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GROWTH ARCHITECTURE OF *THUCYDIA MAHONINGENSIS*, A MODEL FOR PRIMITIVE WALCHIAN CONIFER PLANTS

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A large number of vegetative and fertile branching systems of *Thucydia mahoningensis* provide data for interpreting the growth architecture and life-history pattern of a primitive Paleozoic conifer. Internal anatomy is similar to modern conifers, indicating an arborescent life-history pattern. Three categories of vegetative plagiotropic branching systems are recognized, and these resemble developmental variations among lateral branching systems in juvenile trees of the extant conifer *Araucaria heterophylla* (Salisb.) Franco. *Thucydia mahoningensis* is considered to be a small tree on the basis of the size and branching pattern of the stem and lateral branching systems and on the basis of internal anatomy. Growth architecture of *T. mahoningensis* conforms to Massart's model, but fertile remains reveal interesting differences from living species. The *T. mahoningensis* tree has an orthotropic stem that bears two orders of plagiotropic vegetative shoots. Fertile shoots have a compound ovulate fertile zone and lack vegetative lateral branches. Ovulate branches bear penultimate-type vegetative leaves in the basal region, a compound ovulate fertile zone in the midregion, and ultimate-type vegetative leaves in the distal region. Axillary ovuliferous dwarf shoots of the compound fertile zones correspond to ultimate branches of the vegetative systems. Compound pollen cones are terminal on branches. These and supplementary data from previously described walchian species reveal that the architecture of the most primitive conifers resembles juvenile araucarian conifers and suggest that giant conifers evolved from diminutive trees by the combination of an extended vegetative growth phase and hypermorphoses in leaf development.

Keywords: Araucaria, fossil, growth architecture, Paleozoic, walchian conifer.

Introduction

Conifers have been an important component of terrestrial vegetation since the end of the Paleozoic (Rothwell et al. 1997). The earliest evidence for conifers occurs in Middle Pennsylvanian deposits of the equatorial Euramerican floral province (Scott and Chaloner 1983; Galtier et al. 1992), with conifers appearing in the Early Permian of the Angaran province (Meyen 1997) and the Late Permian of the Gondwanan and Cathaysian provinces (Florin 1950, 1951, 1964; Clement-Westerhof 1988; Kerp et al. 1990, 1996; Mapes and Rothwell 1991; Rothwell et al. 1997; Chandra et al. 1999; Yao et al. 2000; Hernandez-Castillo et al. 2001*a*, 2001*b*). Primitive conifers are most commonly preserved as coalified compressions that display morphological and cuticular characters (Florin 1938–1945, 1950; Pant 1977; Meyen 1978, 1997; Winston 1983, 1984; Clement-Westerhof 1984, 1987, 1988; Archangelsky and Cuneo 1987; Kerp et al. 1990), but some fossil material also reveals internal anatomical features (Rothwell 1982; Mapes and Rothwell 1984; McComas 1989; Rothwell et al. 1997; Hernandez-Castillo 2000).

Although most Paleozoic fossil localities produce only fragmentary and isolated conifer remains (Florin 1938–1945; Clement-Westerhof 1984, 1987; Kerp et al. 1990), a few deposits yield exceptional conifer assemblages with numerous large, well-preserved specimens (Rothwell 1982; Mapes and Rothwell 1988; McComas 1988; Rothwell et al. 1997; Hernandez-Castillo et al. 2001*b*). The latter have provided data for reconstructing several species of conifer plants that are now known with a level of completeness that approaches that of taxonomic species of living plants. Among these, the Upper Pennsylvanian walchian conifer, *Thucydia mahoningensis* Hernandez-Castillo, Rothwell, and Mapes, is currently the most fully characterized and completely understood (Hernandez-Castillo et al. 2001*b*).

This study employs large numbers of interconnected vegetative and fertile branching systems to assess the growth architecture and life-history pattern for the Paleozoic fossil conifer *T. mahoningensis*. Using *T. mahoningensis* as a model for the architecture of walchian species, we compare Paleozoic walchian conifers with living conifers that conform to Massart's model (Hallé et al. 1978). Similarities and differences among the fossil species and living plants are evaluated to interpret the life-history pattern for *T. mahoningensis* and to assess the types of developmental changes that have occurred during evolution of giant modern conifer trees.

Material and Methods

Thucydia mahoningensis is based on 365 specimens, including 342 vegetative shoots, 22 compound ovulate fertile

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zones, and one compound pollen cone (Hernandez-Castillo et al. 2001*b*). The fossil material was collected from the abandoned 7-11 mine, located north of East Liverpool on Ohio Route 7 in Madison Township, Columbiana County, Ohio (McComas 1988; fig. 1 of Hernandez-Castillo et al. 2001*b*). Conifer remains are preserved as coalified compressions and impressions, and several are partly permineralized by pyrite. The age of the fossil material is Pennsylvanian, most likely Desmoinesian (i.e., Westphalian D) or Missourian (i.e., Stephanian A; McComas 1989). The conifer remains are located in a black shale horizon between the Mahoning Coal (Desmoinesian/Westphalian D) and Brush Creek marine unit (Missourian/Stephanian A). Designation of the Mahoning Coal is based on palynological assessment (*Lycospora* and *Thymospora*), while the Brush Creek marine unit is identified by the presence of the ammonite *Pannoceras* and corroborated by palynological assessment (e.g., *Triticites*) of a coal seam designated as Brush Creek Coal by Kosanke (McComas 1989). However, an alternative hypothesis proposed that these strata may be as recent as Stephanian C or even basal Permian based on floral assemblages and their correlation with European sediments (Wagner and Lyons 1997).

Dissecting needles were used to expose partially covered fossil remains, and morphological characters were observed under a dissecting microscope. Specimens were immersed in alcohol and/or water for observation and image capture. Some images were digitized using Leaf Microlumina System version 1.2 (Westborough, Mass.) and were then used as templates for black-and-white line drawings. Images were stored as PSD files and processed with Adobe Photoshop 6.0.

