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PALEOZOIC SEED FERNS: HETERANGIUM KENTUCKYENSIS SP. NOV., FROM THE UPPER CARBONIFEROUS OF NORTH AMERICA[1]

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ABSTRACT

Heterangium kentuckeyensis sp. nov. is described from Lower/Middle Pennsylvanian sediments of eastern Kentucky, based on permineralized stems, petioles, frond members, laminar foliage, and roots, including several organs in attachment. Stems 2.2 to 5.8 mm in diameter are known in several developmental stages. The considerable variability in stelar and cortical histology within this one species emphasizes the need to reassess variability within previously described taxa. Fronds of *H. kentuckyensis* are at least twice pinnate and bear primary pinnae alternately at approximately right angles. Laminar pinnules have dichotomous venation, are at least 2-lobed, and comparable to foliage of the *Sphenopteris*-type. Stomata possess 6–7 subsidiary cells with abaxial papillae. The characters used to distinguish the subgenera of *Heterangium* are evaluated and found to be unreliable. Moreover, suggested phylogenetic schemes both within *Heterangium* and between this taxon and other lyginopterid pteridosperms based on these features are inconsistent with stratigraphic data. Until reproductive features are known, the classification of *Heterangium* species is best based on characters of the vegetative sporophyte, including stelar organization (particularly protoxylem architecture), cortical histology, and frond morphology.

THE GENUS *Heterangium* Corda represents one of the most extensively studied lyginopterid pteridosperms. Stems of *Heterangium* are well known from several European localities (Scott, 1917; Phillips, 1981) including both the British Coal Measures (e.g., Williamson, 1873, 1877; Williamson and Scott, 1895; Scott, 1917), and continental sites (e.g., Renault, 1893, 1896; Kubart, 1911, 1914; Hirmer, 1933). British species, especially *H. tiliaeoides* Williamson and *H. grievii* Williamson formed the basis for some of the earliest and most detailed paleobotanical studies (e.g., Williamson, 1873, 1877; Williamson and Scott, 1895; Scott, 1917). Among continental forms, the most completely known taxon is *H. kukuki* Hirmer, the stelar structure of which has been reviewed in detail (Hirmer, 1933; Beck, Schmid and Rothwell, 1982). The two species recognized from North America are *H. americanum* Andrews, from numerous localities of Middle to Late Pennsylvanian age (Andrews, 1942; Phillips, 1981), and *H. lintonii* Stidd from the Middle Pennsylvanian of Indiana (Stidd, 1979). In addition, Jennings (1976) described specimens of *Heterangium* sp. from the Upper Mississippian (Chester Series) of the Illinois Basin, which he suggested resembled *H. grievii,* but which lacked sufficient diagnostic detail to equate the forms.

Although stems of *Heterangium* have long been recognized from Carboniferous strata, little information is known about the biology and variability of these plants. Taxa traditionally have been classified in an artificial system based on stelar features and leaf trace divergence (Scott, 1917; Hirmer, 1933; Stidd, 1979), but relatively little is understood about the relationships of the other disarticulated organs of the vegetative sporophyte. Reproductive organs have not been found attached, and the architecture of the frond is known only for one anatomically preserved form (Shadle and Stidd, 1975).

A large collection of permineralized organs from the Lewis Creek, Kentucky, coal ball locality provides the opportunity to recognize a

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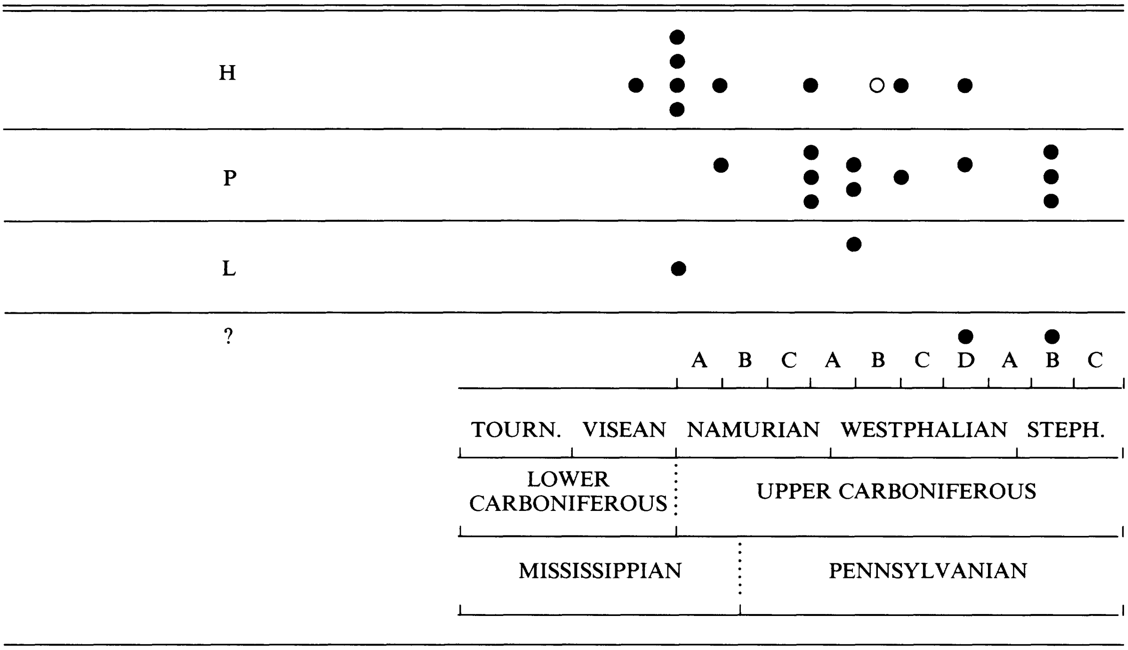
TABLE 1. *Stratigraphic occurrences of species of* Heterangium, *as represented by Subgenus. H = Subgenus* Heterangium, *P = Subgenus* Polyangium, *L = Subgenus* Lyginangium, *? = Subgenus Unknown, 0 = Lewis Creek locality. Data modified from Hirmer (1933), Stidd (1979), and Phillips (1980)*

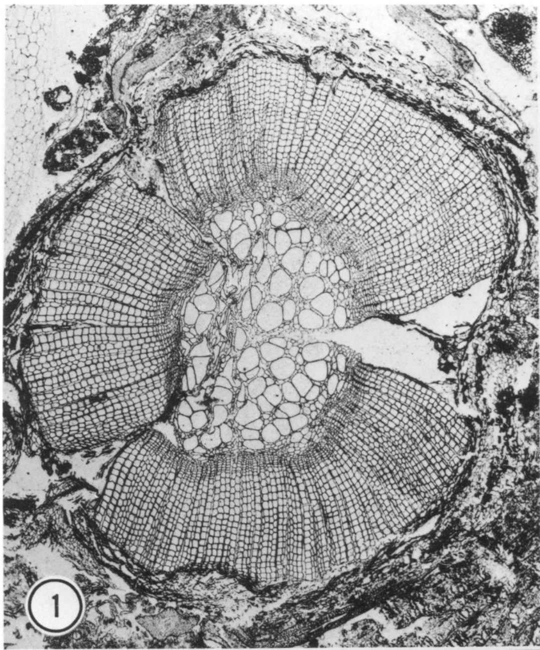


new taxon. The description that follows is based on stems, petioles, frond members, laminar foliage, and roots, including several organs which are organically attached. The taxon represents the most completely characterized species of *Heterangium* to date and adds substantial information about an important member of the lyginopterid seed fern complex.

MATERIALS AND METHODS—A total of 60 specimens, including stems (25 specimens), petioles (9), frond members (17), laminar pinnules (6), and roots (3) were found in coal balls from the Lewis Creek, Kentucky, locality (Table 1). Stratigraphically the locality is considered as either uppermost Lower Pennsylvanian (Good and Taylor, 1970) or lowermost Middle Pennsylvanian (= Westphalian B, Phillips, 1980).

Cellulose acetate peels were prepared with critical sections mounted on microscope slides. Foliage was uncovered using a modification of the "microjackhammer" technique (Rothwell, 1980). Surfaces were gradually uncovered with a Vibro-Graver electric engraver (Model 74, Acme Burgess, Inc., Grayslake, IL) equipped with a carbide tip, while alternately wetting and drying the specimen to weaken the matrix. A serial sequence of pulls was prepared from surfaces to study laminar frond segments. Cuticles of the foliage were macerated from the matrix using 2% hydrochloric acid, washed and mounted on double-sided tape for SEM examination. Slides and peels of *H. kentuckyensis* are stored in the Paleobotanical Collections, Ohio State University, under acquisition numbers 13,840–13,854; 17,269–17,439, and in the Paleobotanical Herbarium, Ohio University, under acquisition numbers 8187–8237.

