The Corystospermales (= Corystosperrmacae Thomas, 1933) are a heterogeneous group of Mesozoic pteridosperms that combine fern-like foliage with seeds enclosed in a cupule. First described from the Molteno Formation of South Africa, the corystosperms are known today to have occurred throughout the Southern Hemisphere during the Triassic, frequently as a dominant component in the flora (Thomas, 1933; Anderson and Anderson, 1983). Anatomy is known for almost every organ comprising corystosperm vegetative and reproductive systems (Pigg, 1990; Taylor, 1992; Meyer-Berthaud, Taylor, and Taylor, 1993; Yao, Taylor, and Taylor, 1995), with the exception of Umkomasia Thomas, the cupulate ovule-bearing structure, which is known only from compression fossils (Thomas, 1933; Lacey, 1976; Holmes and Ash, 1979; Retallick, 1980; Holmes, 1982, 1987; Playford, Rigby, and Archibald, 1982; Kirchner and Muller, 1992; Pole and Raine, 1994; AxsSmith et al., 2000). Although many species of Umkomasia have been described, important details of its morphology have remained ambiguous due to a lack of anatomical information. Additionally, conflicting interpretations of the homologies of the reproductive structures of corystosperms have resulted in poor resolution of their position in reconstructions of seed plant phylogeny (e.g., Nixon et al., 1994; Rothwell and Serbet, 1994; Doyle, 1996).

Here we provide the first description of anatomically preserved Umkomasia and an emendation of the diagnosis for the genus, based on examination of the type material in conjunction with new information. The specimens were recovered from Fremouw Peak in the central Transantarctic Mountains of Antarctica. Histological and morphological features are identified that clearly affiliate these organs with the Corystospermales and with other corystosperm organs described from Fremouw Peak (Pigg, 1990; Taylor, 1992; Meyer-Berthaud, Taylor, and Taylor, 1993; Yao, Taylor, and Taylor, 1995). Anatomical organization of the silicified specimens of Umkomasia is correlated with morphology of compression specimens, which clarifies many characters that have been difficult to interpret since their original description by Thomas (1933). In addition to aiding in assessment of homologies among the Mesozoic pteridosperms and other seed plants, these specimens provide critical insights into recent reconsideration of the corystosperms as potential angiosperm ancestors.

MATERIALS AND METHODS

The description that follows is based on silicified specimens preserved in permineralized peat collected from a col north of Fremouw Peak in the Queen Alexandra Range of the central Transantarctic Mountains (84°17′41″ S, 164°21′48″ E, 2385 m above sea level; Barrett and Elliot, 1973). The peat is found in carbonaceous mudstones of the upper Fremouw Formation, which is early Middle Triassic in age based on palynostratigraphy (Farabee, Taylor, and Taylor, 1990). All specimens were studied using the acetate peel technique (Galtier and Phillips, 1999) after the polished surface was etched in 49% hydrofluoric acid. A thin layer of epoxy was periodically applied under vacuum in order to stabilize specimen surfaces and ensure even etching. Peels were mounted on standard microscope slides, which are housed in the Paleobotany Division of the Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence, Kansas, USA, under accession numbers 20094–20351.

SYSTEMATICS

Order—Corystospermales.

Family—Corystospermaeae.

1933 Unkomasia Thomas, p. 203, Figs. 1–4, and Plate 23, Fig. 56.
1933 Pilophorosperma Thomas, p. 207, Figs. 9–11, and Plate 23, Fig. 58.

Emended diagnosis—Ovulate reproductive organs consisting of a three-dimensional branching system of at least two orders; ultimate branches bearing helically attached cupules; cupules pedicellate or sessile, recurved, ovoid, divided into two well-defined lobes by adaxial and abaxial clefts or unlobed with a single elongate abaxial cleft, each bearing one or two ovules abaxially; ovule with extended bifid integumentary apex.

Species—Unkomasia resinosa sp. nov.

Diagnosis—Cupules glabrous with uniseriate epidermis; cortex heterogeneous with distinct inner and outer zones of parenchymatous tissue, sclerified cells isolated or in clusters, spherical secretory cavities lined with a single layer of epithelial cells; flattened vascular strand with radially aligned xylem and phloem centrally located in each lobe; vascular strand surrounded by up to four rows of tabular cells; ovules small, orthotropous, flattened to rounded in cross section, with basal disk of tracheids in chalaza; nucellus thin with apical nucellar beak; integument comprised of small, isodiamicellular cells, with abundant secretory cavities and tabular, thick-walled cells lining interior surface, fused to cupule wall at base only, apex bifid and protruding past cupule apex; cupule stalk terete to ovoid in cross section, with two-zoned cortex, sclerified cells and abundant secretory cavities, two flattened vascular strands of radially aligned xylem and phloem fusing into single flattened vascular strand distally; cupulate branch determinate, with two-zoned cortex, sclerified cells, secretory cavities, and three flattened vascular strands of radially aligned xylem and phloem at base, producing paired cupule traces from adjacent arms in helical pattern; pith with sclerified cells and secretory cavities.

Holotype—Slide #20094, 11323 DE #6, Figs. 1 and 5 in this paper.

Paratypes—Slide #20095, 11323 DE #23, Figs. 2, 6, and 13; slide #20096, 11323 DE #38, Figs. 3, 8, and 15; slide #20097, 11323 DE #125, Figs. 4 and 9; slide #20098, 11323 DE #51, Fig. 7; slide #20099, 11323 DE #91, Fig. 10; slide #20100, 11323 DE #101, Fig. 11; slide #20101, 11323 DE #13, Fig. 12; slide #20102, 11323 DE #9, Fig. 14.