Results

Thucydia mahoningensis produces three orders of branches (i.e., an antepenultimate stem and penultimate and ultimate branches; fig. 1*A*, 1*B*, 1*H*). All three branching orders are known for both vegetative and reproductive shoots, and all three bear helically arranged simple leaves (fig. 1*A*–1*E*, 1*H*). A fragment of the antepenultimate stem of *T. mahoningensis* is preserved at the base of the specimen in figure 1*A* and 1*B*, where several antepenultimate leaves and plagiotropic penultimate shoots are attached. Most antepenultimate leaves are broken. Nevertheless, they are complete enough to show the same morphology as those found on penultimate and ultimate shoots (fig. 1). The diameter of the antepenultimate stem (7.0 mm) is similar to the largest penultimate shoots in the collection (7.0–9.0 mm), with the attached penultimate shoots corresponding to some of the smallest plagiotropic branching systems at the 7-11 locality (table 1 of Hernandez-Castillo et al. 2001*b*).

Five plagiotropic penultimate shoots extend from the antepenultimate stem, but only four display clear evidence of attachment (fig. 1*A*, 1*B*). These penultimate shoots diverge at almost the same level, forming a pseudowhorl. Therefore, *T. mahoningensis* produced an orthotropic monopodial stem with regular tiers of lateral plagiotropic branches (fig. 1*A*, 1*B*).

The lateral penultimate branches are composed of a penultimate stem that bears series of ultimate shoots, and they typically have a more or less symmetrical form (fig. 1*C*–1*F*). Penultimate systems are the most common conifer branches found at the 7-11 mine. Penultimate shoot systems have different sizes and shapes depending on the diameter and length of the penultimate stem, the number of lateral branches, and the insertion angle(s) of the ultimate branches (fig. 1*C*–1*E*). Three categories of lateral branches are recognized for *T. mahoningensis*. These are ovate (fig. 1*C*), deltoid (fig. 1*D*), and narrowly oblong (fig. 1*E*). Differences in shape are most clearly illustrated by line drawings that are made using fossil specimens as templates (fig. 1*F*). Ovoid plagiotropic branches are the largest shoots (up to 40 cm; fig. 1*C*, 1*F*,*I*), with as many as 92 ultimate branches (fig. 1*C*) that are attached at angles above 50°. Deltoid plagiotropic branches are medium-sized shoots in which ultimate shoots are attached at angles close to 45° (fig. 1*D*, 1*F*,*II*). Narrowly oblong shoots are the smallest, and they have the fewest attached ultimate branches (fig. 1*E*, 1*F*,*III*). Some shoots also display variations in shape, symmetry, and arrangement of ultimate branches (fig. 1*F*,*IV*).

All of these different shapes and sizes correspond to the array of lateral plagiotropic branches produced by juvenile trees of the living species *Araucaria heterophylla* (Salisb.) Franco (figs. 1*G*, 2). *Araucaria heterophylla* displays an orthotropic stem (i.e., an antepenultimate branch) that bears a series of regular tiers of plagiotropic branches (fig. 2*A*; Hallé et al. 1978). Like the fossils, plagiotropic lateral branches of *A. heterophylla* typically display two orders of branching, both of which are covered by helically arranged simple leaves (fig. 2). As in *T. mahoningensis*, leaves on the antepenultimate stem of *A. heterophylla* (*A*) are larger than those of penultimate (*P*) and ultimate shoots (*U*) of lateral plagiotropic branching systems (fig. 2*B*).

The largest plagiotropic branches of *A. heterophylla* are located at the base of the tree (fig. 2*A*) and correspond to the ovoid-shaped specimens of *T. mahoningensis* (figs. 1*C*, 2*C*). Deltoid plagiotropic branches of *A. heterophylla* are located close to the apex of the tree (fig. 2*A*, bracket). Deltoid branches have ultimate shoots that diverge at angles that approach 45°, like the deltoid branches of *T. mahoningensis* (cf. figs. 1*D* and 2*D*). Sizes of deltoid branching systems are always smaller than the ovoid branches (fig. 2*A*). Narrowly oblong branches like those of *Thucydia* do not characterize juvenile trees of *A. heterophylla*. However, this type of morphology does occur at the distal portion of immature (apical) plagiotropic branches of *A. heterophylla* (figs. 1*E*, 2*E*). This suggests that the narrowly oblong specimens of *T. mahoningensis* represent the apical region of immature plagiotropic branches. Like *T. mahoningensis*, *A. heterophylla* also displays variations in size and shape of lateral plagiotropic branches, and adjacent ultimate shoots on each branch may have distinctly dissimilar lengths (cf. fig. 1*F*,*IV*, 1*G*,*IV*).

In contrast to the terminal compound seed cones of living *Araucaria*, the ovulate reproductive organs of *T. mahoningensis* are compound fertile zones (fig. 1*H*). These fertile zones are located on leafy shoots between proximal and distal vegetative regions (fig. 1*H*). Fertile leafy shoots bear leaves of two different sizes that are separated by the ovulate fertile zone (fig. 1*H*). Leaves in the proximal region are longer and wider (mean = 8 mm and 1 mm, respectively) than leaves in the distal zone (mean = 4 mm and 0.9 mm, respectively). Proximal leaves fall within the range of variation for vegetative penultimate leaves (namely, length 5.0–12.5 mm and width

1.0–1.5 mm), while leaves in the distal region fall within the range of variation (namely, length 3.0–6.0 mm and width 0.4–1.0 mm) for vegetative ultimate leaves.

Leaflike appendages of compound ovulate zones (i.e., bracts and sterile scales) also fall within the ranges of variation for penultimate and ultimate vegetative leaves, respectively (Hernandez-Castillo et al. 2001*b*). Bracts are attached to the stem of the ovulate fertile zone and have a mean length and width of 10 mm and 1.2 mm, respectively. Sterile scales are found on axillary ovulate dwarf shoots and have a similar length and width (mean = 3 mm and 0.5 mm, respectively) to vegetative ultimate leaves.