SYSTEMATIC SECTION—*H. kentuckyensis* sp. nov., Pigg, Taylor et Stockey. *Diagnosis*—Stem 2.2–5.8 mm in diameter with stele 0.7–3.0 mm in diameter; central stelar region with large metaxylem tracheids interspersed with ground tissue of varying amounts of thin-walled parenchyma, transfusion tissue-like elements with scalariform to reticulate wall thickening patterns, tabular cells with sclariform thickenings, and sclereids. Protoxylem strands mesarch near margin of stele, not easily distinguished. Wall thickening patterns annular or helical in protoxylem and small peripheral metaxylem strands; multiseriate bordered pits on large metaxylem elements. Secondary xylem up to 26 cells thick with numerous uniseriate rays, tracheids small with conspicuous circular-bordered pits on radial walls; secondary phloem represented by narrow zone of crushed, radially aligned cells. Primary cortex with inner zone of large thin-walled parenchyma and scattered resinous cells, and middle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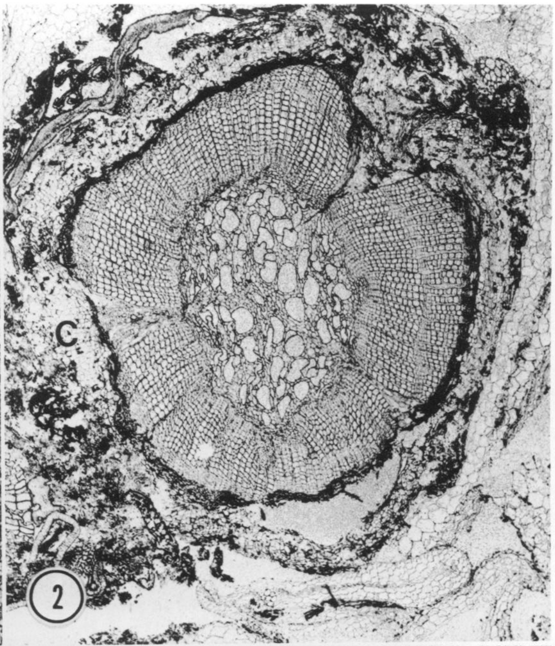
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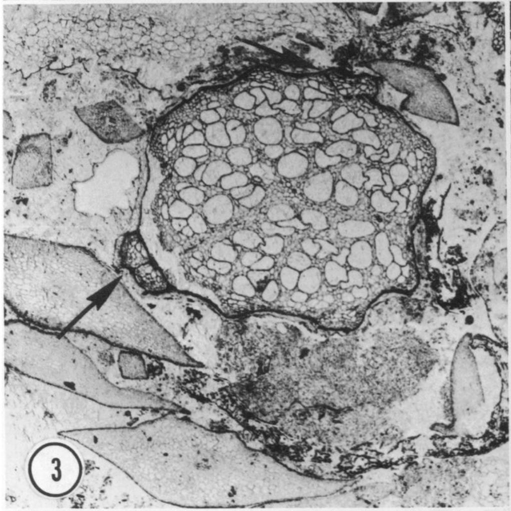
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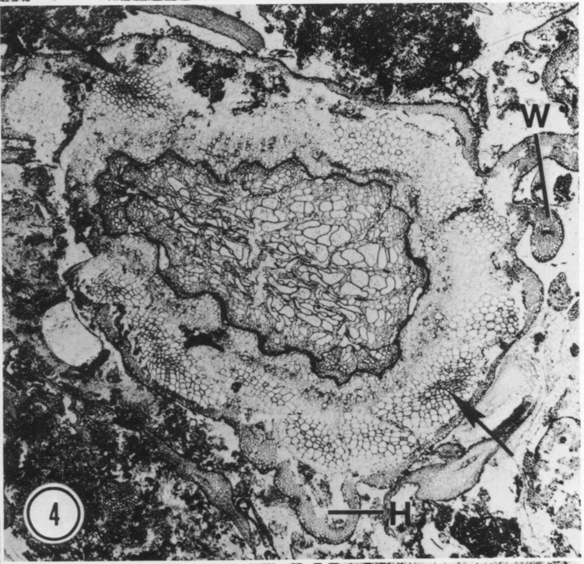
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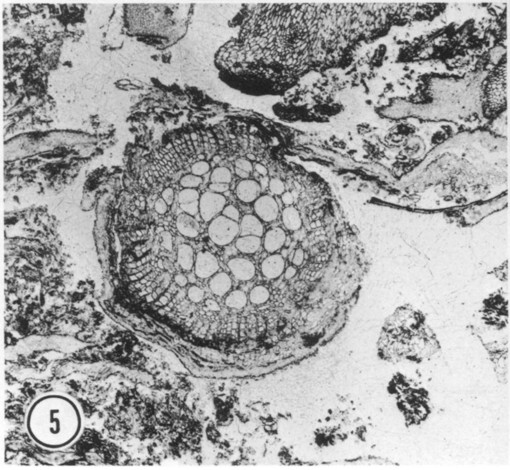
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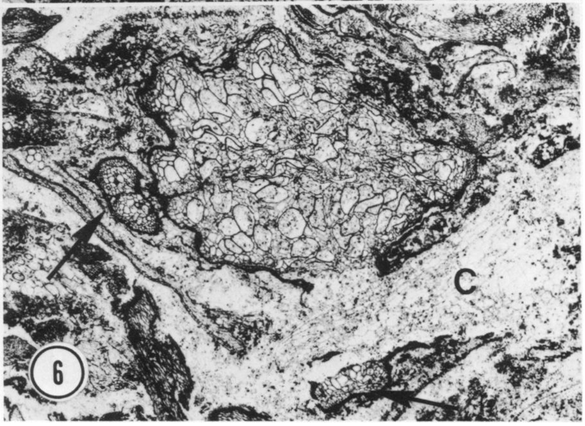
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zone of parenchyma often containing isolated secondary cortical plates or sclerotic nests of tangentially oriented groups of ca. 20 cells; periderm narrow (5–7 cells thick) on largest stems. Hypodermis of compact, isodiametric-rectangular cells and epidermis of large tabular cells with dark contents. Outer margin of stem sometimes irregular with wing-like extensions of tissue. Petiole trace single and bilobed, or double, arising from one area at margin of stele, trace becoming either double or four-stranded (two bilobed strands) at margin of stele or upon entering alate petiole base. Fronds at least twice pinnate; petioles up to 9.3 mm × 2.8 mm wide in transverse section with 4–6 vascular bundles, distal sections of rachis ca. 3 mm × 3 mm wide, each with 3–6 vascular bundles; primary pinnae diverging from main rachis alternately, at approximately right angles, primary pinnae from 1–2 mm wide in transverse section, intermediate foliar members with adaxial, conspicuously grooved projection. Histological features of frond like those of stem. Laminar pinnules of the *Sphenopteris*-type, at least 2-lobed, up to 1.2 mm wide with dichotomous venation, laminae up to 0.4 mm thick in region of midrib, 0.1 mm thick laterally, thickening to 0.2 mm at areas of lateral veins. Trace to pinnule midrib ovoid; mesophyll undifferentiated, thin-walled, parenchymatous, central zone of large resinous cells; pinnules hypostomatic, guard cells thickened, 15 μm wide, 49 μm long; stomata encircled by ring of 6–7 subsidiary cells; blunt, tapering papillae, each about 18 μm wide, 22 μm long, overarching stomata, with 6–7 papillae irregularly grouped around each stoma. Roots up to 1.5 mm in diameter, with diarch primary body 250 μm long; secondary xylem up to 1 mm thick, parenchymatous cortex with scattered resinous cells; thin zone of periderm to periphery.

Holotype—Specimen A (stem with attached petiole bases, showing diagnostic histological features) in coal ball 1781. Figure 6; acquisition number 17,272, in the Paleobotanical Collections, Ohio State University.

Paratypes—Additional specimens of stems and foliage in the following coal balls: OU294, OU330, OU344, OU387, 1446, 1665, 1701, 1737, 1781, 7616, and 8582. Specimens with the prefix OU represent material borrowed from Ohio University collections; unprefixed numbers represent coal balls from Ohio State University. These comprise the remainder of figured specimens and together illustrate features of taxonomic value. Slides are deposited in the Paleobotanical Collections, Ohio State University (acquisition numbers 13,840–13,842; 17,269–17,284) and the Paleobotanical Herbarium, Ohio University (acquisition numbers 8187–8191).

Etymology—The specific epithet, *kentuckyensis,* indicates the location of the Lewis Creek coal ball locality in Leslie County, Kentucky, the source of all specimens described herein.

DESCRIPTION—*Stems*—Stems of *H. kentuckyensis* exhibit a range of variability which includes specimens of differing ontogenetic stages, histology, and degrees of preservation. Including secondary xylem and cortical tissue, the largest stem is 5.8 mm in diameter (Fig. 2), while the smallest is 2.2 mm (Fig. 5). Steles vary from 0.7 mm to about 3 mm in diameter. The stele is best described as a mixed or vitalized protostele, sometimes appearing wedge-shaped in transverse section, due to crushing (e.g., Fig. 4, 6). Wedges of the stele of *H. kentuckyensis* do not represent distinct features delimited by parenchymatous plates as in *H. kukuki* (Hirmer, 1933) or *Microspermopteris aphyllum* (Taylor and Stockey, 1976). Anatomical features of the stele are highly variable. As is characteristic of *Heterangium,* the stele includes large metaxylem tracheids interspersed with small parenchymatous cells. The large metaxylem tracheids (up to 127 μm in diameter) often appear paired (Fig. 1, 5) or clustered in small groups of 4 or 5, however, groups are not delimited as regular packets as in *H. shorense* (Scott, 1917) or surrounded by regular rings of ground tissue as in *H. americanum* (Andrews, 1942).

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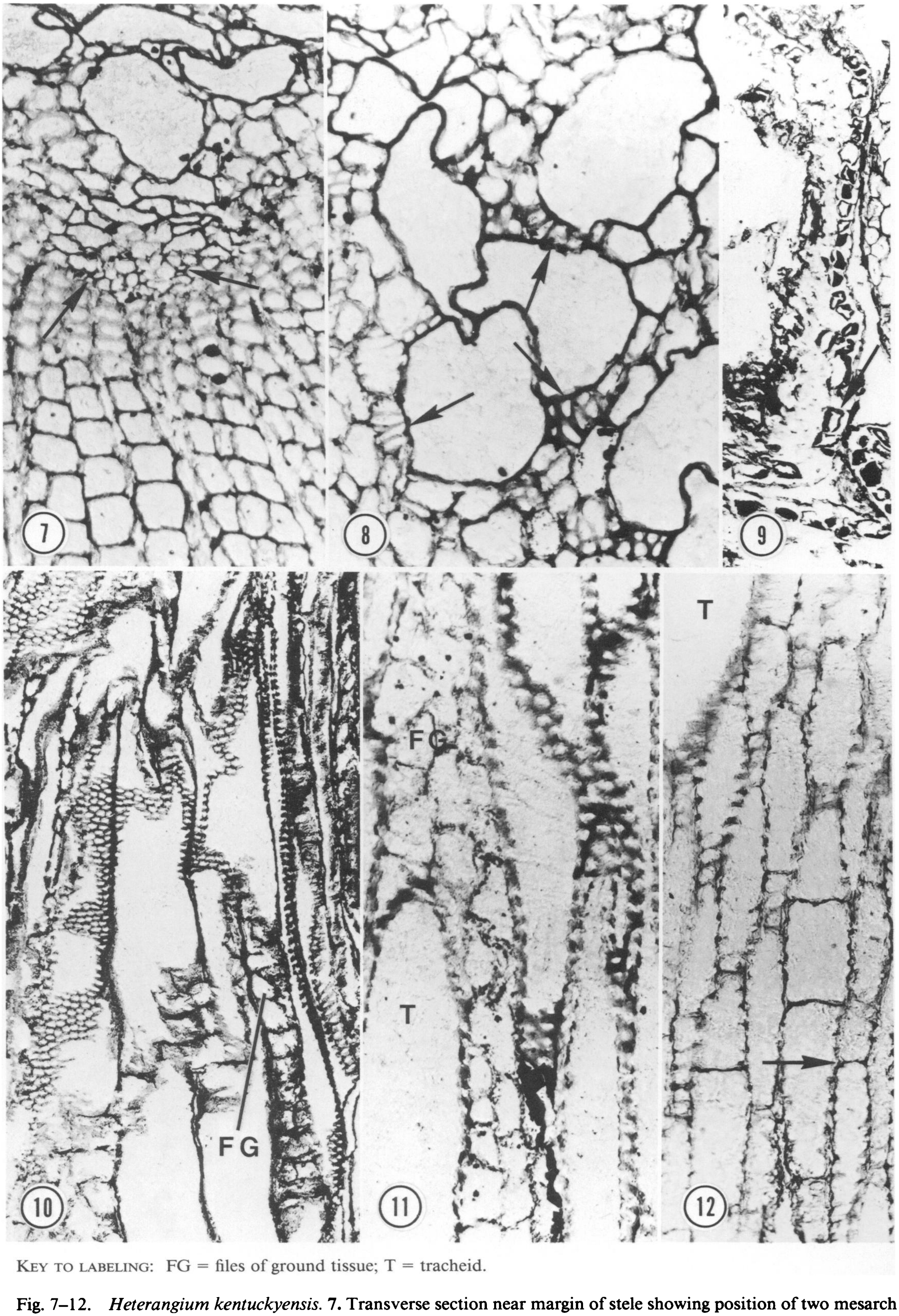
KEY TO LABELING: C = cortex; H = hypodermis; W = epidermal wing.