Repository—Paleobotany Division of the Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence, Kansas, USA.

Type locality—Fremouw Peak, Queen Alexandra Range, Antarctica (84°17′41″ S, 164°21′48″ E, 2385 m above sea level), Buckley Island Quadrangle, Barrett and Elliott, 1973.

Stratigraphic position—Top of the upper portion of the Fremouw Formation.

Age—Early part of the Middle Triassic.

Eymology—The specific epithet resinosa (Latin) refers to the abundant secretory cavities in this organ.

DESCRIPTION

The following description is based on one specimen of an axis with attached cupules and additional specimens of isolated cupules. Unkomasia resinosa is a determinate branching system with cupulate branches at least 15 mm long that bear up to five helically arranged ovulate cupules. The cupules are recurved and ovoid and attached to the branch by short stalks. Each cupule encloses one or two ovules on the abaxial surface of the cupule lobes. Ovules are orthotropous and fused to the cupule wall only at the base. The tip of the ovule integument is bifid and extends past the apex of the cupule.

Cupules—Each cupule is ovoid to somewhat spherical and reflexed toward the base of its stalk. Cupules are bilaterally symmetrical, approximately 7 mm long, 2.7–5.5 mm wide, and 3.3–5.5 mm deep from dorsal to ventral surfaces, with two patterns of morphological organization. A bilobed morphology appears to be more common, with one ovule attached to each lateral lobe (Fig. 1). This organization occurs in a cupule attached at the base of the branch, as well as in isolated specimens. Cupules attached at the apex of the branch are unlobed and possess a single ovule (Figs. 3 and 6–9). In all cupules, the bifid tip of the integument extends past the cupule wall, fused only at the base.

Bilobed cupules are obovate in cross section, with thick lateral walls forming two crescent-shaped lobes (Figs. 1 and 17). During initial sectioning of the permineralized peat block in which Unkomasia resinosa was preserved, approximately 3 mm of the cupulate branch and the middle section of the bilobed cupulate attached to the branch were destroyed. The apex and base of this cupule were subsequently observed on facing surfaces of the blocks. The cupule measures approximately 5.5 mm from dorsal to ventral surfaces and is 4 mm wide at the widest point. Because the cupules are recurved, the apex is oriented downward and the base is at the top of the cupule. In the apical region, only one of the lateral lobes is preserved, with the position of the bifid tip of the integument indicated by two C-shaped structures that ultimately fuse around the micropylar opening. Above this, the two lobes are roughly crescent-shaped in cross-section (Fig. 17). The lobes slightly overlap the stalk on the ventral surface of the cupule and are free from each other on the dorsal surface of the cupule (Figs. 1 and 17). The dorsal opening is narrow (less than 1 mm). A flattened vascular strand occurs centrally in each lobe, at the boundary between the inner and outer cortical tissue zones, but does not extend into the apex of the lobe (Figs. 17 and 18A). At the base of the cupule, the lobes fuse with the stalk and to each other on the dorsal surface (Fig. 2). The epidermis on the inner and outer surfaces of the cupule lobes is smooth, although the outer surface is irregular in outline. This may be due to desiccation or degradation prior to preservation.

Two cupules attached near the apex of the cupulate branch display the second, unlobed morphology, although the more apical cupule is incompletely preserved and slightly distorted (Fig. 3). Both cupules enclose a single ovule. The more completely preserved cupule is roughly ovoid in cross section and measures 2.7 mm wide and 3.3 mm from dorsal to ventral surfaces at its greatest dimensions; its length is estimated to
Figs. 1–5. *Umkomasia resinosa*. 1. Cross section in midregion of bilobed cupule, with two crescent-shaped lobes, integument of aborted ovule attached to right lobe (detail in bracket shown in Fig. 5), ovule (O) attached to left lobe, and cupule stalk (CS); note secretory cavity (arrow) and distinct inner (IC) and outer (OC) cortical zones. Scale bar = 1 mm. Slide #20094, 11323 DE #6. 2. Cross section near base of bilobed cupule, with lobes fused to the cupule stalk on the ventral surface (right) and to each other on the dorsal surface (left); note two vascular strands (arrows). Scale bar = 1 mm. Slide #20095, 11323 DE #23. 3. Cross section of unlobed cupules, each enclosing a single ovule (O); note three cupule stalks (arrows) and numerous secretory cavities (SC) in integuments. Scale bar = 1 mm. Slide #20096, 11323 DE #88. 4. Cross section of lower region of cupule stalk, with two vascular strands (arrows) and distinct inner (IC) and outer (OC) cortical zones. Slide #20097, 11323 DE #125. Scale bar = 500 μm. 5. Detail of area in bracket in Fig. 1, integument of aborted ovule showing sclerified cells along interior wall. Scale bar = 250 μm. Slide #20094, 11323 DE #6.
be approximately 5 mm. At the apex, the bifid tip of the integument extends beyond the lip of the cupule (Figs. 6 and 18B). Above this, the lateral and dorsal walls enclose the ovule; the lateral walls partially overlap the cupule stalk to form an elongate opening on the ventral surface of the cupule (Figs. 7–8 and 18B). A single flattened vascular strand occurs in the center of the dorsal wall and extends to within 1 mm of the cupule apex (Figs. 7–9 and 18B). Both outer and inner epidermal surfaces of the cupule are smooth, but the outer surface is irregular in outline. Near the base of the cupule, the integument of the ovule is fused to the dorsal wall (Figs. 8 and 18B). Ultimately, the lateral walls fuse with the stalk near the base of the ovule (Figs. 9 and 18B).