One specimen demonstrates that the ovulate shoots of *T. mahoningensis* are attached to a larger stem (up to 8.0 mm wide; fig. 1*H*) that has leaves up to 17 mm long and 3.0 mm wide. Such leaves are similar in size to those found on the orthotropic stem that bears vegetative shoots (fig. 1*A*, 1*B*, 1*H*; see table 1 of Hernandez-Castillo et al. 2001*b*). At least three ovulate shoots diverge from this large stem, but only one shows organic connection on the exposed rock surface (fig. 1*H*). The distal region of the large shoot appears to have branches that arise in close succession (fig. 1*H*). They diverge from different radii as if they were borne in a pseudowhorl (fig. 1*H*). A third shoot extends away from the basal part of the stem, but the level of attachment for this branch is not preserved (fig. 1*H*). There are no plagiotropic branches on this specimen or on any other fertile specimen in the collection. We interpret this specimen to be an orthotropic stem that bears a pseudowhorl of ovulate fertile branches (fig. 3*B*).

Only a single compound pollen cone of *T. mahoningensis* has been discovered thus far. The morphology of the branch to which pollen cones are attached remains unknown.

Discussion

Thucydia mahoningensis is represented by three orders of interconnected branches. A complete description of *T. mahoningensis* has been published earlier and includes specimens that preserve external morphology, cuticles, and internal anatomy (Hernandez-Castillo et al. 2001*b*). Organic connection between the plagiotropic branching systems and the orthotropic stem reveals a growth pattern similar to juvenile trees of *Araucaria heterophylla* (fig. 2*A*) and other living species that conform to Massart's model of growth (Hallé et al. 1978). This model is characterized by plants that display an orthotropic stem that bears pseudowhorls of lateral plagiotropic (pinnate) branches (fig. 2*A*, 2*B*; fig. 3*A*).

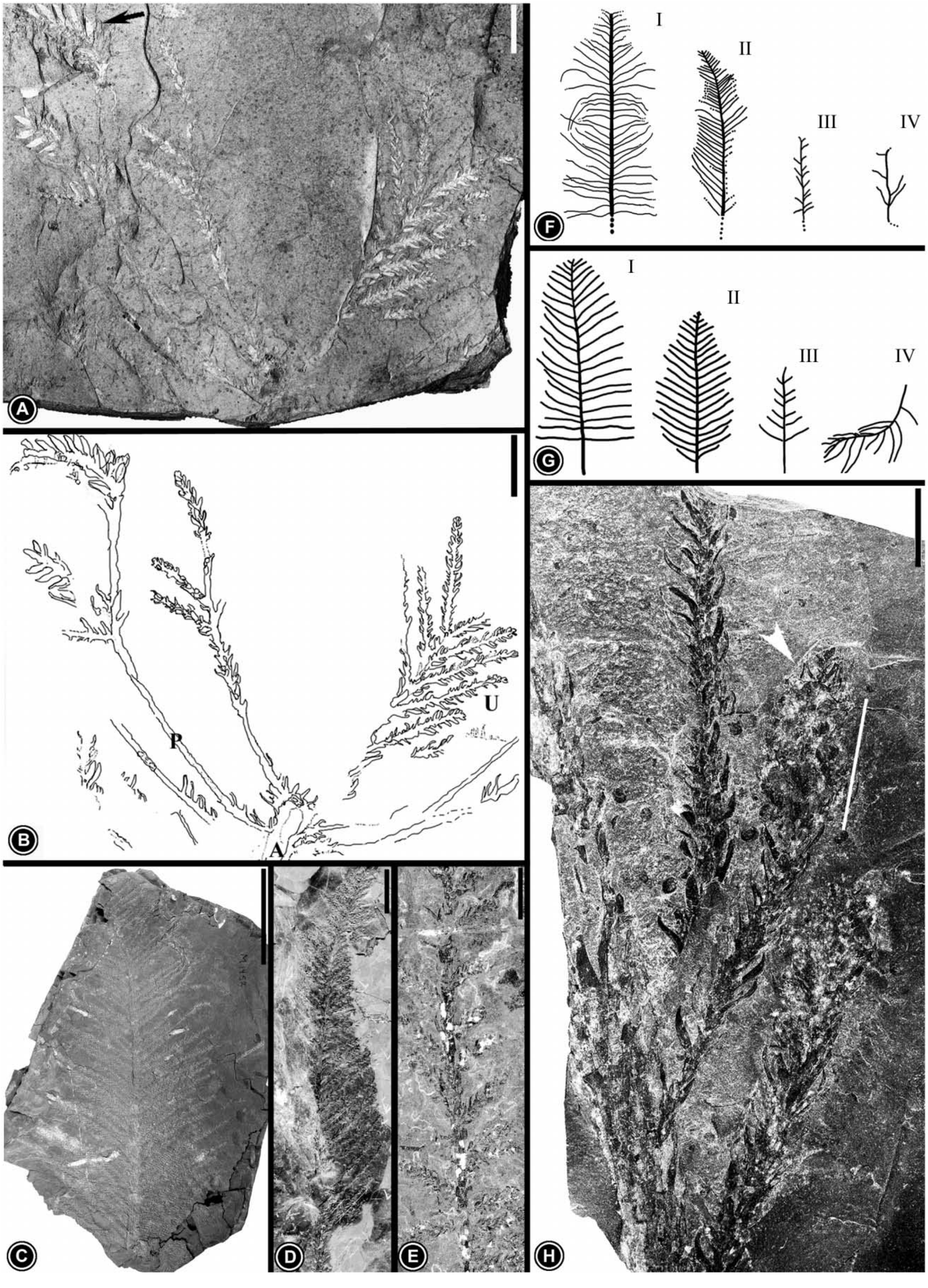
Orthotropic stems with lateral plagiotropic branches, like those of *A. heterophylla* and *T. mahoningensis*, have been proposed as the basic growth form of primitive walchian conifers (pls. IX and X, fig. 14 of Florin 1938–1945, 1951). A specimen described as *Lebachia piniformis* (*sensu* Florin 1938–1945; now *Utrechtia floriniformis* Mapes and Rothwell) shows two plagiotropic branches in organic connection to an antepenultimate stem in a pseudowhorl (pls. IX and X, fig. 14 of Florin 1938–1945). Another specimen described as *L. piniformis* (*sensu* Florin 1938–1945) displays two pseudowhorls of lateral branch scars, and at least one lateral shoot is attached to the upper region of the stem (pls. XIII and XIV, fig. 5 of Florin 1938–1945). The lateral shoots of that specimen appear to be unbranched, as is typical of ultimate shoots. *Lebachia hypnoides* (*sensu* Florin 1938–1945; now *Otovicia hypnoides* [Florin] Kerp et al.) has an antepenultimate shoot that bears at least one plagiotropic branch with terminal pollen cones (pls. XCV and XCVI, fig. 21 of Florin 1938–1945). No pseudowhorl is clearly visible at this level, but this specimen also displays three or more shoots that seem to be borne in a more distal pseudowhorl on the same shoot (pls. XCV and XCVI, fig. 21 of Florin 1938–1945). One specimen described as *Walchia* (*Lebachia*?) spec. (*sensu* Florin 1938–1945) shows a wide antepenultimate shoot (25 mm) with three visible unbranched shoots in a pseudowhorl (pls. CXXXIX and CXL, fig. 7 of Florin 1938–1945).