Fig. 1–6. *Heterangium kentuckyensis.* Transverse sections of stems to show anatomical variability. **1.** Stem with broad zone of secondary xylem. 1446 C_2 top, #20. ×12. **2.** Large stem with secondary xylem and cortex (C). 1665 F top, #60. ×12. **3.** Stele lacking secondary xylem. Note single bilobed leaf traces (at arrows). 1701 D top a, #1. ×15. **4.** Stem lacking secondary xylem with well developed cortical tissue containing sclerotic nests (arrow), hypodermis (H) and cortical wings (W). OU 387 A bottom, #2. ×11.5 **5.** Stem with small amount of secondary xylem, similar in appearance to *H. lintonii.* OU 294 E top, #5. ×16. **6.** Stem lacking secondary xylem. Note bilobed leaf trace and thick cortex (C). 1781 C bottom a, #11. ×16.



KEY TO LABELING: FG = files of ground tissue; T = tracheid.

Fig. 7–12. *Heterangium kentuckyensis.* **7.** Transverse section near margin of stele showing position of two mesarch protoxylem strands (arrows). 1665 F bottom, #17. ×110. **8.** Higher magnification of transverse section of central region

Although it may appear uniform in transverse section, stelar parenchyma is quite variable. Most commonly, in steles of *H. kentuckyensis* metaxylem tracheids are interspersed with relatively isodiametric parenchymatous cells (Fig. 7, top), which superficially appear to be randomly arranged. However, on close examination, the ground tissue is seen to be more ordered. In longitudinal section individual groups of cells occur in elongate, fusiform files (Fig. 10, 11). In stems where the metaxylem tracheids are more widely expanded, these files are offset and appear almost crescent-shaped (Fig. 10). When several metaxylem elements are in close proximity, the resulting stelar parenchyma appears disorganized, depending on the plane of section (Fig. 11). Still other specimens that have a typical *Heterangium* appearance in transverse section (e.g., Fig. 3) contain rectangular cells of the ground tissue with scalariform secondary wall thickenings on their lateral walls (Fig. 12).

Other histological variations occur that are more immediately striking in transverse section. In some stems (i.e., Fig. 5), medullary ground tissue is composed of thick-walled parenchyma while in other cases, individual cells may take on the appearance of transfusion tracheids (Fig. 8). These cells are obliquely oriented and have reticulate-scalariform wall thickenings. In still other stems, a stellate-shaped region of thick-walled sclereids occurs in the central region of the stele (Fig. 13, 15). Individual cells of this tissue resemble stone cells, or brachysclereids (Esau, 1977, fig. 6.1A, B) and have thick walls with simple or branched pits (Fig. 15).

Near the periphery of well-preserved steles protoxylem strands are mesarch and relatively inconspicuous (Fig,. 7, arrows). Because of this it has not been possible to detail the protoxylem architecture. Secondary wall patterns include those typically found in seed ferns. Large metaxylem tracheids are multiseriate bordered (Fig. 10, 11). Protoxylem elements and smaller peripheral metaxylem elements are usually annular or helical: some metaxylem elements near the periphery of the stele and those that vascularize the frond have conspicuous circular bordered pits.

Secondary xylem with numerous vascular rays is present in about one-third of the specimens (Fig. 1, 2, 5), and may be up to 26 cells thick. In a few specimens, one or two concentric rings of slightly smaller tracheids occur within the secondary xylem, giving the appearance of a growth ring (Fig. 2, at right). In this feature, *H. kentuckyensis* is similar to *H. lomaxii* (Scott, 1917). Prominent secondary phloem like that in *H. tiliaeoides* (Williamson, 1877; Williamson and Scott, 1895; Scott, 1917) and *H. americanum* (Hall, 1952) was not observed, but a region of poorly preserved secondary phloem ca. 6 cells thick is present at the margin of the wood (Fig. 14).

The primary cortex is three-parted. The innermost zone is made up of large parenchyma cells (Fig. 4); this layer is surrounded by a region of larger, disrupted cells that contain dark, amorphous material. Cells of this type have been referred to as resinous cells. Near the periphery of the stem, smaller, more compact cells comprise an outer hypodermal layer. This layer is delimited by a conspicuous epidermis of large rectangular cells with dark contents (Fig. 9). In some specimens small, irregular cortical wings and finger-like projections similar to those of *Microspermopteris* (Taylor and Stockey, 1976; Pigg, Stockey and Taylor, 1986), extend from the margin of the axis (Fig. 4), but are generally more extensive than flanges of other species of *Heterangium.*

Two types of secondary cortical tissues are produced. The most prominent type consists of sclerotic nests. They are composed of tangentially oriented, discontinuous plates of ca. 20 cells each (Fig. 4, arrows). The interrupted nature of these plates and their cellular orientation suggests their origin from discontinuous cambia. Individual cells are tangentially elongate and thick-walled, and similar to the brachysclereids found in the central region of some stems (e.g., Fig. 13, 15). In some of the largest stems, a continuous peridermal layer 3–4 cells thick is present (Fig. 14). The periderm is composed of thick-walled, cuboidal cells and is similar to that of *H. lintonii* (Stidd, 1979). Since no evidence of a well-defined phellogen was present, it was not possible to determine the relative positions of cork cambium and its

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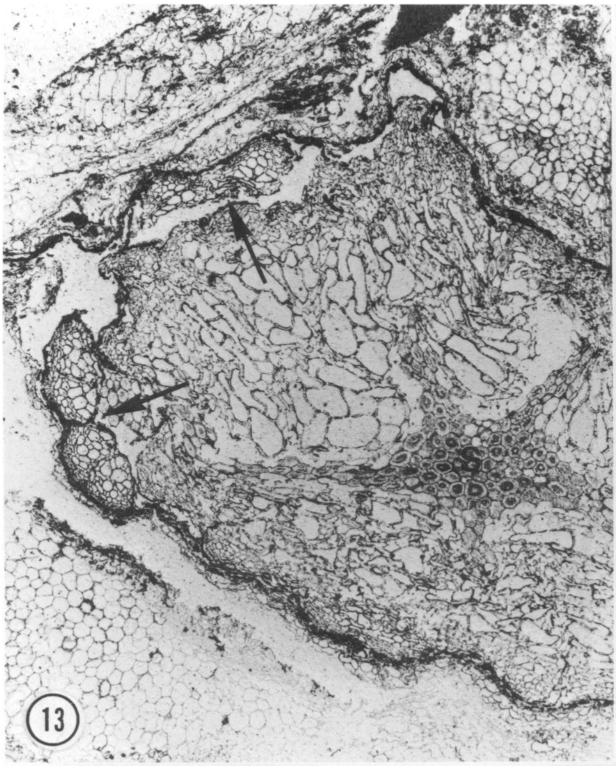
of stele in Fig. 4, showing reticulate wall thickenings (arrows) on cells in the ground tissue. 1665 F bottom, #17. ×135. **9.** Margin of stem showing characteristic epidermal cell histology. 1781 B$_1$ bottom a, #13. ×110. **10.** Oblique longitudinal section showing scalariform wall thickenings on large metaxylem elements of central region of stele. Note crescent-shaped files of ground tissue (FG). 1781 B$_1$ bottom a, #13. ×110. **11.** Longitudinal section through stele of specimen in Fig. 15 showing large metaxylem tracheids (T) and patches of smaller, isodiametric parenchyma cells aligned in files (FG). 1737 A$_1$ side$_2$, #4. ×110. **12.** Longitudinal section of stele of specimen in Fig. 2 showing large metaxylem tracheids (T) adjacent to smaller cells of the ground tissue with sclariform lateral walls (arrow). 1701 D$_2$ side, #11. ×110.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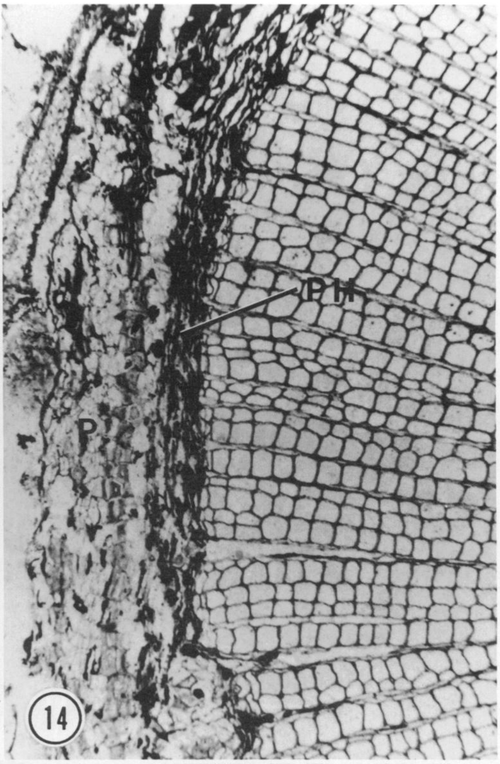
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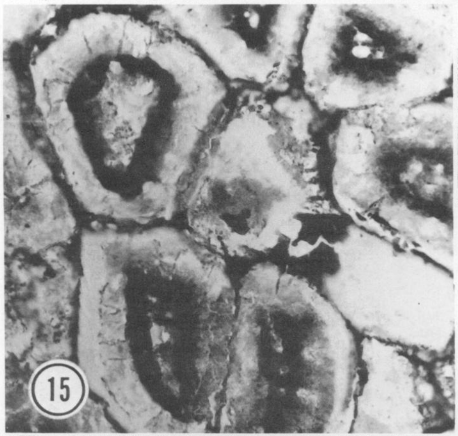
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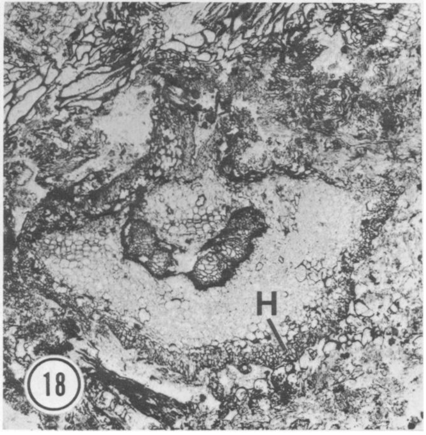
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derivatives, nor to determine whether the region represents phellem (as described by Stidd [1979] for similar tissue in *H. lintonii*), phelloderm, or a combination of the two. For this reason the more general term periderm is used.

