

NEW PERSPECTIVES ON THE MESOZOIC SEED FERN ORDER CORYSTOSPERMALES BASED ON ATTACHED ORGANS FROM THE TRIASSIC OF ANTARCTICA¹

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A new Triassic corystosperm is described from the Shackleton Glacier region of Antarctica. The compression fossils include cupulate organs (*Umkomasia uniramia*) and leaves (*Dicroidium odontopteroides*) attached to short shoot-bearing branches. The cupulate organs occur in groups near the apices of the short shoots, and each consists of a single axis with a pair of bracts and a subapical whorl of five to eight ovoid cupules. This unique architecture indicates that the cupules are individual megasporophylls rather than leaflets of a compound megasporophyll. A branch bearing an attached *D. odontopteroides* leaf provides the first unequivocal evidence that *Umkomasia* cupulate organs and *Dicroidium* leaves were produced by the same plants. Although this had previously been assumed based on organ associations, the new specimens are important in demonstrating that a single species of corystosperm produced the unique cupulate organs described here and the geographically and stratigraphically widespread and common *D. odontopteroides* leaf. Therefore, biostratigraphic, paleoecological, and phylogenetic studies that treat *Dicroidium* leaf morphospecies as proxies for biological species of entire plants should be reconsidered. Phylogenetic analysis suggests that the corystosperm cupule is an unlikely homologue for the angiosperm carpel or outer integument.

Key words: Antarctica; Corystospermales; *Dicroidium*; Gondwana; Mesozoic; pteridosperms; Triassic; *Umkomasia*.

Fossil remains of the Mesozoic seed fern order Corystospermales (= Corystospermaceae Thomas, 1933) are the dominant component of most Southern Hemisphere Triassic paleofloras (Anderson and Anderson, 1983), and are therefore of particular interest to paleobotanists. Furthermore, the widespread and highly variable corystosperm leaf genus *Dicroidium* has been used extensively in biostratigraphic, phylogenetic, and paleoecological research (e.g., Retallack, 1977; Anderson and Anderson, 1983). Despite the important role the corystosperms have played in Gondwanan paleobiology and geology, the numerous species of ovulate organs (*Umkomasia*), pollen organs (*Pteruchus*), and leaves (*Dicroidium*) typically attributed to southern hemisphere representatives of this group have never been found organically attached. Consequently, the corystosperms exist only as a synthetic group in which these organs are conceptually united entirely on the basis of locality associations, general cuticular similarity, and the occurrence of similar pollen grains in *Pteruchus* pollen sacs and ovules within *Umkomasia* cupulate organs (Thomas, 1933). The resulting lack of specific reconstructions is reflected in persistent controversies regarding the morphology and phylogeny of the group (Crane, 1985). This situation is particularly problematic and relevant to broader questions of seed plant phylogeny and character evolution as the ovulate organs of the corystosperms and other so-called Mesozoic seed ferns (pteridosperms) have been focal points in discus-

sions of angiosperm carpel (Taylor, Del Fueyo, and Taylor, 1994) and/or outer integument origins (Doyle, 1996).

Here we describe a remarkable new assemblage of compressed corystosperm remains from the Shackleton Glacier region of Antarctica that includes specimens of a unique *Umkomasia* cupulate organ with a whorled cupule arrangement and the common leaf species *Dicroidium odontopteroides* attached to branching systems bearing distinctive short shoots. A new *Pteruchus* pollen organ that was probably produced by the same species of corystosperm is also described. In addition to providing the first unequivocal evidence based on attached organs that *Umkomasia* cupulate organs and *Dicroidium* leaves were produced by the same plants, this material has important implications for our understanding of the morphology, phylogeny, and paleoecology of the corystosperms, as well as the biostratigraphy of the Gondwanan Triassic.

MATERIALS AND METHODS

The new fossils were collected from exposures of the upper Fremouw or lower Falla Formation on an unnamed ridge informally known as "Alfie's Elbow" in the Shackleton Glacier region of Antarctica (Fig. 1). The precise stratigraphic position is uncertain due to the isolated nature of the outcrop and lack of previous geological study. The outcrop is ~42 m thick and represents a fluvial deposit including several cycles of channel, levee, floodplain, crevasse splay, and paludal facies (Fig. 2). Plant fossils occur in at least six levels that apparently represent low-energy braided stream deposits based on the fine-grained siltstones and shales and the well-articulated plants.

