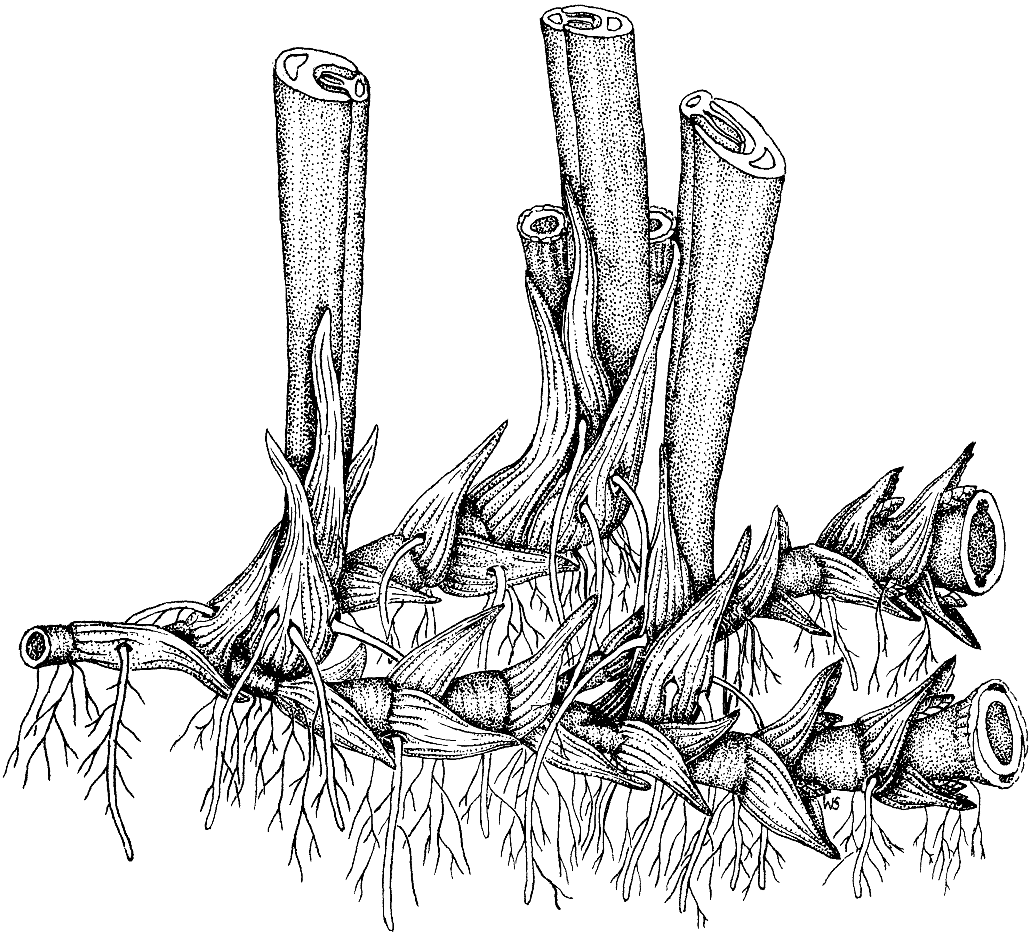

Fig. 23 Partial reconstruction of the sympodial rhizome system of *Eorhiza arnoldii*

The scalelike ensheathing leaves that surround *Eorhiza* axes are also common in many monocot families. Their protective function for monocot stems has been noted by Holttum (1955). However, in *Eorhiza* axes these ensheathing leaves were not fibrous or rigid but mostly aerenchymatous and probably did not afford much protection for rhizomes. Holttum's (1955) suggestion that the common occurrence of leaf sheaths in the monocots is "an adaptation directly related to the lack of a cambium" does not seem supported by our study of *Eorhiza* plants that have both leaf sheaths and a vascular cambium.

Vegetative buds on *Eorhiza* rhizomes are very similar in appearance to those described for many monocots, e.g., *Iris* (Arber 1925, figs. lxxx, 5). Conduplicate-plicate ptyxis, characteristic of *Eorhiza,* also occurs in the Liliales, Iridaceae, and some Asparagales (Dahlgren and Clifford 1982); in the bud, *Eorhiza* leaves are most similar in shape to *Tritonia* (Iridaceae). The characteristic abaxial lacuna is similar to that of *Sisyrhinchium* (Iridaceae); however, the vasculature differs in that *Eorhiza* leaves have two series of vascular bundles, one adaxially and one abaxially oriented. At more distal levels, *Eorhiza* leaves become slightly foliated or folded. No septations or other indications of blade suppression, as occurs in some dicots with similar appearing leaves (Kaplan 1975), have been observed.

This type of ensiform leaf with an equitant base and an isobilateral lamina is very similar to many Iridaceae (Rudall 1994); however, as Dahlgren and Clifford (1982) point out, this leaf type occurs scattered throughout unrelated monocot families and probably evolved independently many times. Its presence in the dicot *Eorhiza* indicates that this leaf type may have evolved independently in the dicots as well. Arber (1925) cites several dicots with monocot-like leaves and some that also lack laminae. Only one of these, *Oxalis,* contains aquatic species, and these plants have slender floating stems with leaves that arise from a bulb (Cook 1990). However, the "leaves" in *Oxalis* have been shown to be "phyllodes" in a "petiolar derivative sense" (D. R. Kaplan, personal communication, 1994) and, thus, are not homologous with the leaves of *Eorhiza.*

In addition to lateral branches that continue the sympodial rhizome system, small branches are present that themselves bear subopposite branches, with each resulting axis bearing scale-leaves. We suggest that they may prove to be floral axes. Some groups of monocots, e.g., the Zingiberaceae, reportedly have flowering axes that bear only scale-leaves while others bear inflorescences on leafy shoots (Holttum 1955).