In both morphotypes, the cupule wall possesses distinct inner and outer zones of tissue organization (Figs. 1 and 7). Inner cortical cells are thin-walled, isodiametric to polygonal, and measure up to 105 μm in diameter. Many of these cells are filled with dark contents. Outer cortical cells are more thin-walled, isodiametric, and larger (up to 150 μm in diameter); these cells lack contents. Sclerified cells with unevenly thickened walls occur in the cortex, usually isolated but occasionally in clusters of up to five cells (Fig. 14). These cells are polygonal in cross section, measure up to 102 μm in diameter with cell walls approximately 14 μm thick, and possess simple pits (Fig. 15). Spherical secretory cavities (Figs. 1 [arrow] and 14) are large (up to 264 μm in diameter) and occur throughout the cortex, but are more common in the outer cortical zone. Each secretory cavity is lined by a single row of thin-walled, elongate epithelial cells, which measure up to 117 μm long and 36 μm wide. An amber to dark brown inclusion is frequently present within the cavities. Epidermal cells are occasionally preserved along the smooth interior surface of the cupule lobes (Fig. 14). These cells are thin walled, square to rectangular, and measure up to 12 μm wide and 33 μm long.

Cupules are helically arranged on the cupulate branch, borne on short stalks that are terete to ovoid in cross section. The cortex of the stalk is bizoned, with a narrow inner cortex consisting of 2–3 rows of cells (Fig. 4). Secretory cavities and sclerified cells are present throughout the length of the stalk. Two flattened vascular strands form a wide V-shaped trace in the base of the stalk (Fig. 4). The two strands fuse into a single vascular strand distally (Fig. 18A, B). Phloem is oriented abaxially.

**Ovules**—Ovules are small, ranging from 1.0 mm to 3.5 mm in diameter, and are somewhat flattened in cross section when they appear in pairs (Figs. 1 and 17). When ovules occur singly in a cupule, they are more irregular in outline (Figs. 3 and 7). In most specimens, only the integument and nucellus are preserved. The integument is a thin, heterogeneous tissue, approximately 150 μm thick, with abundant secretory cavities, which are identical in organization to those observed in the cupule and cupule stalk. The principal tissue of the integument consists of small, thin-walled, isodiametric cells measuring up to 75 μm in diameter. In cross section from the base to near the apex of the nucellus, however, 2–3 layers of small, thick-walled, tabular cells line the interior surface of the integument (Fig. 5). These cells measure up to 53 μm in diameter and have cell walls up to 4 μm thick. At the apex, the integument extends approximately 1 mm past the cupule lobes and is bifid (Fig. 6). The bifid morphology is indicated in serial cross sections by two C-shaped structures that eventually fuse around the micropylar opening. Within the cupule, the integument is free from the cupule wall and attached only near the chalaza (Fig. 8). The point of attachment of the ovule to the cupule wall is broad, extending up to 1.1 mm in cross section, and delineated by a zone of small, thin-walled, isodiametric cells (Fig. 10). These cells may represent an abscission layer. A single trace to the ovule is produced by the vascular strand of the cupule lobe (Fig. 11). The vasculature expands in the base of the ovule and forms a basal disk of scalariform tracheids (Fig. 12). The nucellus is thin and papery and appears to be fused to the integument only at the chalaza. In the unlobed cupules, the nucellus is much more irregular in outline than those occurring in the bilobed cupules (compare Fig. 1 with Fig. 3). This may, however, be attributable to shrinking of the delicate tissue during preservation. In a few ovules, the tip of the nucellus consists of a mass of tissue, perhaps corresponding to a nucellar beak (Fig. 7). None of the ovules show evidence of megagametophyte tissue.

**Bisaccate pollen grains** occur within the integument and at the apex of the nucellus (Figs. 6 and 13). The grains measure up to 85 μm (mean = 75 μm) long (saccus to saccus) and 45 μm wide in polar view; the height of the corpus measures approximately 47 μm and the sacci up to 40 μm in equatorial view. Endoreticulations occur on the distally inclined sacci. These grains appear to resemble pollen allied with the *sporae dispersae* taxon *Alisporites* Daugherty emend. Jansonius from the pollen sacs of *Pteruchus fremouwensis* Yao, Taylor et Taylor (Osborn and Taylor, 1993). The grains associated with *Umkomasia resinosa*, however, are larger on average than those reported by Osborn and Taylor.

**Cupulate branch**—The branch that bears cupules is ovoid in cross section and measures 1.4–3 mm in diameter (Fig. 6). At the base of the branch, three separate flattened vascular strands are embedded in a bizoned cortex and surround the central pith (Fig. 19A). The vascular strands produce traces in a helical phyllotaxy to the five cupules on the branch (Fig. 19B–E). Surrounding the pith (440 μm to 660 μm) is a bizoned cortex that is 0.4–1 mm thick. The inner zone consists of thin-walled cells frequently filled with dark contents while the outer zone is composed of thin-walled cells lacking contents and is often poorly preserved. Secretory cavities and sclerified cells occur throughout the cortex and pith. They are identical to those observed in the cupules. The outer surface of the branch consists of poorly preserved cells, and it is difficult to discern an epidermal layer.