The frond—The architecture of the frond is interpreted from an assemblage of interconnected and fragmentary foliar remains, and petiole bases attached to the stem (Fig. 6, 13, 16–22, 24–28, 33). The frond is at least twice pinnate and bears two-lobed laminar pinnules of the *Sphenopteris*-type. Petiole traces occur at the periphery of the stele as either single or double bilobed strands. Figures 3, 6, and 13 (top) illustrate a single bilobed strand, while Fig. 4 (left) and 13 (left) show a double bilobed trace. This variation may reflect either variability in trace production or a condition in which traces divide at different levels in the cortex. In one specimen (Fig. 13) both configurations are present, suggesting that considerable variability may occur in a feature that was previously thought to have taxonomic significance (Hirmer, 1933). Since strands are produced from one area of the stele, *H. kentuckyensis* would presumably be assignable to the subgenus *Heterangium* sensu Stidd (1979) (= *Euheterangium* sensu Scott, 1917).

Isolated petioles and numerous higher-order frond fragments are found throughout the coal ball matrix. In transverse section the largest petiole (Fig. 16) is 9.3 mm × 2.8 mm wide, elongate-triangular in shape, and vascularized by four large, bilobed vascular strands. Histological features of the petioles and all frond members are identical to those of the stem cortex. They are composed of large parenchyma cells with an inner region of larger cells and scattered resinous cells, a middle zone of parenchymatous tissue, and an outer hypodermal layer of small, compact cells (Fig. 16–18). Secondary tissues are represented by prominent, tangentially-to-radially oriented plates (= sclerotic nests) that are scattered in the ground tissue (Fig. 17, 21).

Specimens illustrating a major dichotomy of the frond rachis, a feature that characterizes the petioles of lyginopterids (Shadle and Stidd, 1975), have not been found. However, the largest petioles (Fig. 16) are at least twice as large as the next order (Fig. 17, 18), suggesting that either: 1) a dichotomy occurred, 2) that specimens represent extreme distal and proximal areas of large fronds, or 3) that fronds were quite variable in size (Fig. 33). The next order, presumably the primary rachis (sensu Shadle and Stidd, 1975) is 3 mm in diameter and produces alternately arranged primary pinnae ca. 1 mm in diameter that diverge from the rachis at nearly right angles (Fig. 17, 18, 21, at right). Most of the intermediate foliar members of the frond are characterized by grooved, adaxially directed projections (Fig. 16–18, top, 33). Secondary pinnae 1–2 mm wide are attached to the primary pinnae (Fig. 20, 33). Several specimens (e.g., Fig. 20) show a primary pinna in organic connection to a secondary pinna and pinule base.

Pinnules are laminar and lobed (Fig. 22, 24, 25, 33). Organic connections occur infrequently, and most of the laminar specimens are found as isolated fragments in the coal ball matrix. Laminar pinnules with dichotomous venation (Fig. 22) are at least 2-lobed and 1.2 mm wide. In transverse section the pinnules are slightly revolute, up to 0.4 mm thick in the region of the midrib, 0.1 mm thick laterally, and up to 0.2 mm thick at areas of lateral veins (Fig. 24). Histologically, the pinnules are composed of relatively undifferentiated mesophyll tissue that contains intermittent zones of dark, possibly resinous cells (Fig. 22, 24–26, 28). Vascular strands are ovoid (Fig. 24, 28), and contain about 20 tracheids, mostly with scalariform secondary thickenings or circular bordered pits.

Pinnules are hypostomatic, with individual stomata encircled by a ring of 6–7 subsidiary cells (Fig. 27). Subsidiary cells form a blunt, abaxial papilla up to 22 μm long and 18 μm wide that extends prominently beneath the leaf surface (Fig. 26, 29, 30). Rings of papillae are sometimes found intact (Fig. 30), or are occasionally distorted where individual papillae

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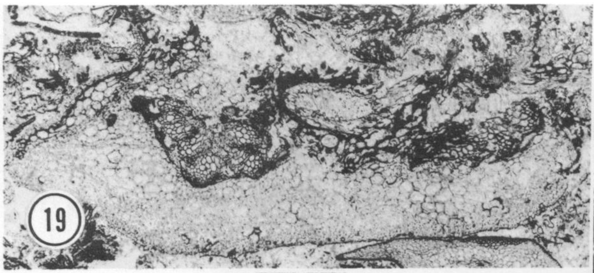
KEY TO LABELING: H = hypodermis; P = periderm; PH = phloem; S = sclereids.

Fig. 13–18. *Heterangium kentuckyensis*. **13.** Transverse section of stem showing stellate-shaped cluster of sclereids (S) in the central region of stele. Note diverging double (left) and single (top) bilobed leaf traces (arrows). 1737 A_2 side$_2$, #4. ×26. **14.** Transverse section of stem in Fig. 1 to show extrastelar tissues. Note zone of secondary phloem (PH) and periderm (P). 1446 C_2 top, #20. ×35. **15.** Transverse section of several sclereids from the center of the stem illustrated in Fig. 13. 1737 A bottom, #14. ×275. **16.** Transverse section of large petiole with conspicuous vascular bundles. Note irregularly-shaped hypodermis (arrow). OU 330 E bottom, #5. ×9.7. **17.** Transverse section of frond segment, at more distal level. Note sclerotic plates (arrow), and adaxial, grooved projection. OU 344 D top, #13. ×16. **18.** Frond segment showing conspicuous hypodermis (H). OU 344 C top, #4. ×16.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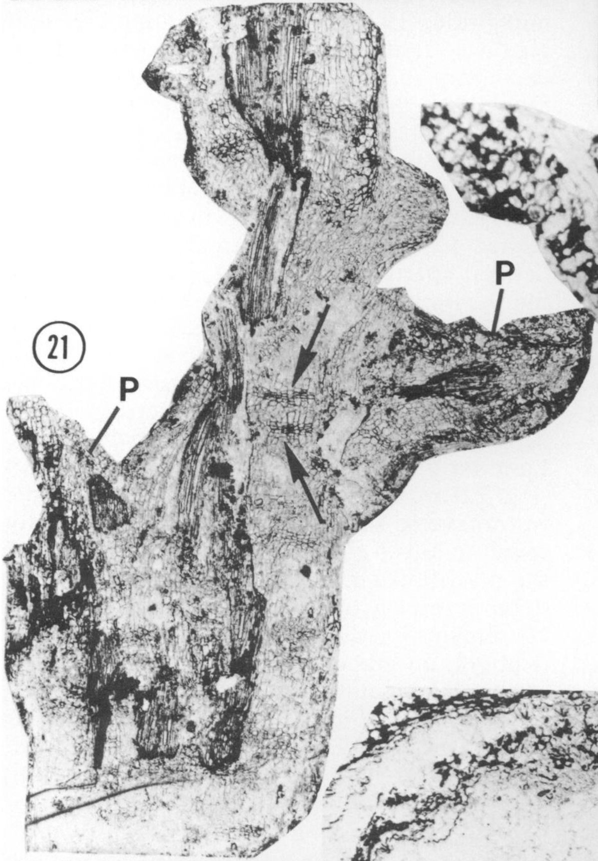
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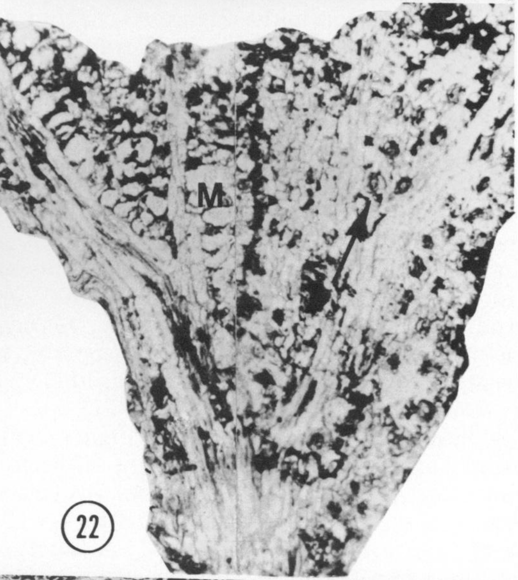
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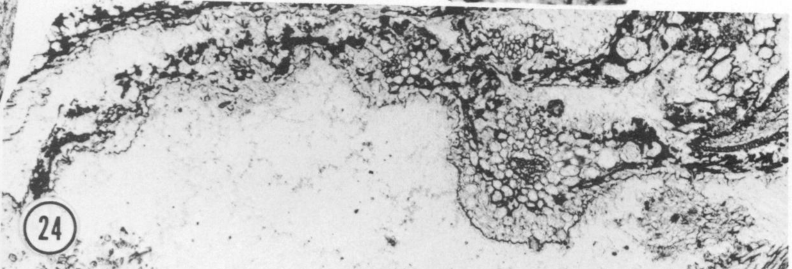
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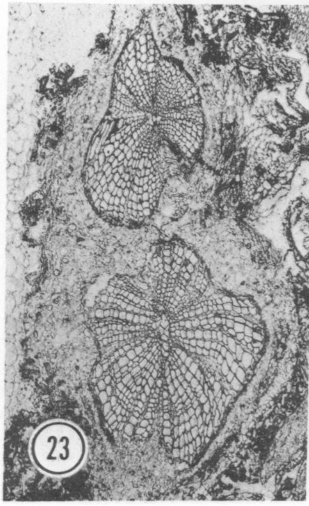
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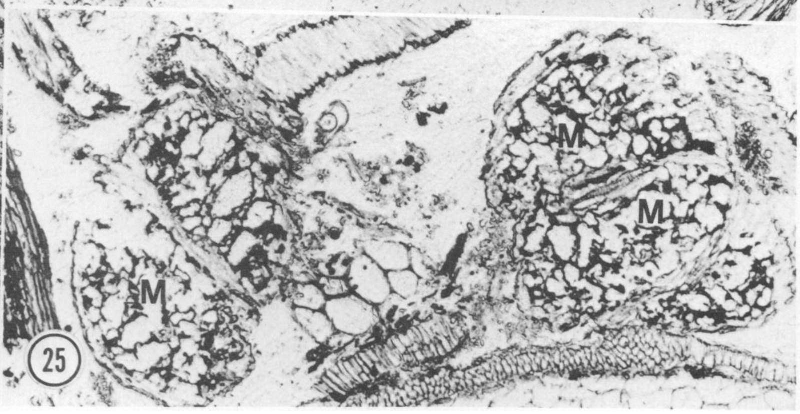
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have collapsed inwardly (Fig. 29). Papillae with a more regular arrangement have been reported surrounding the stomata of other seed fern foliage (e.g., Mickle and Rothwell, 1982; Reihman and Schabilion, 1985). The ring of papillae in *H. kentuckyensis* apears to be more loosely arranged than in other seed ferns, and papillae apparently overlap slightly to cover the stoma (Fig. 31, 32).