Taxodiella bardaeana (Zalessky) Meyen from the Permian of western Angaraland appears to have three orders of branching, but the arrangement of ultimate branches is irregular (pl. 28, fig. C of Meyen 1997). Therefore, *T. mahoningensis*, *U. floriniformis*, and *O. hypnoides* are the only species of primitive conifers for which unequivocal orthotropic stems with attached pinnate plagiotropic lateral branching systems have been documented thus far. However, the morphogenus *Tylodendron* Weiss consists of Paleozoic conifer stem casts or permineralizations that also display pseudowhorls with branch scars of lateral shoots. *Tylodendron* specimens are widely distributed throughout Europe and North America, and they suggest that orthotropic stems were produced by many species of walchian conifers (Rothwell et al. 1997).

Vegetative Branches

Although the lateral plagiotropic branching systems of *T. mahoningensis* conform to three categories on the basis of overall shape, size, numbers of ultimate branches, and angles of insertion of ultimate shoots (i.e., ovoid, deltoid, and narrowly oblong; fig. 3*A*), specimens within each category display broad ranges of variation in length and width of penultimate and ultimate shoots (fig. 1*A*–1*F*). Generally, ovoid branches have the longest length, breadth, and widest angles of insertion (45°–90°) where the distal regions of the ultimate shoots often overlap each other (fig. 1*F*,*I*; fig. 4 of Hernandez-Castillo et al. 2001*b*), but the length and angles of insertion of ultimate shoots also overlap among the three types of branches. These large ovoid branches (fig. 1*F*,*I*) conform to the basal plagiotropic branches of juvenile *A. heterophylla* (fig. 2*A*, 2*C*).

Deltoid branches of *T. mahoningensis* are smaller than ovoid branches and have narrower angles of insertion, ranging between 45° and 50°. Length of ultimate shoots of deltoid branches is considerably shorter (5–10 cm) than those of ovoid branches (7–15 cm) (fig. 1*C*, 1*D*; fig. 3*A*). These branches also show a similar pattern as in juvenile trees of *A. heterophylla*, where deltoid branches occur closer to the apex of the tree than do the ovoid branches (fig. 2*A*, 2*D*). Narrowly oblong branches of *T. mahoningensis* have the shortest length (0.6–1 cm) and narrowest width (0.5–0.8 mm), as do young branches near the apex of *A. heterophylla* (fig. 1*E*, 1*F*,*III*; fig. 2*A*, 2*E*). In this type of branch, ultimate shoots are absent or very short near the apex of the penultimate shoot, and they also have the smallest number of ultimate shoots per plagiotropic branching system (fig. 1*E*, 1*F*,*III*; figs. 2*E*, 3*A*). Progressively, larger pen-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ultimate shoots have successively larger numbers and lengths of ultimate shoots.

Because juvenile trees of *A. heterophylla* display relatively large, ovoid plagiotropic branches, deltoid medium-size branches, and narrowly oblong small branches near the apex, variations among lateral branching systems of *T. mahoningensis* are equivalent to developmental differences in branches of *A. heterophylla*. These developmental variations include different interbranch distances in both *T. mahoningensis* and *A. heterophylla* (figs. 1*F*, 1*G*, 2*F*, 3*A*). Other members of *Araucaria* section *Eutacta* also display a similar growth architecture and branching pattern to that of *Thucydia*. For example, young trees of *Araucaria columnaris* (Forster) Hooker share the same tree architecture and shape, size, and distribution of plagiotropic lateral branching systems (G. R. Hernandez-Castillo, personal observation). Some *A. columnaris* trees even produce odd, narrowly oblong branches at the base of 1–2-yr-old trees (G. R. Hernandez-Castillo, personal observation).

Fertile Branches

Architecture of the ovulate fertile branches of *T. mahoningensis* differs from that of vegetative branches. Compound ovulate zones are located in the middle region of fertile shoots that bear vegetative leaves in both proximal and distal regions (figs. 1*H*, 3*B*, 3*C*; Hernandez-Castillo et al. 2001*b*, fig. 10). Length and width of leaves at opposite ends of the fertile shoots are similar to different categories of vegetative leaves. Proximal leaves on fertile shoots are similar in length to penultimate leaves on vegetative shoots, while distal leaves are similar to proximal leaves of ultimate shoots. Subtending bracts and sterile scales of compound ovulate zones are also similar in length and breadth to vegetative penultimate and ultimate leaves, respectively. Therefore, the axillary ovulate dwarf shoots are equivalent to ultimate branches on vegetative shoots in both branching complexity and leaf size (fig. 3*B*, 3*C*).