**Vascular system**—The cupulate branch is determinate, with the stele in the base consisting of three flattened vascular strands (Fig. 19A). Each strand is approximately 30–40 cells wide and consists of 3–4 rows of radially aligned tracheids and a poorly preserved zone on the abaxial side of the xylem corresponding to the position of phloem. These radially aligned cells are interpreted as primary xylem since there is no evidence of vascular rays. The pattern of cupule trace departure suggests a helical phyllotaxy, with traces to the basal cupules consisting of a pair of vascular strands derived from the ends of two adjacent strands in the axis (Fig. 19B–C). The strands of each cupule trace form a wide, open V shape, with the bottom of the V oriented away from the vascular cylinder (abaxially). The trace to the basal cupule consists of two strands, each 13–15 cells wide, each with 2–3 rows of radially aligned tracheids. At a more distal level, the width of each of
Figs. 6–13. *Unkomasia resinosa*. 6. Cross section of unlobed cupule near apex, showing dorsal cupule wall (CW), bifid integument (I) in paradermal section, and cupule stalk (CS) still partly attached to the cupulate branch (CB); note pollen (arrow) at micropylar opening and secretory cavities in cupule wall and integument. Scale bar = 1 mm. Slide #20095, 11323 DE #23. 7. Cross section of unlobed cupule near apex of ovule, with distinct inner (IC) and outer (OC) cupule cortex zones, central vascular strand (white arrow) in dorsal wall, lateral walls of the cupule enclosing a single ovule, numerous secretory cavities in integument (I), mass of tissue at nucellar apex (N), and cupule stalk (CS). Scale bar = 1 mm. Slide #20098, 11323 DE #51. 8. Cross section of unlobed cupule near base of ovule, with central vascular strand (V) in dorsal wall, integument (I) fused to dorsal wall, distorted nucellus (N), and cupule stalk (CS).
the stelar vascular strands that produced part of the trace is reduced to 20–25 cells. In the next cycle of cupule traces, one strand of the trace originates from the opposite end of the stelar strand that produced part of the first trace; the other half of the trace originates from the next adjacent stelar vascular strand (Fig. 19C). The vascular strand that produced two successive cupule traces in the helix is much reduced in width and further dichotomizes to form two small strands (Fig. 19D). The remaining two strands also dichotomize, producing a total of five cupule traces (Fig. 19E). Traces to the two basal cupules are produced in a distance of less than 1 mm between nodes. Attachment of the next cupule is estimated to be approximately 4 mm above the basal cupules. Separation of the stalks of the penultimate and terminal cupules is estimated to occur less than 1 mm above this.

Two flattened vascular strands are present at the base of each cupule stalk (Figs. 4 and 18A–B) and fuse to form a single strand distally (Figs. 9 and 18A–B). Xylem is composed of 3–4 rows of radially aligned tracheids measuring 9–13 μm in diameter (Fig. 15). Phloem is also organized into radial files of cells measuring 9–11 μm in diameter (Fig. 15). A narrow tissue consisting of 2–3 rows of sclerified cells surrounds the vascular strand and may represent the bundle sheath (Fig. 15).

In the bilobed cupules, the vascular strand dichotomizes in the base of the cupule to produce a vascular strand for each lobe (Figs. 2, 18A). The vascular strand of each lobe extends nearly to the apex. In unlobed specimens, the vascular strand does not dichotomize, remaining as a single strand in the center of the dorsal cupule wall (Fig. 18B). In the most apical cupule on the cupulate branch, the vascular strand extends approximately half the length of the cupule wall; in the next lower cupule, the strand terminates within 1 mm of the apex of the dorsal wall. The flattened vascular strand in these cupules consists of 2–3 rows of radially aligned tracheids, each up to 36 μm in diameter (Fig. 10). Phloem is oriented toward the interior of the cupule (abaxially) and is organized into radial files of at least two rows. Transfusion tracheids with scalariform thickened walls occur in patches on either side of the vascular strand. A bundle sheath, which consists of up to four rows of tabular sclerified cells that range from 9 to 45 μm in diameter, surrounds the vascular strand (Fig. 9). The vascular strand produces a single trace to the ovule (Figs. 11

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Scale bar = 1 mm. Slide #20096, 11323 DE #88. 9. Cross section near base of cupule; note bundle sheath (B) at sides of the single central vascular strand (arrow) seen in longitudinal section. Scale bar = 1 mm. Slide #20097, 11323 DE #125. 10. Cross section of unlobed cupule showing vascular strand (vertical arrow), abscission layer (horizontal arrow), integument (I), and nucellus (N). Scale bar = 250 μm. Slide #20099, 11323 DE #91. 11. Cross section of cupule vascular strand (arrow pair) and trace to the ovule (horizontal arrow). Scale bar = 250 μm. Slide #20100, 11323 DE#101. 12. Cross section through base of an ovule showing chalazal disk of scalariform tracheids. Scale bar = 100 μm. Slide #20101, 11323 DE #13. 13. Pollen grain occurring at micropylar opening of ovule in Fig. 6. Scale bar = 50 μm. Slide #20095, 11323 DE #23.
Fig. 17. Reconstruction of a cross section near the base of a bilobed cupule of *Umkomasia resinosa* showing two developing ovules. Dotted lines = transition from outer to inner cortex; circles = secretory cavities; black/white bundles = xylem/phloem; stippled area = interior of ovule.

and 18A–B), which expands into a basal disk of tracheids with scalariform wall thickenings in the chalaza of the ovule (Figs. 12 and 18A–B).

**Associated axis**—An axis with several similar histological characters occurs in close proximity to the cupulate branch but is not organically attached to it. This axis is oval in oblique cross section and approximately 3 mm in diameter. Pith is about 660 μm in cross-sectional diameter and similar in organization to that observed in the cupulate branch. Secretory cavities occur in the pith and cortex. The vascular system consists of at least two separate flattened vascular strands with radially aligned tracheids that suggest an endarch maturation pattern. Metaxylem tracheids are isodiametric in cross section, measuring up to 30 μm in diameter. Phloem is not preserved. Traces consist of two strands, each derived from the tips of adjacent arms of the stele. The cortex is bizoned, with the cells of the inner zone small and frequently filled with dark contents. Many cells in this zone appear to be sclerified. Cells in the outer zone have thin walls, lack cell contents, and are generally poorly preserved.