Evidence that *Eorhiza* rhizomes are found in situ (in growth position) comes from several sources. First, *Eorhiza* roots are some of the most common organs found in the chert. Roots bearing delicate secondary and tertiary roots, attached to rhizome axes, further suggest that these plants were preserved in situ in the peat. Second, the degree to which we can trace these extensive rhizome systems (some up to 41 cm) would indicate that the plants preserved here are relatively complete and could not have been transported any great distance without becoming more fragmented. Third, the growth position of the rhizomes within the chert blocks is consistent with their in situ preservation.

Evidence of an aquatic or semiaquatic habitat for *Eorhiza* and many of the other Princeton chert plants comes from three sources: the presence of anatomical features indicative of aquatic habitats; affinities of the plants with those of known aquatics; and the association with animal remains (Cevallos-Ferriz et al. 1991). The presence of turtle bones silicified in the chert layers (R. C. Fox, personal communication, 1986) along with the plants, as well as those of a soft-shelled turtle in the shales immediately above the chert zones (J. Gardner, personal communication, 1993) and the freshwater fish *Amia* (Wilson 1977, 1982) strongly suggest a permanent shallow freshwater lake or pond as the probable habitat. Association of *Eorhiza* rhizomes with seeds of *Allenbya collinsonae* (Nymphaeaceae) (Cevallos-Ferriz and Stockey 1989), *Keratosperma allenbyensis* (Araceae) (Cevallos-Ferriz and Stockey, 1988*a*), and *Decodon allenbyensis* (Lythraceae) (Cevallos-Ferriz and Stockey 1988*b*) also indicates the edge of a shallow water system.

The presence of extensive aerenchyma in the rhizome and leaves of *Eorhiza* is also indicative of an aquatic habitat (Sifton 1945, 1957; Williams and Barber 1961; Sculthorpe 1967). The large honeycomb-like system similar to that in the cortex of *Eorhiza* has been suggested to provide strength with the least amount of tissue (Williams and Barber 1961; Esau 1965). The presence of a large air lacuna in the leaves of *Eorhiza* further indicates that they were at least partially submerged.

In growth habit *Eorhiza* also demonstrates a remarkable similarity to *Acorus* L. (Cook 1990). Both plants have unifacial, medianly flattened leaves and a horizontal rhizome bearing small scale-leaves that are punctured by roots (Kaplan 1970). These plants are also similar anatomically, with broad parenchymatous and aerenchymatous ground tissue (Ogden 1974). In contrast to *Eorhiza, Acorus* rhizomes have amphivasal vascular bundles and lack secondary tissues. However, *Eorhiza* has a bifacial vascular cambium and secondary tissues in the major leaf bundles.

Recent phylogenetic analyses of the monocots using molecular data (Chase et al. 1993; Duvall et al. 1993) have supported a basal position among monocots for *Acorus calamus* L. Although *Acorus* has previously been classified in the Araceae on the basis of its apparent similarities with *Gymnostachys anceps* R. Br., a number of authorities (e.g., Grayum 1987) have suggested that it would be better classified in its own monotypic family. Given the morphological and anatomical similarities between *Eorhiza* and *Acorus,* it would be interesting to speculate a possible connection between these taxa; however, more rigorous analysis of the phylogenetic position of *Eorhiza* awaits the description of its reproductive remains.

We now know a great deal of information on the growth and morphology of the vegetative body of *Eorhiza arnoldii.* Plants grew from a sympodial rhizome system similar to many living monocots and exhibited subopposite branching. Branches gave rise either to rhizome sympodia or to branches bearing small scale-leaves. Foliage leaves arose from axillary buds on the rhizome system and leaves with ensheathing bases were similar to the ensiform equitant unifacial (isobilateral) foliage of some monocots. While growth habit and leaf morphology were monocot-like, rhizome axes show typical dicot anatomy.

On the basis of number and size of specimens, *Eorhiza* was clearly a dominant plant in the aquatic habitat represented in the Princeton chert. The ubiquity of this taxon in the chert suggests that *Eorhiza* may have grown in near monotypic stands like many aquatic plants today.

Acknowledgments

We thank Sergio R. S. Cevallos-Ferriz, UNAM, Mexico City, for help in specimen preparation; Charles B. Beck, University of Michigan Museum of Paleontology, for the loan of the type specimens; Gar W. Rothwell, Ohio University, Athens, for technical assistance and use of laboratory facilities; and Donald R. Kaplan, University of California, Berkeley, who read an early draft of the manuscript. The reconstruction in figure 23 was kindly rendered by Wilson N. Stewart. Supported in part by the Natural Sciences and Engineering Research Council of Canada (NSERCC) grant A-6908 to Ruth A. Stockey, NSERCC-ICR grant to Ruth A. Stockey, NSF-NATO Postdoctoral Fellowship RCD-885474 to Kathleen B. Pigg, and NSF grant BSR-9006625 to Kathleen B. Pigg.

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