Roots—A small number of diarch roots have been found associated with stems and foliage of *H. kentuckyensis.* They are small (up to 1.5 mm in diameter) and possess a narrow zone of secondary xylem (Fig. 23). Although not attached to the stems, the roots display histological features that are identical to those of stems, petiole and other foliar members.

DISCUSSION—*Species of Heterangium—Stele:* Species of *Heterangium* have been traditionally classified by type of leaf trace divergence, protoxylem maturation and stelar configuration. Scott (1917) first grouped the species of *Heterangium* described by Corda (1845), Renault (1893, 1896), Kubart (1908, 1909, 1911, 1914), Williamson (1873, 1877), and Williamson and Scott (1895) into three subgenera (i.e., *Euheterangium, Polyangium,* and *Lyginangium*). Members of Subgenus *Euheterangium* were defined by a single leaf trace, while those assignable to Subgenus *Polyangium* possessed traces that arose from two separate areas at the margin of the stele. Taxa included in Subgenus *Lyginangium* were believed to represent members of a sequence intergradational between most species of *Heterangium* (which had vitalized protosteles) and those of the eustelic genus *Lyginopteris,* which were characterized by a broad parenchymatous pith (Scott, 1917, 1923; Beck et al., 1982). This classification was further augmented by Hirmer (1933) who described several new species and added further hierarchical subsections of his own. Hirmer's classification is based not only on the mode of trace origin, but also on the pattern of vascularization in the cortex and petiole. Most recently, Stidd (1979) pointed out nomenclatural problems with *Euheterangium,* and suggested the substitution of the name *Heterangium* for that subgenus.

It is now apparent that the taxonomic characters traditionally used for *Heterangium* are, for most species, either difficult to define, intergradational, or only superficially known. Confusion has resulted over what components of the stelar concept were being discussed, and how to compare them. Moreover, the tendency for certain characters to occur together has resulted in a classification based on superficial evaluation. In order to sort out what is currently known about *Heterangium,* each component of previous classifications must be considered separately. The major stelar features can be delimited as follows: 1) primary xylem organization (i.e., metaxylem and ground tissue), 2) primary xylem maturation, 3) protoxylem architecture, 4) leaf trace divergence from the stele, and 5) vascularization of the petiole.

1) Primary xylem organization—The generic concept of *Heterangium,* as set forth by Corda (1845) is based solely on the distinctive organization of metaxylem and ground tissue in a vitalized protostele. Corda's type specimen, *H. paradoxum,* represents a crushed and poorly preserved fragment of a stele, and thus the generic diagnosis reflects only those features of the central stelar region (i.e., large metaxylem elements surrounded by smaller parenchymatous cells, and types of tracheary pitting patterns). Basically all the heterangiums (with the possible exception of members of Subgenus *Lyginangium,* i.e., *H. andrei* and *H. intermedium,* which apparently have a pith) conform to the generic concept as it stands.

Authors have repeatedly attempted to make some sense of the organization of metaxylem and cells of the ground tissue, using such terminology as "tracheid clusters" or "packets," "parenchymatous plates," etc. (Table 2). In the most general terms, the steles of *Heterangium* have a central region composed of a mixture of metaxylem elements and parenchymatous

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KEY TO LABELING: M = mesophyll; P = primary pinna; S = secondary pinna.

Fig. 19–25. *Heterangium kentuckyensis.* **19.** Transverse section of pinna rachis. 1701 F top, #61. ×23. **20.** Transverse section of primary pinna rachis bearing secondary pinnae (S) and laminar pinnules (arrow). 7616 C top, #11. ×16. **21.** Longitudinal section of pinna rachis showing alternately attached primary pinnae (P). Note sclerotic nests (arrows). Top of photograph represented by section of pinna axis in Fig. 19. 1701 F, #7. ×12.5. **22.** Montage of laminar pinnule. Note dichotomous venation, mesophyll (M), and stomata (arrow). 1701 F, #2. ×64. **23.** Diarch roots found in association with *H. kentuckyensis* stems. 1665 E bottom, #27. ×16. **24.** Transverse section of laminar pinnule. 1701 F top, #63. ×43. **25.** Oblique paradermal section through pinnule lobes. Note mesophyll (M). 8582 D bottom, #53. ×60.

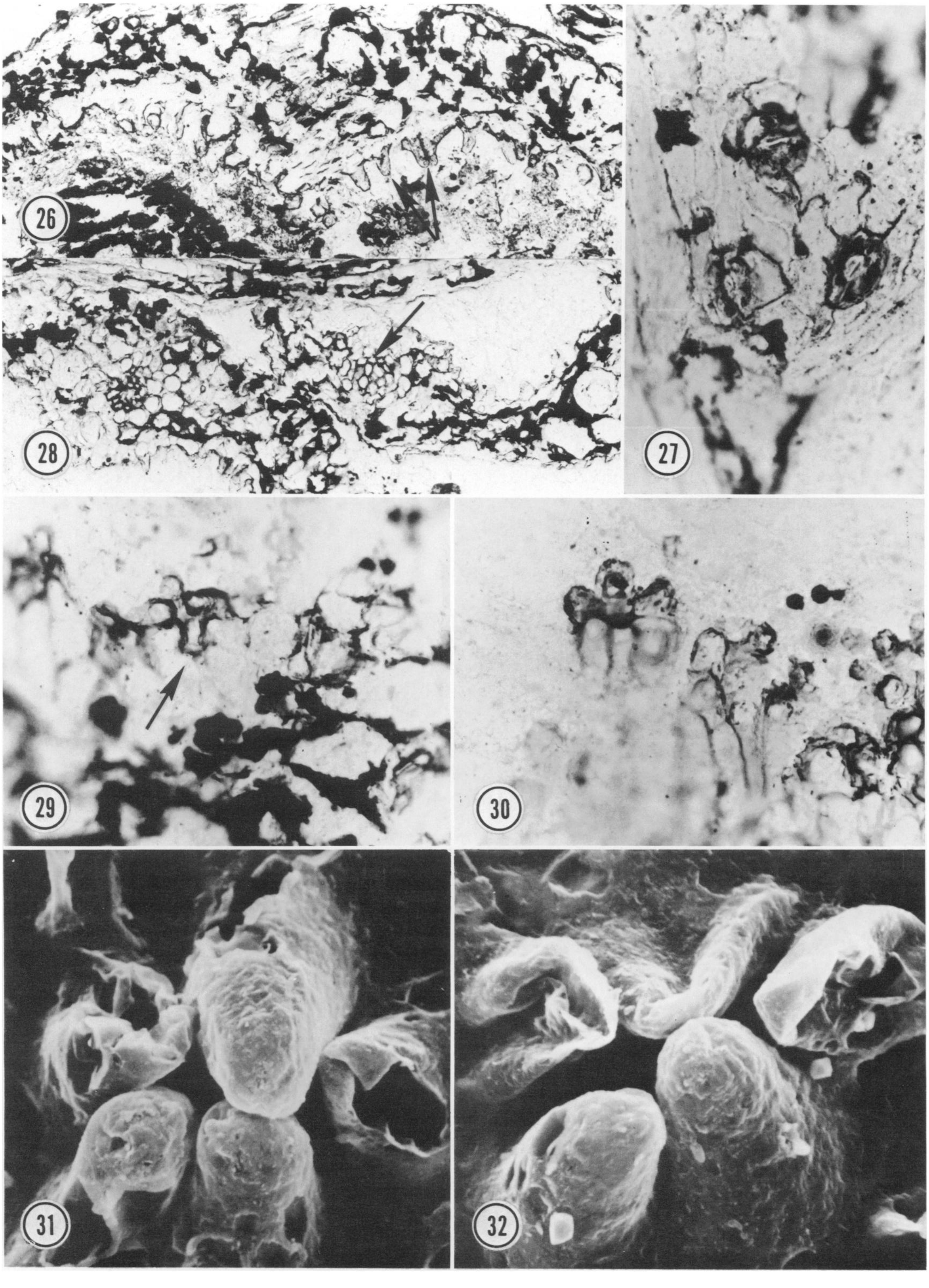

Fig. 26–32. *Heterangium kentuckyensis.* **26.** Transverse section of laminar pinnule. Note mesophyll cells with dark contents and prominent abaxial papillae (arrows). 8582 D bottom, #37. ×135. **27.** Three stomata with prominent guard cells, and ring of subsidiary cells. 1701 D, #2. ×264. **28.** Transverse section of laminar pinnule showing ovoid vascular strand (arrow). 1701 F_1 top, #63. ×110. **29.** Ring of four abaxial papillae extending from pinnule. 1701 D,