**DISCUSSION**

The genus *Umkomasia* was established based on compression fossils of cupulate structures from the Triassic Molteno Formation of South Africa (Thomas, 1933). Thomas’s brief diagnosis was emended many years later by Holmes (1987), who synonymized two additional genera, *Pilophorosperma* and *Karibacarpon* Lacey, with *Umkomasia*. The anatomically preserved specimens described here conform morphologically to the emended diagnosis of *Umkomasia* in all but two characters. The first character was added by Holmes, who characterized *Umkomasia* as possessing “one or more opposite pairs of sessile or pedicellate cupules” (Holmes, 1987, p. 166). This arrangement, however, is not consistent, even in Thomas’s type specimen (Fig. 16). More recently, a whorled organization of cupules was described for *Umkomasia uniramia* Axsmith, Taylor, Taylor et Cúneo, based on compression specimens and specimens macerated from the matrix (Axsmith et al., 2000). The anatomically preserved specimens of *Umkomasia resinosa* clearly demonstrate that the cupules are arranged in a helical pattern on the cupulate branch (Fig. 20). Based on these findings, it is apparent that this character has been misinterpreted in previous descriptions, since a helical phyllotaxy could appear as opposite or alternate in compression fossils, depending on the length of the internodes between cupules and the plane of compression. The second character, cited by both Thomas (1933) in his circumscription of the Corystospermaceae and Holmes (1987) in his emendation, is the presence of a single ovule in each cupule. While this character is difficult to assess in compression specimens, anatomically preserved specimens indicate that either one or two ovules may be present in each cupule. We are uncertain as to the systematic significance of this character. Ovule number
may vary based on the position of the cupules on the cupulate branch or on whether a second ovule in the cupule aborted.

Nineteen species of Umkomasia, including those originally assigned to Pilophorosperma or Karibacarpon, have been described to date from Argentina, South Africa, Germany, Australia, New Zealand, and Antarctica (Thomas, 1933; Lacey, 1976; Holmes and Ash, 1979; Retallack, 1980; Holmes, 1982, 1987; Playford, Rigby, and Archibald, 1982; Kirchner and Müller, 1992; Pole and Raine, 1994; Axsmith et al., 2000). Species delimitation is problematic, compounded by a lack of data on the range of developmental and positional variation within a single compound cupulate structure. An overall revision of the known species of Umkomasia based on a better understanding of the range of variation in the genus is needed. As there is no single species that the anatomically preserved material most closely resembles, we have chosen to assign these cupulate structures to a new species of Umkomasia.

Further support for assigning these specimens to the Corystospermales is provided by similarities with the anatomical organization of other corystosperm taxa described from Fremouw Peak (Pigg, 1990; Taylor, 1992; Meyer-Berthaud, Taylor, and Taylor, 1993; Osborn and Taylor, 1993; Yao, Taylor, and Taylor, 1995). The frond Dicroidium fremouwensis Pigg displays several characters that resemble those observed in Umkomasia resinosa, including primary xylem with radially aligned tracheids and transfusion tracheids. Most notable are the secretory cavities lined with a single layer of epithelial cells and sheath of cuboidal cells surrounding the vascular strand. Small stems of Kykloxylon fremouwensis Meyer-Berthaud, Taylor et Taylor, like U. resinosa, also possess secretory cavities, radial alignment of tracheids in the primary xylem, and organization of the vascular strands in pairs in the apical region of the shoot (Meyer-Berthaud, Taylor, and Taylor, 1993). Although the characters that link U. resinosa with D. fremouwensis and K. fremouwensis are noteworthy, they are not conclusive in that there remains the possibility that other corystosperm vegetative organs corresponding more convincingly with U. resinosa may yet be described from Fremouw Peak. There is, however, strong histological support for the hypothesis that the cupulate structures of U. resinosa were borne by the same plant that also bore the pollen organ Pteruchus fremouwensis (Yao, Taylor, and Taylor, 1995). The organization of the vascular tissue in the microsporophyll-bearing axis of P. fremouwensis is similar to that of the cupule-bearing axis of U. resinosa. The vasculature in the microsporophyll stalk of P. fremouwensis consists of a V-shaped pair of vascular strands comprised of radially aligned tracheids with the base of the V oriented abaxially, as also occurs in U. resinosa (compare Figs. 15–16 of Yao, Taylor, and Taylor [1995] with Figs. 4 and 15). Both taxa display helical organization of the ultimate units (= sporophylls), have a layer of cuboidal cells sheathing the vascular strand, and possess abundant secretory cavities lined with a single layer of epithelial

Fig. 19. Reconstructions of cross sections of Umkomasia resinosa showing the vascular system of the cupulate branch. (A) Base of branch showing three vascular strands. (B) Production of trace to the basal cupule (1) from two adjacent vascular strands. (C) Production of trace to second cupule (2) from the opposite end of one vascular strand and the next adjacent strand. (D) Dichotomy of one vascular strand (upper right pair) to ultimately form a trace to the terminal cupule. (E) Dichotomy of remaining strands to form traces to apical cupules (3–5).
Fig. 20. Suggested reconstruction of a cupulate branch of *Umkomasia resinosa* showing nature of cupules with bifid ovule tips and arrangement on axis.

Correlation of anatomy with morphology—Interpretation of the morphology of *Umkomasia* has varied since the initial description because the cupulate organ has been known only from compression fossils. As a result, precise homologies of reproductive structures in the corystosperms have been debated for decades. The anatomical organization observed in *Umkomasia resinosa* provides data that clarify many of these contested characters.