Using this rationale, the stem to which ovulate fertile shoots are attached (fig. 1*H*) may be considered an antepenultimate branch (fig. 3*B*). This is equivalent to the orthotropic vegetative stem (namely, antepenultimate branch; fig. 1*A*, 1*B*), and it accounts for the apparently pseudowhorled arrangement of ovuliferous branches on the fertile specimen of *T. mahoningensis* (fig. 1*H*). Additional specimens of *T. mahoningensis* that show attachment of the pollen cones will be required to determine whether the pollen-bearing branches conform to the same general pattern of organization as the vegetative and ovulate lateral branches (i.e., two levels of organization).

Growth Patterns among Walchian Conifers

From these data, we interpret the mature *T. mahoningensis* tree to be roughly equivalent to a juvenile *A. heterophylla* tree in branching pattern and branching complexity (fig. 3*A*). *Thucydia mahoningensis* produces fertile ovulate zones on lateral branches near the top of the small tree and vegetative plagiotropic branches at more basal pseudowhorls. These fertile and vegetative lateral shoots are of comparable branching complexity (i.e., two orders of branching), in which the ultimate branches are either ovuliferous dwarf shoots or leafy vegetative shoots (fig. 3*A*–3*C*). The axis of the ovulate zone is the penultimate branch, and the branch to which this fertile branch is attached represents an antepenultimate orthotropic stem.

An ovulate shoot with two orders of complexity has been described previously for *O. hypnoides* (=*L. hypnoides* of Florin 1938–1945, 1951). This specimen (i.e., pls. CI, CII, fig. 2 of Florin 1938–1945) shows a terminal compound ovulate cone attached to the apex of a penultimate shoot, and the rest of the shoot bears short, ultimate vegetative branches. Therefore, the ovulate-branching systems of *O. hypnoides* and *T. mahoningensis* are both constructed of two orders of branching. The two species differ in architecture because (1) *T. mahoningensis* produces compound ovulate zones in the midregion of the branch, whereas *O. hypnoides* produces terminal compound ovulate cones; (2) the *T. mahoningensis* fertile branch lacks subtending vegetative branches found in *O. hypnoides*; and (3) *T. mahoningensis* ovulate shoots are radial in organization, while those of *O. hypnoides* are planar. The fertile branches of *U. floriniformis* (=*L. piniformis sensu* Florin 1938–1945, 1951) are more complex, showing three orders of branching (i.e., pls. XXVI–XXVII, fig. 7, and pls. XXIX–XXX, figs. 6, 7 of Florin 1938–1945). *Utrechtia floriniformis* specimens have ovulate cones attached to the lateral branches of a plagiotropic system. Therefore, the lateral branches with a terminal cone are compound shoots. The other

Fig. 1 *Thucydia mahoningensis* Hernandez-Castillo, Rothwell, and Mapes vegetative and fertile shoots. *A*, Antepenultimate orthotropic stem with lateral plagiotropic branching systems. Note entirely different leaf shapes according to splitting of rock (arrow). OUPH 13411 (G200), scale = 1 cm. *B*, Line drawing from specimen on fig. 1*A*. Note attachment of lateral plagiotropic branching systems to orthotropic antepenultimate stem (*A*) and shape and size of penultimate (*P*) and ultimate (*U*) leaves on same branching system (upper left side). OUPH 13411 (G200), scale = 1 cm. *C*, Large plagiotropic branching system. Note overall ovate shape of branching system, size, and insertion angles (45°–50°) of ultimate shoots. OUPH 13412, scale = 10 cm. *D*, Medium-sized plagiotropic branching system. Note overall deltoid shape of shoot and size and angles of insertion (≤45°) of ultimate shoots. OUPH 13413 (G8), scale = 2.5 cm. *E*, Small lateral plagiotropic branching systems. Note narrowly elongate shape and small size of ultimate shoots. OUPH 13419 (GPC-1), scale = 3 mm. *F*, Line drawings of four specimens showing different types of lateral plagiotropic branches. Size of drawings is proportional to size of original specimens. *I*, Ovate (from specimen OUPH 13414); *II*, deltoid (OUPH 13413); *III*, narrowly oblong (OUPH 13419); and *IV*, abnormal lateral plagiotropic branch that lacks symmetry and ultimate shoots (G201). *G*, Line drawings of four lateral plagiotropic branching systems of juvenile tree of *Araucaria heterophylla*. Shape of branches is similar to that of *T. mahoningensis*, and size of drawings is proportional to size of original branches. *I*, Ovate (at base); *II*, deltoid (second pseudowhorl from apex to base); *III*, deltoid, narrowly oblong (youngest apical branch); and *IV*, abnormal lateral plagiotropic branch that displays variations in symmetry and number of ultimate shoots. *H*, Fertile specimen in which lateral shoots are borne in a pseudowhorl. Compound ovulate zones are located between two vegetative zones (line). Lateral branches are unbranched and broken at the distal region, where stem continues to produce more leaves (arrowhead). OUPH 13450 (GR-1), scale = 1 cm.