cells, with protoxylem strands confined to the margin of the stele. Differing proportions of parenchyma to metaxylem occur, and from species to species the degree of organization of these cell types is variable. At one extreme are steles with "packets" or clusters of tracheids surrounded by anastomosing rings of parenchymatous cells (e.g., as in *H. shorense,* Scott, 1917), while at the other are those with parenchymatous plates that radiate both eccentrically and from the center of the stele (*H. kukuki,* Hirmer, 1933; Beck et al., 1982). In some species, both parenchymatous plates and tracheid clusters are present (*H. grievii,* Scott, 1917); in others there is no discernible pattern (e.g., *H. kentuckyensis*).

Of the 22 known permineralized species, at least 11 were described from a single specimen, many from only one transverse section, with no information provided about the three-dimensional nature of the stem (Table 2). In the best known species where specimens showing lateral continuity have been available (i.e., *H. kukuki*), radial plates of parenchyma are present, as in *Microspermopteris* (Taylor and Stockey, 1976; Pigg et al., 1986). Other taxa that may have a similar organization are *H. minimum* and *H. lintonii* (Stidd, 1979).

2) Primary xylem maturation—Among species, primary xylem maturation shows a complete intergradation, including mesarch, marginally mesarch, marginally exarch and exarch patterns (Table 2). Within individual species, the intergradation of maturation type, coupled with the difficulty in identifying protoxylem strands in many specimens, results in an ambiguous and unreliable taxonomic character.

3) Protoxylem architecture—Perhaps the feature of greatest potential usefulness in understanding stelar patterns in gymnosperms is the three-dimensional architecture of the protoxylem (Beck et al., 1982). The absence of suitable material and problems encountered with identifying protoxylem strands have precluded the analysis of this character in most species of *Heterangium,* including *H. kentuckyensis.* In *H. kukuki,* the only stem studied extensively with respect to protoxylem, Hirmer (1933) was unable to identify a continuous system of cauline protoxylem strands. A similar pattern may be seen in some members of the woody Ranales (Benzing, 1967), and some cordaites (Trivett and Rothwell, 1985). A pattern of discontinuous protoxylem strands would presumably be caused by elongation of procambial strands prior to differentiation, re-

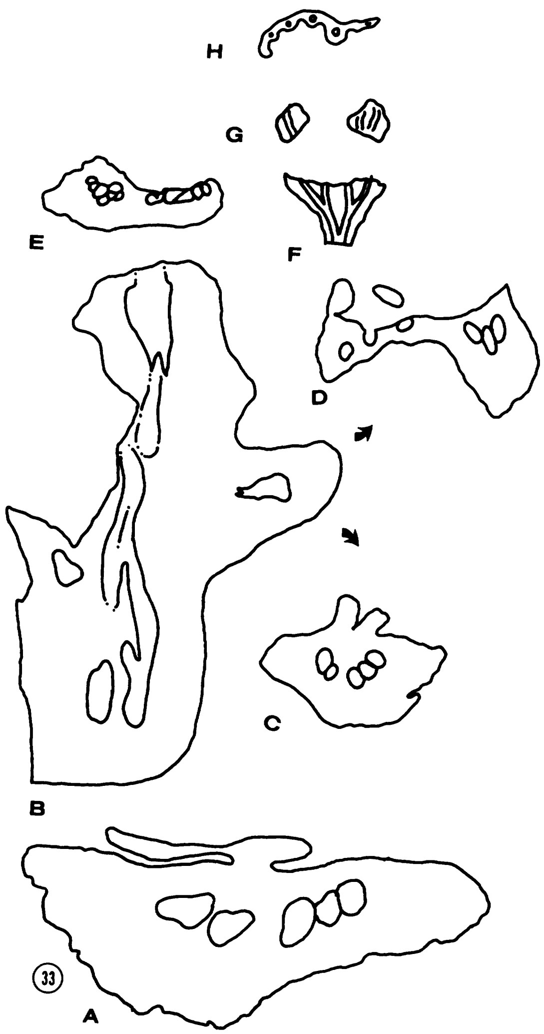

Fig. 33. Line diagram of frond segments of *H. kentuckyensis* illustrated to scale. A = transverse section of petiole (= Fig. 16), B = paradermal section of main rachis (= Fig. 18), C = transverse section of primary pinna (= Fig. 21), D = transverse section of primary pinna with attached secondary and pinnule lobe (= Fig. 20), E = transverse section of main rachis (= Fig. 19), F (= Fig. 22) and G (= Fig. 25) represent paradermal views of laminar foliage, and H = transverse section of laminar pinnule (= Fig. 24). ×10.

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#2. ×320. **30.** Oblique transverse section of ring of five subsidiary papillae, showing papillae in more lateral view. 1701 F, #5. ×264. **31.** Ring of five papillae showing blunt tips. 1701 F. ×1,150. **32.** Several collapsed papillae showing general shape and features of the wall. 1701 F. ×1,150.

TABLE 2. *Comparative chart contrasting morphological features of all permineralized species of* Heterangium

Species (* = described from one specimen)	Stem diameter Stele diameter (mm)	Primary xylem maturation	Stelar features	Stelar parenchyma thickenings	Secondary xylem	Secondary phloem	Traces to petiole origin/divison
Section H							
H. alatum Kubart Namurian A, Ostrau	6.5 4.0	mesarch	random arrangement	?	small amount	+ (produced, poor)	1 (10/section)
H. grievii Williamson Visean, Pettycur	7–15 ?	mesarch	tracheid clusters reticulate parenchyma	? (not observed)	7–8 cells uneven thickness	?	1–2
H. "*grievii*"* Jennings Namur A/B, Illinois	15 (crushed)	?	tracheid clusters	?	none	?	?
H. kentuckyensis Westphalian B, Kentucky	2.2–5.8 0.7–3.0	mesarch	irregular arrangement	reticulate scalariform, thick-walled, sclereids	up to 26 cells	+ (produced, poor)	1–bilobed–2
*H. lintonii** Stidd Westphalian D, Indiana	5–8 3–4	mostly exarch	parenchyma plates (inconsistent)	spiral, scalariform reticulate	less than 0.5 mm	+ (produced, poor)	1–bilobed +/ridges
*H. minimum** Scott Westphalian A, UK	2.9 × 1.7 1.6 × 1	mesarch	parenchyma plates (few), mostly tracheids	?	7 cells	?	1–bilobed
H. polystichum Kubart Namurian A, Ostrau	10 5.3	mesarch	tracheid clusters	?	small amount	?	1–divides–2 (13/section)
*H. schusteri** Kubart Namurian A, Ostrau	8.6 ?	nearly exarch	random arrangement	?	10 cells	?	1–2 (3/section)
H. sturii Kubart Namurian A, Ostrau	5.4 2.6	nearly exarch	random arrangement	?	none	?	1 (large) (5/section)
Section P							
H. americanum Andrews Stephanian B, US (Namurian A/B, Westphalian D)*	1.7–4 ?	mesarch, nearly exarch	random arrangement	?	small amount	?	2–2 bilobed–4
*H. duchartrei** Renault Stephanian B, France	6.5 2.0	?	random arrangement	?	+, up to 5 mm broad rays	+, (produced, poor)	2

TABLE 2. *Continued*

Species (* = described from one specimen)	Stem diameter Stele diameter (mm)	Primary xylem maturation	Stelar features	Stelar parenchyma thickenings	Secondary xylem	Secondary phloem	Traces to petiole origin/divison
*H. hoppstaedteri** Hirmer Westphalian B, Ruhr	? 4.0 (stele)	?	parenchyma plates (irregular)	?	+	–	1
H. kukuki Hirmer Westphalian B, Ruhr	3–5.5 ?	exarch to mesarch plates	parenchyma plates	?	+, uneven	?	1—2 in cortex
H. lomaxii Williamson Westphalian A, UK	5–13 ?	mesarch, nearly exarch	some tracheid clusters (not regular)	?	+, uneven thickness	+	2 widely-spaced
*H. punctatum** Renault Stephanian B, Autun	5.5 1	?	?	?	+, small amount	+, dialated rays	?
*H. renaulti** Brongniart (Renault)	5.5 ?	?	?	?	–	?	2–4
*H. shorense** Scott Westphalian A	17–18 7	mesarch	conspicuous tracheid packets, reticulate parenchyma	?	5 cells, uneven	?	2–4
H. tiliaeoides Scott Westphalian A	10–16 ?	mesarch	xylem packets (irregular)	?	+, thick	+, dialated rays	2–4
Section L							
H. andrei Kubart Namurian A, Ostrau	14 4.8	?	parenchymatous pith containing few tracheids	?	+, broad zone	?	1—2—4
*H. intermedium** Kubart Westphalian B, Ruhr	? ?	?	parenchyma pit with few tracheids	?	?	?	?
Section ?							
*H. paradoxum** Corda Westphalian D, Radnitz	? ?	?	slight tracheid clusters; much parenchyma	?	?	?	?
*H. bibractense** Renault Stephanian B	16–17 1–1.5	?	small primary body no clusters, no plates	?	+, extensive	+ (produced, poor)	none known

Data modified from Corda (1845), Williamson (1873, 1877), Williamson and Scott (1895), Renault (1896), Kubart (1914), Scott (1917), Benson (1933), Andrews (1942), Hirmer (1933), Shadle and Stidd (1975), Jennings (1976), and Stidd (1979).