Thomas (1933) originally suggested that *Pteruchus* and *Umkomasia* were fertile branching systems, based on his interpretation of the position of the reproductive structures as occurring in the axils of bracts. Bracts have not been observed in *Umkomasia resinosa* and Holmes (1987) noted that many compression specimens lack bracts, suggesting that they may have been shed prior to preservation. Thomas (1933) ultimately concluded that the ovulate and pollen-bearing structures were not foliar (= sporophylls), but rather were “expanded receptacles” at the apices of branches. An alternative interpretation, that the entire reproductive organ represents a single compound sporophyll bearing pollen sacs or ovules on modified pinnules, was proposed by Townrow (1962). The specimens from Antarctica, in addition to descriptions of compressed corystosperm reproductive structures from India (Pant and Basu, 1973, 1979) and Antarctica (Yao, Taylor, and Taylor, 1995; Axsmith et al., 2000), demonstrate that the structure is not a single compound sporophyll; the cupules rather are individual sporophylls borne in a helical arrangement on a branch-like axis (Fig. 20). Further support for this interpretation is provided by the anatomical organization of both the cupule-bearing axis of *U. resinosa* and what we interpret as the main axis found associated with it. These axes display stem-like anatomy with a radially symmetrical, endarch vascular cylinder embedded in a pith. Moreover, the vascular organization of these axes more closely resembles that of *Kykloxylon* than the frond rachis of *Dicroidium*. Based on these data, it is clear that both cupulate and pollen-bearing reproductive structures (= “pinnae” of Doyle, 1996: p. S29) in corystosperms are determinate branches bearing sporophylls, a slight modification of the organization proposed by Thomas (1933). The overall organizational complexity of these organs varies from simple, exemplified by the whorled organization of *U. uniramia*, to compound, demonstrated in most other compression taxa of *Umkomasia*. It is likely that *U. resinosa* was a compound structure comprised of several determinate fertile branches helically arranged on a main fertile axis. Axsmith et al. (2000) were able to further demonstrate that the whorled fertile branches of *U. uniramia* were attached to a short shoot on a branch bearing *Dicroidium* leaves. No evidence of attachment to the next order of branching has yet

cells. Additionally, secretory cavities occur in the walls of the pollen sacs and are also observed in the integument of *U. resinosa*. Pollen found associated with the ovules of *U. resinosa* resembles the pollen produced by *P. fremouwensis* (compare Fig. 3 of Osborn and Taylor [1993] and Fig. 25 of Yao, Taylor, and Taylor [1995] with Fig. 13). Some of these characters (e.g., helical arrangement of sporophylls) will undoubtedly be shown to occur generally in the corystosperms as additional anatomically preserved specimens are described. Specific anatomical and morphological characters in both *U. resinosa* and *P. fremouwensis* nevertheless strongly suggest that both taxa represent organs of the same Triassic seed plant.
been found for \textit{U. resinosa}, but it is possible that they were borne in a similar manner.

The number of cupule lobes is a feature frequently utilized in the identification of corystosperm ovulate organs. Thomas (1933) originally distinguished \textit{Umkomasia} from \textit{Pilophorosperma} based on cupule lobing and epidermal patterns; \textit{Umkomasia} has been interpreted as a bilobed structure with an elongate opening on the dorsal and ventral surfaces of the cupule, whereas \textit{Pilophorosperma} has only a single opening on the ventral surface. Holmes (1987) stressed the importance of gross morphological characters in identifying corystosperm reproductive structures. He noted that cuticular features are not always preserved and that the degree of lobing may vary based on stage of development and plane of compression. Morphological variation among the cupules on the cupulate branch may be developmental (Holmes, 1987), suggesting that maturation of the cupules in \textit{U. resinosa} was acropetal. One major difference among the cupules is that the basal cupule is bilobed, whereas the more apical cupules possess only a ventral opening (Figs. 1, 2, and 20). It remains unknown whether the apical cupules would have ultimately achieved a bilobed morphology as they matured, but it seems unlikely based on the dorsal position of the single vascular strand. The narrow dorsal opening between lobes in the bilobed cupules, however, does not represent a line of dehiscence, as suggested by Axsmith et al. (2000); the lobes are histologically separate and distinct structures. Most of the anatomically preserved specimens of \textit{U. resinosa} contain ovules and, in the bilobed cupules, the lobes are closely appressed to one another. In compressions and macerated specimens of \textit{U. uniraminia} described by Axsmith et al. (2000), no ovules were observed within the cupules and the lobes appear to have separated (see particularly Fig. 13, Axsmith et al., 2000). This may represent a post-dispersal morphology. Alternatively, greater separation of cupule lobes observed in \textit{U. uniraminia} may reflect effects of fossilization and diagenetic processes. Further support for a developmental interpretation of differences in \textit{U. resinosa} include the greater size of the basal cupule when compared with the apical cupules, as well as the degree of development of the vascular strands in the two apical cupules. The lower (more mature) cupule displays greater acropetal differentiation of the vascular strand than that observed in the more apical (less mature) cupule. It appears that the vascular strand in \textit{U. resinosa} developed acropetally in the cupule, a condition that is known during leaf development in a number of modern seed plants (e.g., Pray, 1955; De Sloover, 1958; Postek and Tucker, 1982).