The new collection consists of over 500 slabs. The best preserved specimens that form the basis of this study are listed below. The plant parts are preserved as dark black compressions on a fine-grained, dark to medium gray shale and siltstone matrix. Many of the rock surfaces

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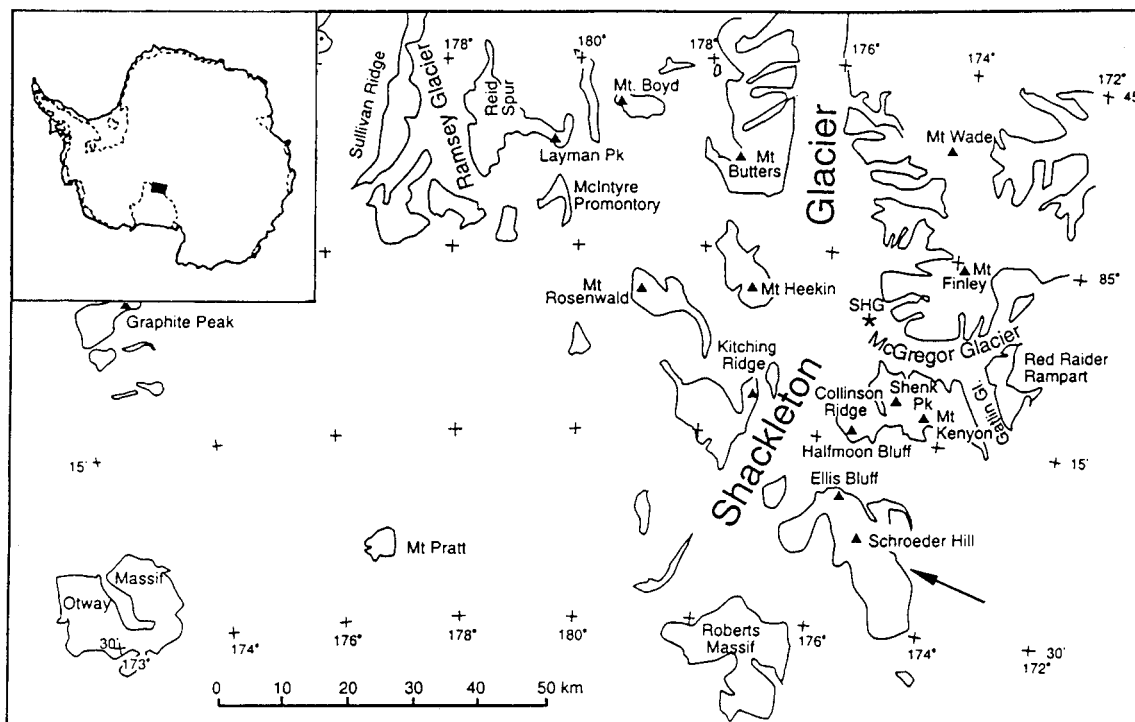


Fig. 1. Map of the Shackleton Glacier region of Antarctica. Arrow indicates location of the "Alfie's Elbow" site.

are covered with isolated leaves of *Dicroidium odontopteroides* and the new *Umkomasia uniramia* cupulate organs described here. Less common are *Dicroidium dubium*, *D. elongatum*, *Dictyophyllum* sp., *Heidiophyllum elongatum*, *Pteruchus* sp., *Taeniopteris* sp., *Telemachus elongatus*, and branching systems bearing short shoots. Larger in situ stumps and oriented logs also occur.

Photographs of compressed specimens on the gray shale matrix were taken under polarized light to increase contrast. Where necessary, specimens were exposed on the rock surfaces using needles. A combination of the bioplastic transfer and bulk maceration techniques was used. Three slabs were embedded in Ward's Bioplastic and cut transversely. The exposed surfaces were then carefully macerated in 48% hydrofluoric acid. The reverse sides of specimens exposed on the original surface were retained on the bioplastic block as a transfer. The plant organs originally preserved deeper within the matrix were extracted from the acid during maceration and subsequently rinsed in distilled water and air dried. The cupulate organs recovered in this way were fragile but could be handled for study; however, the delicate *Pteruchus* pollen organs rarely survived the maceration process intact. Therefore, several features of the pollen organs, such as the total number of pollen sacs and the precise arrangement of microsporophylls, were difficult to discern conclusively. Specimens of all organs are too coalified for cuticular analysis using oxidative maceration techniques. Some specimens were mounted on stubs for scanning electron microscopy (SEM) study, but the surfaces are generally not well enough preserved for detailed epidermal analysis. Many poorly preserved in situ pollen grains were extracted from *Pteruchus* pollen organs by removal of the pollen sacs followed by maceration in 48% hydrofluoric acid. Because the grains are very fragile, gravity settling of the grains from solution was required, and no oxidative procedures were performed.

SYSTEMATICS

Order—Corystospermales

Family—Corystospermaceae

Genus—*Umkomasia* Thomas 1933

Species—*Umkomasia uniramia* sp. nov.