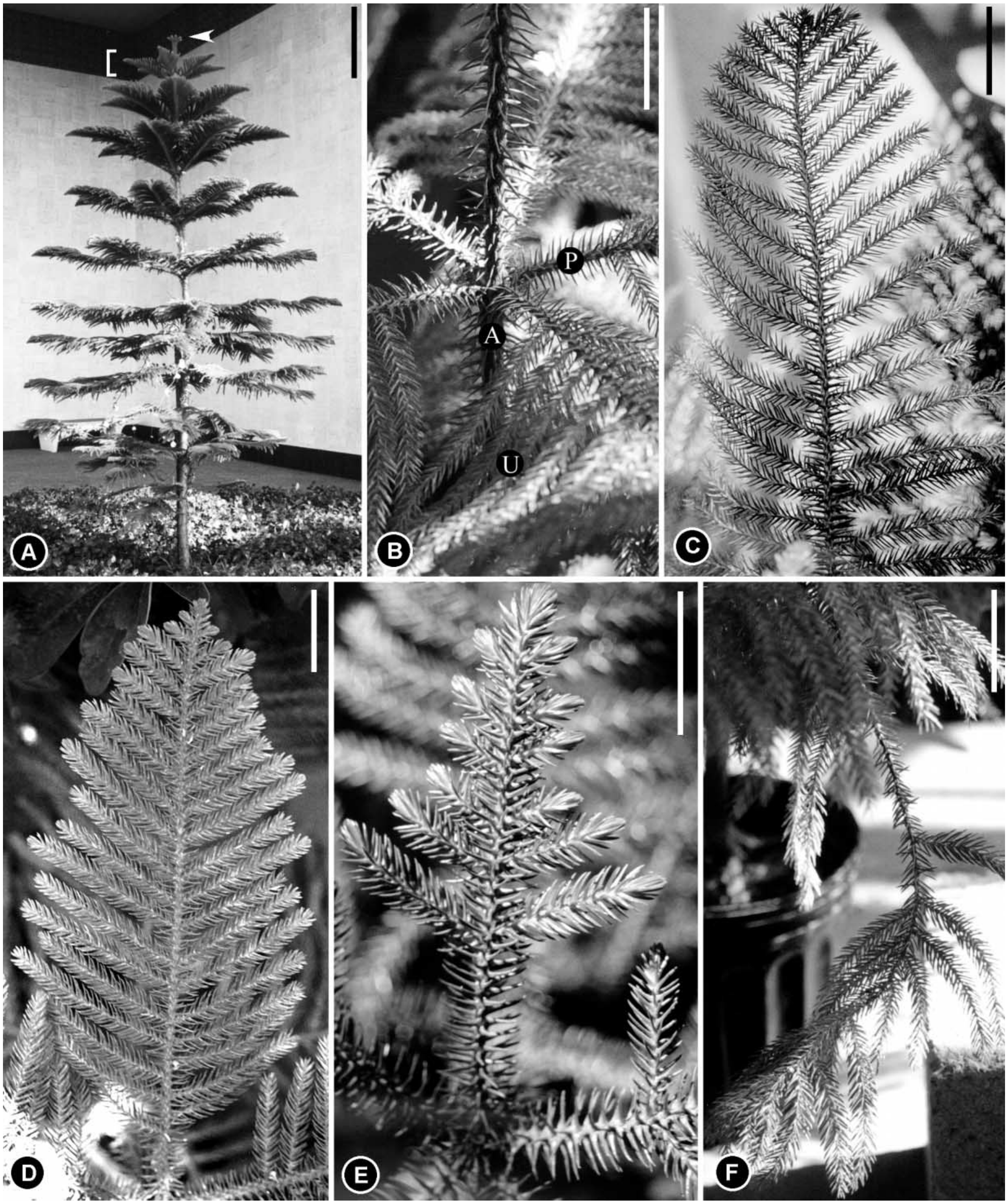

Fig. 2 Juvenile tree of *Araucaria heterophylla* (Salisb.) Franco. *A*, Tree showing an orthotropic stem with pseudowhorls of lateral plagiotropic (pinnate) branches. Youngest and smallest plagiotropic branches (arrowhead) shown at apex; second node (apex to base) displays medium-size branching systems that are deltoid in shape (bracket); and remaining nodes display large plagiotropic branching systems that are ovate in shape. Scale = 30 cm. *B*, Third node from apex to base showing orthotropic antepenultimate stem with five lateral plagiotropic branches. Note size of antepenultimate (*A*), penultimate (*P*), and ultimate leaves (*U*). Scale = 1 cm. *C*, Ovoid lateral plagiotropic branching system. Note angles of insertion of distal (45°–50°) and basal (>50°) ultimate branches. Scale = 10 cm. *D*, Deltoid plagiotropic lateral branching system showing overall shape, angles of insertion of ultimate shoots (45°–50°), and triangular apex. Scale = 10 cm. *E*, Apical lateral branching system (apical node) that shows triangular shape where distal portion of branch has narrowly oblong shape. Scale = 1 cm. *F*, Basal lateral plagiotropic branching system showing lack of ultimate shoots and abnormal shape caused by lack of sunlight. Scale = 10 cm.