The bilobed morphology of corystosperm cupules first noted by Thomas (1933) has been reinterpreted in recent reconstructions, particularly that of Crane (1985) and subsequent illustrations based on this reconstruction (e.g., Crane, 1988; Taylor, 1996). These reconstructions illustrate the cupules as solid structures with an apical pore through which the ovule integument protrudes. The reconstruction of \textit{Umkomasia uniraminia} proposed by Axsmith et al. (2000) also portrays cupules with this morphology. Reexamination of Thomas’s type specimen of \textit{U. macleani} (Fig. 16) and Axsmith et al.’s type material of \textit{U. uniraminia}, considered with the anatomical evidence provided by \textit{U. resinosa}, supports Thomas’s original interpretation that some cupules of \textit{Umkomasia} possess two separate lobes, as illustrated in Fig. 20. Thomas (1933) also described unlobed cupules with an elongate cleft on the abaxial side, which he assigned to \textit{Pilophorosperma}. The presence of bilobed and unlobed morphotypes in \textit{U. resinosa} supports Holmes’s (1987) suggestion that \textit{Pilophorosperma} and \textit{Umkomasia} are identical. On the other hand, Karibacarpon, which Holmes also synonymized with \textit{Umkomasia}, has five to nine distinct lobes that form a star-shaped outline when compressed and is more than twice as large as cupules of \textit{Umkomasia} (Lacey, 1976; Holmes and Ash, 1979). Based on new information provided by the structurally preserved specimens of \textit{U. resinosa}, this synonymization, as well as identification of other multilobed cupule compressions as \textit{Umkomasia} (e.g., Retail-lack, 1977), should be reconsidered.

Many authors have commented on the irregular, wrinkled surface of \textit{Umkomasia}, although several reconstructions illustrate the cupules with a smooth epidermis (Crane, 1985; Axsmith et al., 2000). The wrinkled surface has been interpreted as indicating fleshiness (Thomas, 1933; Petriella, 1980; Holmes, 1987; Axsmith et al., 2000). In \textit{U. resinosa}, the cortex is composed of two distinct zones of parenchyma; the outer zone forms what might have resulted in a fleshy layer with an uneven epidermal surface (e.g., Figs. 1–3), supporting interpretations of previous researchers. One possible function of the fleshy cupules may have been protection of the enclosed developing ovules. Interestingly, the sporophyll lamina of \textit{Pteruchus fremouwensis}, with its pendant pollen sacs, is not thickened as it is in \textit{U. resinosa}.

The cupules in \textit{Umkomasia resinosa} possess a large number of what we interpret as secretory cavities in the lobes and integument. Structures such as these occur in numerous gymnosperm taxa, from secretory cavities in Carboniferous pteridosperms (Delevoryas and Morgan, 1954; Krings, 2000) to resin canals in extant Pinaceae. It is of interest that such structures are found in all corystosperm organs known from Antarctica. Although in extant plants these structures function in sequestration of secondary metabolites, many additional functions have been suggested, including protection from herbivory, prevention of excessive water loss from transpiration, and wound healing (Fahn, 1979; see also Krings, 2000 and references therein). There is much that is still unknown about the biology of plants that lived at high latitudes during the Mesozoic. There is evidence that the corystosperms of Antarctica were seasonally deciduous, based on mats of \textit{Dicroidium} leaves occurring in association with large in-situ trunks, as well as the presence of a periderm layer beneath leaf bases in stems of \textit{Kykloxyylon} (Meyer-Berthaud, Taylor, and Taylor, 1993; Taylor, 1996; Taylor, Taylor, and Cúneo, 2000). One hypothesis to account for the large number of secretory structures in Antarctic corystosperms is that a high metabolic rate was required in order to produce a large amount of biomass during the relatively short growing season. Taylor, Taylor, and Cúneo (2000) note that wide growth rings in silicified wood from the Triassic of Antarctica indicate that these plants did, in fact, undergo exceptional growth during the summer. This, in turn, might result in production of large quantities of secondary metabolic compounds, necessitating greater storage area in plant tissues. As an added benefit, it is possible that the high concentrations of these substances in all parts of the plant would have made them unpalatable to herbivores seeking forage during the brief period in which it was abundant.

The presence of secretory cavities in the integument of \textit{Umkomasia resinosa} is one of the features that distinguishes it from \textit{Ignatospernum monili}, an ovule of unknown affinities that also occurs at Fremouw Peak (Perovich and Taylor, 1989). These isolated ovules are characterized by a three-parted scler-
otesta that differs substantially from the delicate tissues observed in the ovules of *U. resinosa*. Additionally, *I. monilii* is radially symmetrical in cross section and does not possess a bifid micropyple. Based on these differences, it seems unlikely that these ovules were produced in cupules of *U. resinosa*, but it remains possible that they belonged to another corystosperm species. Other ovules found at Fremouw Peak include those occurring within cupules of *Petriellaea angulata* and ovulate cones of *Parasciadopitys aequata*, both of which are morphologically and anatomically different from *U. resinosa* (Taylor, Del Fueyo, and Taylor, 1994; Yao, Taylor, and Taylor, 1997).

The anatomy of the ovules of *Umkomasia resinosa* differs substantially from other Triassic ovules. The ovules are small, with an estimated maximum length of 7 mm, including the bifid extension of the integument. A significant difference between *U. resinosa* and other known anatomically preserved ovules is the apparent lack of a sclerified layer in the integument. There is no evidence for any type of specialized, protective tissue surrounding the megagametophyte beyond that afforded by the cupule, thin integument, and nucellus. One hypothesis to account for this is that protective tissues might have developed in mature ovules with fully developed megagametophytes, which have not yet been found. On the other hand, lack of a sclerified layer may indicate that these ovules did not undergo a period of dormancy and instead germinated soon after abscission from the cupule. In an environment with a comparatively short growing season, early and rapid germination may have been crucial to seedling establishment.