TABLE 2. *Continued*

Species (* = described from one specimen)	Winged petioles	Primary cortical sclerenchyma	Secondary cortical sclereids	Periderm	Hypodermis	Resinous cells	Trichomes/ glands	Wings
Section H								
H. alatum Kubart Namurian A, Ostrau	+	?	?	–	?/dictyoxylon	?	?	+/stem
H. grievii Williamson Visean, Pettycur	–, but "decurrent"	sparganum grades into dictyoxylon	–	–	?/sparganum	+	?	– ("ribbed" due to petioles)
H. "*grievii*"* Jennings Namur A/B, Illinois	–	sclerotic nests—inner, fibrous bands—outer	–	?	?/sparganum	?	?	ridges (preservational?)
H. kentuckyensis Westphalian B, Kentucky	+	sclerotic nests (?)	+, nests	+	6 cells	+	–	+/stem
*H. lintonii** Stidd Westphalian D, Indiana	+	–	–	+	2–3 elongate cells	+	+ 1–2 cell	–
*H. minimum** Scott Westphalian A, UK	–	sparganum (small amount)	?	–	sparganum	?	?	+/ridges
H. polystichum Kubart Namurian A, Ostrau	–	?	?	?	?	?	?	–
*H. schusteri** Kubart Namurian A, Ostrau	–	dictyoxylon	?	?	?/dictyoxylon	?	?	?
H. sturii Kubart Namurian A, Ostrau	–	dictyoxylon	?	?	?/dictyoxylon	?	?	–
Section P								
H. americanum Andrews Stephanian B, US (Namurian A/B, Westphalian D)*	–	sclerotic nests sparganum	–	?	?	?	?	?
*H. duchartrei** Renault Stephanian B, France	–	?	?	+	?	?	?	?
*H. hoppstaedteri** Hirmer Westphalian B, Ruhr	–	stone cells (inner cortex) sparganum	–	–	sparganum	?	–	?

TABLE 2. *Continued*

Species (* = described from one specimen)	Winged petioles	Primary cortical sclerenchyma	Secondary cortical sclereids	Periderm	Hypodermis	Resinous cells	Trichomes/ glands	Wings
H. kukuki Hirmer Westphalian B, Ruhr	–	–	+, nests (plates)	–	–/little	–	+ multicellular	?/ridges
H. lomaxii Williamson Westphalian A, UK	–	sclerotic nests (massive); sparganum grading into dictyoxylon	+, nests	?	+	+ 2/3 cells elongate	?	+
*H. punctatum** Renault Stephanian B, Autun	?	?	?	?	?	?	?	?
*H. renaulti** Brongniart (Renault)	–	?	?	?	?	?	?	?
*H. shorense** Scott Westphalian A	–	"masses" + in "pericycle" and cortex	+, nests (inner cortex)	–	dictyoxylon	+ (esp. cortex)	?	?
H. tiliaeoides Scott Westphalian A	–	sclerotic nests + in "pericycle" and cortex	?	+ little	?/ sparganum	+/ = "secretory sacs"?	?	?
Section L								
H. andrei Kubart Namurian A, Ostrau	–	dictyoxylon	?	?	?	?	+/stalked glands	–
*H. intermedium** Kubart Westphalian B, Ruhr	?	?	?	?	?	?	?	?
Section ?								
*H. paradoxum** Corda Westphalian D, Radnitz	?	?	?	?	?	?	?	?
*H. bibractense** Renault Stephanian B	?	?	?	+	?	?	?	?

sulting in metaxylem but not protoxylem production. This may explain, in part, the difficulty in identifying protoxylem strands in *Heterangium* stems, if differentiation prior to elongation occurred in the leaf primordia but seldom in the stem apex proper. This feature may prove to be widespread in the genus as it becomes better understood (Stidd, 1979), however, it may not be the only pattern that is present. There is further uncertainty whether the continuity or discontinuity of protoxylem strands in a given stele can be correlated with presence or absence of an underlying sympodial organization. Thus it appears that the long-held notion that *Heterangium* occupies an intermediate position in the evolution of the eustele remains equivocal, based on protoxylem architecture.

4) Leaf trace divergence from the stele—Scott's original distinction between the subgenera *(Eu)heterangium* and *Polyangium* was based on whether leaf traces diverged from one or two areas of the stele (Scott, 1917), although he recognized correlations with other features. Where this reflects a basic and unambiguous pattern, it is probably a valid and useful distinction.

5) Vascularization of the petiole—Hirmer (1933) further divided the subgenera of *Heterangium* on the basis of trace bifurcation and vascularization of the petiole. There are several problems with this approach. The level at which the vascular strand divides may be variable for a stem. For instance, at comparable levels, petiole traces in *H. kentuckyensis* may be either single or double (Fig. 13). Without extensive specimens it may not be possible to determine whether traces reflect the condition at the point of origin from the stele, or a subsequent bifurcation. In many instances the number of vascular strands is difficult to determine in the cortex and throughout the petiole since protoxylem strands are not easy to identify and the resulting number may be solely a remnant of preservation. Furthermore, vascularization of the frond by large or small, single or double traces may be determined by the size of the frond. Many taxa possess the same basic pattern of petiole vascularization in which a single trace becomes bilobed within the stem and emerges into the petiole base as either a single bilobed or double strand (Table 2). This may be either a generalized pattern from which minor variations occur, or the basic pattern present in all members of the group, including incompletely known taxa.

The foregoing analysis of stelar features suggests that *Heterangium* represents a heterogeneous mixture of forms that intergrade within intermediate taxa, while a combination of features are correlated in either end member of the sequence. For instance, at one extreme, taxa that best characterize Subgenus *Polyangium* (e.g., *H. shorense, H. tiliaeoides*) have well-defined clusters of tracheids, mesarch protoxylem maturation, and traces that originate as two strands at the margin of the stele (Table 2). At the other extreme, typical representatives of the *Heterangium* group (e.g., *H. grievii, H. lintonii*) have less distinct protoxylem strands, tend toward exarchy, and produce a single petiole trace that later bifurcates. Since these features have been considered only superficially to date, it has been difficult to determine their biological and taxonomic significance. Upon understanding more fully the three-dimensional configurations of primary xylem organization and protoxylem architecture, several patterns may emerge that suggest a more biologically sound classification of taxa currently recognized as species of *Heterangium.* Until the heterogeneous assemblage that comprises *Heterangium* is more carefully assessed it is premature to use stelar characters as important components of phylogenetic schemes (e.g., Stein, 1986).

Perhaps since Scott (1917), there has been an underlying assumption that the stratigraphic distribution of stelar types reflected phylogeny within the lyginopterids. The oldest, simplest forms conformable to Subgenus *Heterangium* were thought to have given rise to the later, more sophisticated taxa included in the subgenera *Polyangium* and *Lyginangium.* However, a careful analysis of the species characters placed within a stratigraphic framework suggests something quite different (Table 1, Table 2). Although the oldest *Heterangiums* belong to Subgenus *Heterangium,* they occur concurrently with *Polyangium* types throughout the Upper Carboniferous (Table 2; Bertram, 1986).

Heterangium kentuckyensis—Biological and developmental variability: In the past it has been difficult to correlate features of *Heterangium* due to a lack of comparative data (Table 2). Many species of *Heterangium* have been based on the anatomy of a single organ (i.e., the stem), and frequently only from one or a few transverse sections. Some species (e.g., *H. americanum*) are recognized from numerous localities (Phillips, 1980) based solely on stems that include a wide range of structural variability. It is probable that geographical and geological ranges of these species are overestimated, since features other than stems might better distinguish taxa.

The data base for the description of *H. kentuckyensis* is established from a single locality. Based on the presence of some or all of a combination of diagnostic features, at this time it is our belief that all specimens investigated are referable to a single species. The material thus provides, for the first time, a sufficient sample of variability within a single species of *Heterangium* so that it is possible to delimit features that are ontogenetically and taphonomically diverse from those that are taxonomically significant. This increased level of resolution thus allows for a more accurate analysis of those features which may be of potential taxonomic importance.

Stems—The variability in the stem of *H. kentuckyensis* is extensive in both stelar and cortical histology. While no particular arrangement of xylem parenchyma and tracheids is apparent in transverse section, longitudinal sections suggest that parenchyma is ordered. The occurrence of parenchyma in elongate, fusiform files (Fig. 10, 11) suggests that the ground tissue in steles of *H. kentuckyensis* arose from the transverse divisions of elongate procambial initials, rather than directly from a ground meristem. The files are displaced laterally by the expansion of large, adjacent metaxylem tracheids, but in most cases they are still recognizable (Fig. 10, 11). In stems that produce xylem parenchyma with scalariform wall thickenings, the putative procambial origin of parenchyma is more convincing, since in this instance the parenchymatous cells are not distorted by the expansion of adjacent tracheids (Fig. 12). To our knowledge, the meristematic origin of xylem parenchyma in *Heterangium* has not been addressed.

In *H. kentuckyensis,* cortical tissues also demonstrate histological variability, most of which may be attributed to ontogenetic and preservational states. Sclerotic plates appear to be produced as secondary tissues, from distinct discontinuous cambia, since it is possible to follow tangential files of cells within each group (Fig. 4, 17, 21). Within the genus, sclerotic plates and sclerotic nests are almost always present (Table 2), although there is considerable variability in histological detail from species to species. Plates in *H. grievii,* for example, are narrow and distinct and may be of primary rather than secondary origin since the cells are not aligned in rows. Periderm from a radially continuous cambium is also produced to a limited extent in *H. kentuckyensis,* as well as *H. lintonii* and several other taxa (Table 2). In cases where fronds are found in association with stems (e.g, *H. kentuckyensis*; *H. grievii,* Williamson, 1873; *H. kukuki,* Hirmer, 1933), cortical features are usually identical to frond histology.

Still other species of *Heterangium* illustrate additional histological variability (Table 2). In addition to sclerotic plates or nests and periderm, species may have zones of massive sclerotic patches that can be traced to a primary origin (e.g., *H. lomaxii*), narrow bands (*H. grievii*), a distinct banding pattern that can be considered as sparganum cortex (e.g., *H. minimum*), the intergradation of sparganum into anastomosing dictyoxylon-type cortex (*H. lomaxii*), and well-defined dictyoxylon cortex (*H. schusteri*). These cortical types can further occur in differing zones within stems and probably, in combination, represent one of the best suites of features for recognizing species of *Heterangium,* and for correlating stems with foliage. Resinous cells, trichomes, and the presence and type of hypodermis are also distinctive features of *Heterangium* species.