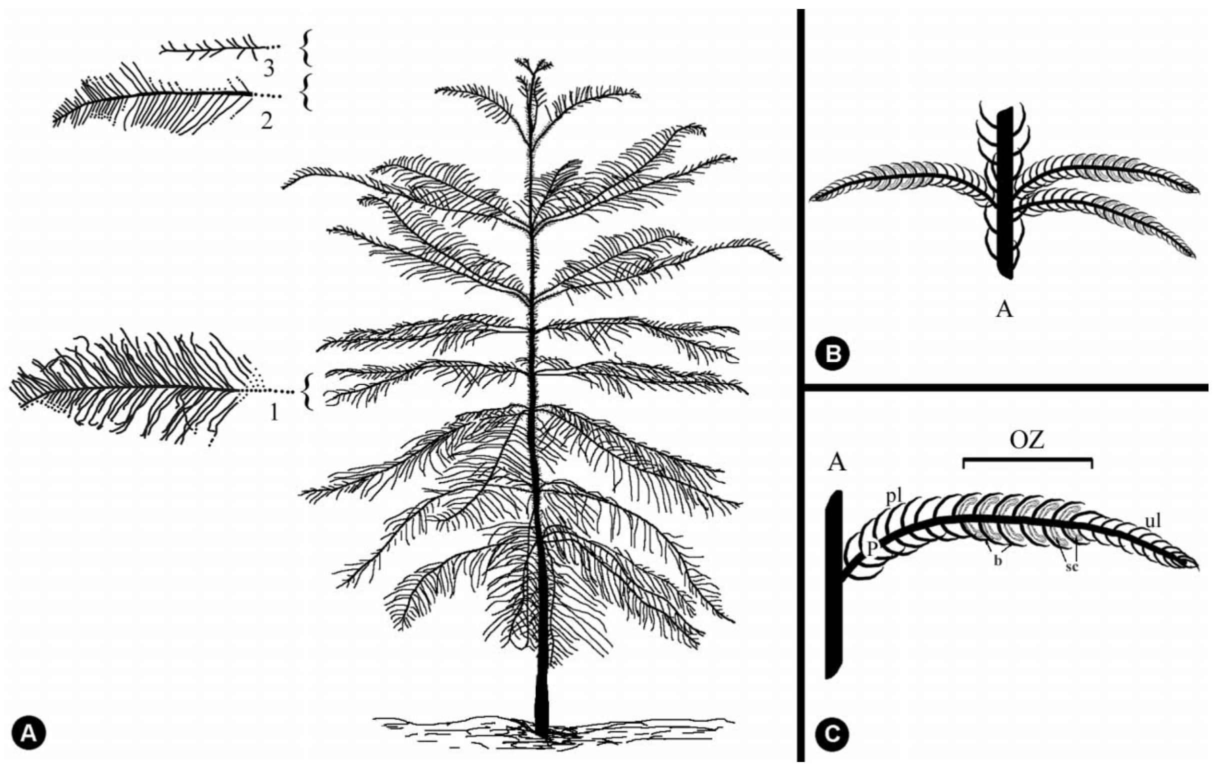

Fig. 3 *Thucydia mahoningensis* Hernandez-Castillo, Rothwell, and Mapes plant reconstruction. *A*, Reconstruction of the plant showing a small tree with an orthotropic stem that bears several nodes with lateral plagiotropic branching systems. Note types (*1*, oblong; *2*, deltoid; and *3*, narrowly oblong) and distribution of vegetative lateral plagiotropic branches. *B*, Fertile branching systems of *T. mahoningensis* in which orthotropic stem (*A*) bears unbranched lateral fertile shoots. *C*, Fertile lateral branching system composed of penultimate stem (*P*) that bore proximal penultimate leaves (*pl*), an intermediate compound ovulate zone (*oz*), and distal ultimate leaves (*ul*). Penultimate stem (*P*) is also compound ovulate zone axis, where ultimate shoots are represented by axillary dwarf shoots (*ds*). Bracts (*b*) of compound ovulate zones are similar in size to vegetative penultimate leaves. Sterile scales (*sc*) of axillary dwarf shoots are similar in size to vegetative ultimate leaves.

laterals are ultimate branches, being either vegetative or terminating in a simple pollen cone.

Additional information about the architecture of walchian conifers was obtained from specimens recently described as *Culmitzschia laxifolia* and *Hermitia germanica* from the Fischbach-Niederwörresbach locality in the northern Saar-Nahe Basin, Germany (Lausberg 2002). These specimens show orthotropic stems with several lateral plagiotropic branches that resemble juvenile trees of living *Araucaria* (Hallé et al. 1978; Veillon 1978; Hallé 1999; Grosfeld et al. 1999). Other variations known from previously described walchian specimens (Florin 1938–1945), such as plagiotropic lateral branches with orthotropic tendencies and apparently unbranched laterals, etc., need to be reassessed and compared with extant species that share such variations.

Plant Stature and Growth Architecture

The pseudowhorled, orthotropic branching pattern of *T. mahoningensis* stems demonstrates that the plant had a monopodial stem with regular tiers of plagiotropic branches, as do juvenile trees of *A. heterophylla*. On the basis of the size of the stems, branching patterns of shoot systems, size and shapes of vegetative branching systems, and internal anatomy of the plant (Hernandez-Castillo et al. 2001*b*), we interpret *T. mahoningensis* to have grown as a small tree. The woody stems indicate that the plant lived for an extended period, but the consistently small size of the branching systems demonstrates that it probably was a very small tree. By comparing the largest plagiotropic laterals of *T. mahoningensis* to similar sized basal branches of *A. heterophylla*, we estimate that *T. mahoningensis* attained a height of only ca. 2 m. A comparison of the diameter for the known orthotropic *Thucydia* stem specimens (i.e., 5–8 mm) with stems of *A. heterophylla* also supports this interpretation. This interpretation is consistent with walchian branches from other localities (Florin 1938–1945; Rothwell et al. 1997) and also with the diameter of the only *in situ* walchian forest known thus far (Calder 1995; G. W. Rothwell and G. Mapes, personal observation).

Several models have been developed to characterize growth architecture for arborescent vascular plants (Hallé et al. 1978; Bell 1991). The growth of many extant conifers is explained either by Rauh's model or Massart's model (Hallé et al. 1978; Veillon 1980; Bell 1991; Hill 1997; Hallé 1999). Trees with a monopodial stem and series of regular plagiotropic branches, such as *T. mahoningensis*, conform to Massart's model (Hallé et al. 1978). These include all of the walchian conifers for which growth architecture can be determined (Mapes and Rothwell 1991), and this supports Florin's original interpretation for the most ancient conifers (Florin 1927; 1938–1945; 1951). Massart's model is typical for many living species of the Araucariaceae, Pinaceae, and Taxaceae (Hallé et al. 1978).