The number and attachment of ovules in *Umkomasia* are characters that may be significant in further refining analyses of phylogenetic relationships of the corystosperms. Since Thomas’s initial description, the number of ovules in the cupulate structures has been assumed to be one, although morphology observed in the type specimen of *U. macleani* (Fig. 16) does not support this interpretation unequivocally (Thomas, 1933; Holmes, 1987). Some authors have suggested that corystosperms had two ovules per cupule (Crane, 1988; Stewart and Rothwell, 1993; Yao, Taylor, and Taylor, 1995; Frohlich and Parker, 2000), but this seems to be based on inclusion of the Cretaceous genus *Ktalenia circularis* Archangelsky in the group (Archangelsky, 1963; Taylor and Archangelsky, 1985). Although interpreted as the youngest-known Mesozoic pteridosperm, there is little evidence that *K. circularis* is in fact a corystosperm, and comparisons with the Caytoniales are much better supported, as noted by Taylor and Archangelsky (1985) and Taylor, Del Fueyo, and Taylor (1994). The occurrence of two ovules within cupules of *U. resinosa*, on the other hand, is direct evidence for this character in corystosperms. It is interesting to note that it is not a consistent feature and is dependent not only on successful development of the second ovule within a cupule but apparently also upon position of the cupule on the cupulate branch. Although the second ovule in the basal cupule on the cupulate branch described here may have aborted, other isolated cupules with two ovules were observed. There is no evidence, however, that a second ovule ever developed in the apical cupules.

Ovule attachment in the corystosperms has previously not been clear from examination of compression fossils. Based on interpretation of the cupules of *Umkomasia uniramia* as sporophylls, Axsmith et al. (2000) predicted that the ovules would be found on the abaxial surface; the anatomical organization of *U. resinosa* confirms this organization. This further supports interpretation of the corystosperm cupule as formed by abaxial, conduplicate folding of the sporophyll laminae (Axsmith et al., 2000). Assessment of the corystosperm cupule as a homologue to cupules of other Mesozoic pteridosperm groups such as the Caytoniales (Thomas, 1925; Harris, 1940) and Petriellales (Taylor, Del Fueyo, and Taylor, 1994), in which ovules are adaxially attached, no longer appears to be tenable.

**Implications for phylogenetic analysis**—The new data provided by *U. resinosa* emphasize the significant differences that exist among the orders of Mesozoic pteridosperms as they are currently understood. There are several lineages of seed plants in the Mesozoic that experimented with variations on ovule enclosure within an enveloping structure. The abaxial position of the ovules, however, definitively separates Corystosperms from Petriellales (Taylor, Del Fueyo, and Taylor, 1994) and Caytoniales (Thomas, 1925; Harris, 1940), which bear adaxial ovules. Organization of the cupule, formed by circinate folding of the sporophyll lamina in these other orders, also indicates an evolutionary history that is divergent from that of the corystosperms. In recent analyses, corystosperms have been interpreted to form a clade with some representatives of the Peltspermales (Nixon et al., 1994; Doyle, 1998). Although the peltasperms are as yet poorly understood as whole plants, there are some general similarities between the organization of *Umkomasia* and the ovulate organs of *Autunia conferta* from the Permian of west and central Europe (e.g., helical arrangement of megasporophylls on the ovulate organ and abaxial attachment of a pair of ovules on the megasporophyll; Kerp, 1988). Further assessment of homology among these orders is greatly enhanced by correlation of the Antarctic corystosperm organs to reconstruct an entire plant, which provides a terminal taxon for use in future phylogenetic analyses.

The historically uncertain phylogenetic position of the Corystospermales with respect to other seed plants was recently reviewed by Axsmith et al. (2000), who also recoded characters in selected previously published analyses to include their new data (Nixon et al., 1994; Doyle, 1996). When we attempted a similar recoding with data obtained from *U. resinosa*, we found that no further changes in tree topology or length resulted. Some controversial characters of ovules that have been utilized in the past, such as symmetry (platyspermy vs. radiospermy), should not be included in future analyses, particularly since the presence of both symmetries in *U. resinosa* further reinforces arguments provided by Rothwell (1986) on the difficulties inherent in interpreting this character. Characters that might prove to be more informative include organization of integumentary tissues and patterns of vascularization of the megasporophyll and ovule.

With mounting molecular evidence that the Gnetales are not the sister group to the angiosperms (Samigullin et al., 1999; Winter et al., 1999; Bowe, Goat, and dePamphilis, 2000; Chaw et al., 2000), attention is turning once again to fossils as a source of evidence for angiosperm ancestors. The corystosperms have recently been suggested as a possible ancestral group, based on a theory proposed by Frohlich and Parker (2000) incorporating genetic control of development of reproductive structures. In their “mostly male theory,” Frohlich and Parker hypothesize that one step in the development of floral organization might have been the result of ectopic repositioning of ovules onto the flattened adaxial surface of microsporophylls, such as those found in *Pteruchus*. Abaxial position of the ovules in *Umkomasia*, however, does not support interpretation of corystosperm sporophylls as homologues for the
angiosperm carpel. Furthermore, derivation of the carpel wall from the lamina of the microsporophyll would result in enclosure of ovules with a single integument, suggesting de novo origination of the outer integument of angiosperm ovules. Some Mesozoic pteridosperms do possess characters that point in the direction of an angiosperm lineage. Nevertheless, as this study emphasizes, the relationship of the corystosperms to other seed plants is still poorly understood and requires reanalysis each time morphological characters are described based on structurally preserved organs. As our data on the anatomy of *Umkomasia* indicate, interpretation of the Corystospermales as a possible ancestral group for the angiosperms has become less feasible.

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