The frond—The frond of *H. kentuckyensis* is at least twice pinnate and bears lobed pinnules of the *Sphenopteris* type. Petioles contain four to six vascular strands, and have histological features similar to those of stems, including resinous cells and cortical sclerotic plates. Primary pinnae diverge alternately at nearly right angles to the main rachis: frond members contain resinous cells and a prominent adaxial groove. Hypostomatic pinnules bear blunt papillae on each of the 6–7 subsidiary cells.

The only other *Heterangium* frond that is known in detail (Shadle and Stidd, 1975) has bicellular trichomes unlike those of *H. kentuckyensis.* The leaves also have a palisade layer in contrast to general, undifferentiated parenchyma in *H. kentuckyensis.* Stomata were not found on laminar pinnules, but those discovered on the frond rachis lacked papillae (Shadle and Stidd, 1975). Furthermore, no notch or groove like that of *H. kentuckyensis* was reported on the frond members (Shadle and Stidd, 1975). Sclerotic nests in the ground tissue of petioles of *H. kentuckyensis* are large and conspicuous compared to those in the frond described by Shadle and Stidd (1975).

The exact affinities of all specimens described by Shadle and Stidd (1975) with one or several species of *Heterangium* is uncertain, since the specimens include material from two localities of differing stratigraphic level: Berryville (Upper Pennsylvanian) and Sahara (Middle Pennsylvanian), and because fronds were not found in attachment to stems. The only previously described stem from these localities is *H. americanum* Andrews (Phillips, 1981). However, *H. americanum* was also described based on material from two localities representing middle and late Pennsylvanian age and the localities of specific specimens are not distinguished in Andrews' (1942) illustrations. Shadle and Stidd (1975) have suggested that more than one stem may be present at Berryville, and a number of different forms of *Heterangium* from several localities in the Illinois Basin have been observed by us that probably represent more than a single taxon. For these reasons it appears that specimens currently recognized as *H. americanum* probably represent a heterogeneous assemblage.

The frond of *H. grievii* is partially known as a result of Williamson and Scott's (1895) work, and was inferred from the distinctive, narrow sclerotic plates in the cortex of frond members. The frond architecture, however, has yet to be reconstructed. The suggestion that certain compression species of *Sphenopteris* (e.g., *S. elegans,* and *S. dissecta*) represent the frond of *Heterangium* is conjectural. These ideas are based on the presence of transverse striations on frond axes, which have been thought to represent taxonomically diagnostic sparganum- or dictyoxylon-type cortex (Seward, 1917; Scott, 1923; Jennings, 1976). However, cortical tissues of these types are common to many seed ferns, and, especially at the level of resolution possible with compression forms, are probably not unique to the fronds of *Heterangium.*

Hirmer (1933) illustrated several large frond segments and neuropterid pinnules found in association with *H. kukuki,* which he suggested together represented the frond of that taxon. While the petioles and other large frond segments are histologically similar to the stems of *H. kukuki* and probably represent the foliage of this species, there is no evidence to support the connection between these segments and the neuropterid pinnules.

Jennings (1976) described a compressed frond system with *Heterangium* affinities from the Upper Mississippian Chester Series of Illinois. These fronds bear the highly dissected *Rhodea*-type foliage and petrified *Telangium* or compressed *Telangiopsis*-type synangia. The narrow, banded sclerotic plates in the cortex are similar to those of *H. grievii* (Williamson and Scott, 1895). Unfortunately, stems are poorly preserved and lack the sufficient diagnostic detail necessary to equate the form with *H. grievii* or compare it with other species of *Heterangium.* The presence of different pinnule types (i.e., *Rhodea* and *Sphenopteris*) on fronds of *Heterangium* species further underscores the heterogeneous nature of plants with *Heterangium*-type stems, and suggests strongly that stems referred to as *Heterangium* do, in fact, represent different taxa that can only be understood as whole plants by the reconstruction of stems and their frond systems.

Roots and plant habit—Roots known to be attached to *Heterangium* are rare and apparently quite variable. Diarch roots are known in association with *H. kukuki* (Hirmer, 1933), while masses of small, diarch and triarch adventitious roots have been described in attachment to stems of *H. grievii* (Williamson, 1873; Benson, 1933). Adventitious roots are said to occur in association with leaf trace production in *H. lomaxii* (Scott, 1917) and large, tetrarch roots with abundant secondary xylem are found in *H. tiliaeoides* (Scott, 1917). The roots found in association with stems of *H. kentuckyensis* are small and diarch, and histologically similar to the stems, but nothing is known regarding their origin or attachment. The axis described by Renault (1893, Pl. LXV, fig. 3) as *H. bibractense* which exhibits a tetrarch stele, large amounts of secondary xylem, and periderm, is root-like in organization. It may perhaps be the root of *H. duchartrei,* found in the same sediments.

The presence of numerous adventitious roots in some taxa, the relatively small size of stems, the uneven production of secondary xylem (Table 2), and the frond-like leaves all suggest that at least some *Heterangium* plants may have had a vine-like or liana habit like that proposed for many other Carboniferous seed ferns. Although branching specimens of *Heterangium* have been reported (e.g., *H. grievii,* Williamson and Scott, 1895), the mode of branch production and association of branches with subtending petioles has not been demonstrated. However, the paucity of specimens investigated suggests this, as well as connections with fertile parts, may yet be found.

Lyginopterid pteridosperm evolution—The relationship of *Heterangium* to other lyginopterid pteridosperms has remained difficult to resolve. Since *Heterangium* has been known almost entirely as a stem, its putative relationships with other lyginopterids have been explained on the basis of stelar concept. Indeed, the distinctive vitalized protostele of *Heterangium* has played a pivotal role in concepts concerning the origin of the eustele in the early radiation of the gymnosperms (Beck et al., 1982).

One early theory of gymnospermous stelar evolution was that of Kubart (1914), who proposed that species assignable to Subgenus *Lyginangium* (e.g., *H. andrei*) were similar in many ways to *Lyginopteris* stems since they possessed dictyoxylon cortex, capitate glands, and a pith. Because of a few tracheids in the central parenchymatous pith zone of these forms Kubart placed them in the genus *Heterangium,* suggesting they represented intermediate members of a lineage extending from protostelic to eustelic stems. Whether the species included in Subgenus *Lyginangium* are actually conformable to *Heterangium* at all remains equivocal. A review of diagnostic features in the present study suggests that *H. andrei* (Kubart, 1914), at least, may conform more closely to the genus *Lyginopteris.* Recent investigation of material from Kubart's locality has substantiated this conclusion (Bertram, 1986). Bertram (1986) has suggested that three species of *Heterangium* described by Kubart (i.e., *H. sturii, H. schusteri,* and *H. andrei*) represent protostelic taxa more appropriately assignable to *Lyginopteris.*

Other attempts to link *Heterangium* with the eustele involved *H. kukuki* (Hirmer, 1933; Beck et al., 1982). An analysis of the protoxylem architecture of this taxon (Hirmer, 1933; Beck et al., 1982), however, revealed a vascular system unlike the continuous sympodial system of (cauline) protoxylem strands that was expected among eustele progenitors. This type of evidence, together with the contemporaneous occurrence of protostelic *Heterangium* stems and eustelic seed ferns (e.g., *Lyginopteris*), suggests that the role of any heterangiums in the evolution of eusteles is doubtful.

Heterangium kukuki, and possibly *H. minimum* and *H. lintonii* (Stidd, 1979), are reported to have permanent parenchymatous plates like those of *Microspermopteris* (Taylor and Stockey, 1976; Pigg et al., 1986) and possibly *Syncrama* (Holden, 1954, Pigg et al., 1986). The single curved petiole trace, morphology of the petiole, cortical histology, presence of multicellular trichomes on the stem, axillary branching, and foliage type distinguish *Microspermopteris* from *Heterangium* (Pigg et al., 1986). Although some heterangiums (*H. minimum, H. kukuki*) have steles that are similar to those of *Microspermopteris,* it is premature to equate these taxa by assigning them to *Microspermopteris* based on stelar features alone, as has been suggested by other authors (Taylor and Millay, 1981; Bertram, 1986). Foliage of *Microspermopteris* is known to be distinct from that of *Heterangium* both morphologically and anatomically (Pigg et al., 1986) and will undoubtedly be of significance in resolving this problem. It is now apparent that the *Microspermopteris* complex, including *Microspermopteris aphyllum* (Taylor and Stockey, 1976), *M. aphyllum* var. *kansensis* sensu Baxter (1952), *Syncrama lirata* Holden (Pigg et al., 1986), and the three new species of *Microspermopteris* recognized by Bertram (1986) represent a plexus of plants that are distinct from *Heterangium.* The genus *Syncrama,* based on one species, *S. lyrata* Holden, was invalidly published by Phillips (1980) as a species of *Microspermopteris* (i.e., *M. lyrata,* table 2.17, Phillips, 1980). Until individual *Microspermopteris*-like plants can be reconstructed more completely, preferably from single localities, it seems premature to make taxonomic conclusions of this sort.

The morphological variability of *H. kentuckyensis* has provided an opportunity to evaluate ontogenetic, taphonomic and structural features of the genus and to demonstrate both inter- and intraspecific heterogeneity within the genus. Characters traditionally used to distinguish subgenera of the genus now appear unreliable. Furthermore, members of the heterogeneous assemblage currently recognized as *Heterangium* are certainly generically distinct from other lyginopterid taxa, particularly *Lyginopteris* and *Microspermopteris.* Previous attempts to link these genera through proposed intermediate forms and stelar similarities are not supported by our present understanding. Only the reconstruction of whole plants in this light will solve many of the unanswered problems with respect to the phylogeny of these lyginopterid pteridosperms. Until reproductive parts are known in organic attachment, stelar organization (particularly protoxylem architecture), cortical histology, and frond morphology represent the most reliable features for reconstructing the sporophytes of plants with *Heterangium* stems.

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