While vegetative lateral shoots of *T. mahoningensis* are always plagiotropic with many ultimate branches, ovulate shoots have no vegetative branches (fig. 3*B*). Most other conifers produce their seed cones on highly branched lateral systems. These include the other walchian conifers for which this feature is known (i.e., specimens described as *L. piniformis* [= *U. floriniformis*] and *O. hypnoides*). One exception is the recently discovered living araucarian species *Wollemia nobilis* Jones, Hill, and Allen (Hill 1997), in which none of the fertile laterals are branched (pinnate) and cones terminate the branches of mature trees. However, *W. nobilis* differs from *T. mahoningensis* by having reiteration of the lateral branches. After a cone of *W. nobilis* senesces, the entire branch abscises and a new adventitious branch is produced in the same location (Hill 1997).

Living conifers typically produce terminal seed cones, but continued activity of the apical meristem sometimes produces a vegetative branch from the tip of the cone (Chamberlain 1935). Species from several groups of living conifers occasionally show this pattern, which is considered to be a teratology rather than a characteristic growth pattern (Chamberlain 1935; Gifford and Foster 1989). Terminal cones have also been described as the typical condition in primitive conifers (Florin 1927, 1938–1945, 1951), but *T. mahoningensis* and several other Paleozoic species with ovulate fertile zones (e.g., *Voltzia hexagona* [Bischoff] Geinitz and *Concholepis harrisii* Meyen and other coniferophyte-like plants [Rothwell and Mapes 2001]) show that compound ovulate zones or intercalary ovulate cones may be more common than previously realized (Hernandez-Castillo et al. 2001*b*; Rothwell and Mapes 2001). Nevertheless, the exact nature of fertile structures is not a diagnostic component of Massart's model. Therefore, *T. mahoningensis* and other species with unbranched ovulate shoots and/or ovulate fertile zones, rather than compound cones, may be included.

Because evolutionary changes commonly result from alterations of ontogeny (Gould 1977; Rothwell 1987), a comparison of *T. mahoningensis* with living conifer trees allows for the recognition of consistent differences in growth and for the identification of evolutionary changes that may be responsible for the differences. One of the most obvious differences between *T. mahoningensis* and living conifers is in the morphology of ovulate fertile structures. Transformation of the compound ovulate fertile zones in *T. mahoningensis* to the terminal compound cones of living conifers requires only maturation of the apical meristem with differentiation of tissues at the cone apex. The ease of this transformation is evident from the teratologies that are well known for living conifers (Chamberlain 1935; Gifford and Foster 1989), and the nearly universal production of terminal ovulate cones in Mesozoic and more recent species indicates that this change occurred early in conifer evolution.

A striking similarity between walchian conifers and juvenile plants of several araucarian conifers was first recognized by Florin (1927). This is clearly illustrated by comparing our reconstruction of *T. mahoningensis* (Hernandez-Castillo et al. 2001*b*) or Florin's reconstruction of *U. floriniformis* (*L. piniformis sensu* Florin 1938–1945, 1951) with juvenile plants of the genus *Araucaria* such as *A. heterophylla* (fig. 2*A*). All three have an orthotropic monopodial stem with pseudowhorls of lateral plagiotropic shoots that produce two orders of branches with helically arranged needle-like leaves. Whereas *T. mahoningensis* and other walchian conifers were apparently all small trees that produced a single morphology of leaves on the ultimate branches throughout the life of the plant, many living conifers grow to giant stature, and some produce leaves with different morphologies during different stages of growth. For example, seedlings of some living species of the Cupressaceae produce needle-like taxodioid leaves, while older plants produce scalelike leaves (e.g., *Sequoiadendron giganteum*; Falder 1999). Many species of *Araucaria* (including *A. heterophylla*) produce needle leaves as juvenile plants (e.g., fig. 2*A*) and one or more additional morphologies of leaves on older plants (de Laubenfels 1972). This age-related heterophylly characterizes several species of the *Eutacta* section of *Araucaria* (de Laubenfels 1972).

Using *T. mahoningensis* as a model, walchian conifers (including *Ernestiodendron* Florin, *Otovicia* Kerp et al., *Emporia* Mapes and Rothwell, and *Utrechtia* Mapes and Rothwell [= *Lebachia sensu* Florin]) can be characterized as surprisingly small conical trees with monopodial orthotropic stems that produced plagiotropic branches in pseudowhorls. The production of abundant wood in *Thucydia* (Hernandez-Castillo et al. 2001*b*) and *Emporia* (Mapes and Rothwell 1984) indicates that these plants were long-lived woody perennials. Thick cuticles and needle-like leaves in most walchian species, combined with evidence for the existence of seed dormancy in the walchian genus *Emporia* (Mapes et al. 1989), indicate that walchians were stress-tolerant plants that lived in relatively dry habitats (Rothwell et al. 1997), as do many extant conifers.

If living araucarian conifer trees became reproductive at a comparable size to walchians such as *Thucydia*, then all would share common features of growth architecture, leaf morphology, and phenology. However, the living species are extremely long-lived plants that grow to a giant size before reaching reproductive maturity and often show distinct age-related heterophylly (de Laubenfels 1972; Stockey 1982). Nevertheless, only two important developmental changes would be required to transform the architecture of *T. mahoningensis* and similar walchian species to that of living members of the Araucariaceae. These are (1) an extended delay in the onset of reproductive maturity and (2) a change in leaf morphology associated with an extended period of growth. Both of these can be understood as resulting from changes in the relative timing and rates of growth for different features of an organism that are encompassed by the concept of heterochrony (Gould 1977). Delay in the onset of fertility is explained by the process of postdisplacement, while the change in leaf morphology associated with increased size can be attributed to the process of hypermorphosis (McNamara 1986).

Interpretations of growth, development, phenology, and life-history patterns for extinct species, such as those developed here, provide an additional dimension of understanding about plant evolution. *Thucydia mahoningensis* is an excellent example of how the fossil record can be used to infer roles that individual species played in ancient plant communities and ecosystems, thus allowing us to increase our knowledge of primitive representatives of living groups and the changes that have resulted in the living representatives.

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