Diagnosis—Cupulate reproductive organs attached to vegetative branching systems of at least three orders, lower vegetative branch orders at least 2.3 cm wide, lateral short shoots alternately or distichously arranged, up to 6.5 cm long with closely spaced, slightly raised lenticular leaf bases with thickened lateral extensions, leaf attached to long shoots conforming to *Dicroidium odontopteroides*; cupulate reproductive structures in groups of at least three near apex of lateral short shoots, each organ consisting of a single axis and a subapical whorl of 4–8 cupules; cupulate organ axis up to 7.5 cm long \times 4.0 mm wide, base slightly expanded, axis bearing an oppositely arranged pair of bracts in variable positions along upper quarter; bracts up to 5.0 mm long with broad bases and acute apices; cupules ovoid, up to 1.4 cm long \times 1.3 cm wide, borne on recurved stalks up to 1.5 cm long, stalk expanding at point of attachment to cupule and partially extending over upper cupule surface as a midrib, dehiscent cupules consisting of two flaps attached to midrib; cuticle of main axis and inner cupule surface smooth, outer cupule surface irregular.

Holotype—T12–990a&b (Figs. 3, 4)

Paratypes—T12–1002 (Figs. 6, 8, 9), T12–1019a (Fig. 10), T12–1028a (Fig. 5), T12–1036a (Fig. 11), T12–1049 (Fig. 14), T12–1074 (Fig. 7), T12–1076 (Fig. 17), T12–1078 (Fig. 12), T12–1080 (Fig. 15), T12–1081 (Fig. 13), T12–1082 (Fig. 16).

All described and figured specimens are deposited in

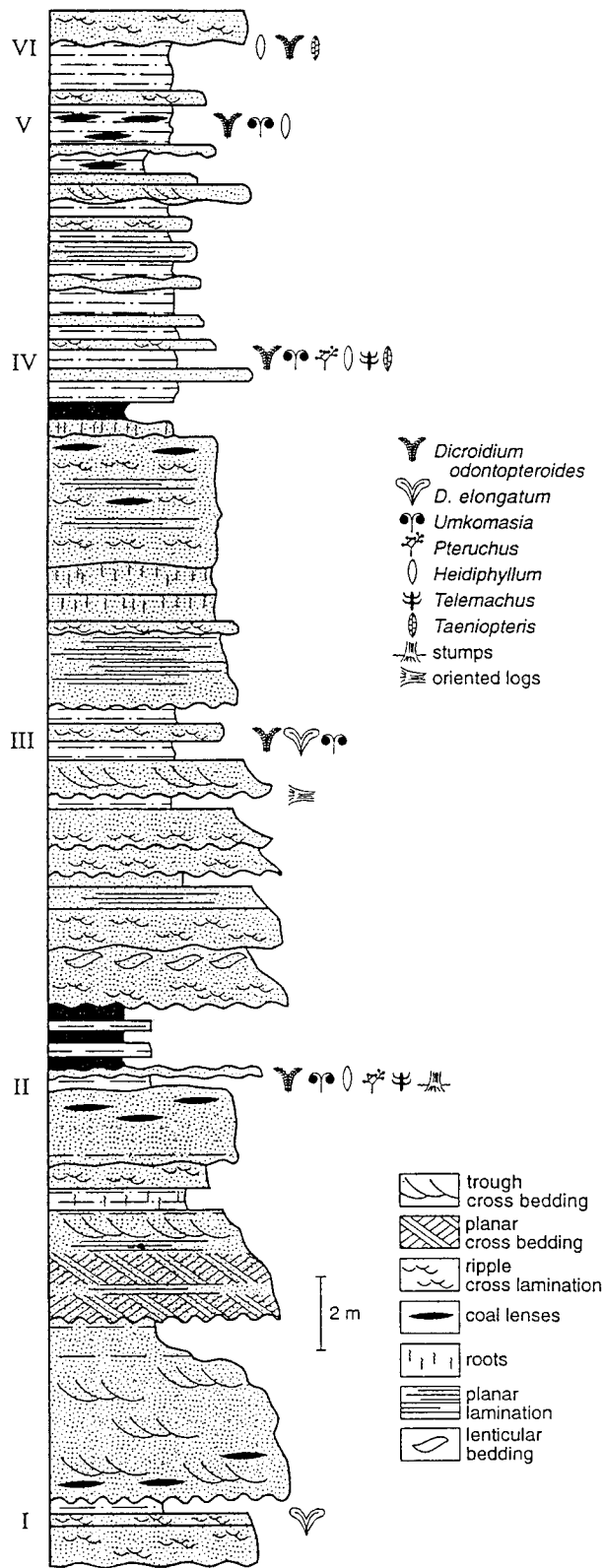


Fig. 2. Stratigraphic section of the upper Fremouw or lower Falla Formation at the new locality showing the distribution of fossil plant horizons.

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Type locality—A ridge southeast of Schroeder Hill in the Shackleton Glacier region of Antarctica (~85° 23' 717" S, 174° 49' 916" W) (Fig. 1).

Stratigraphic position—Upper Fremouw or lower Falla Formation.

Age—Late Middle to early Late Triassic.

Etymology—The specific epithet *uniramia* refers to the unbranched architecture of the cupulate organ axis relative to other *Umkomasia* species that typically consist of two branch orders.

DESCRIPTION

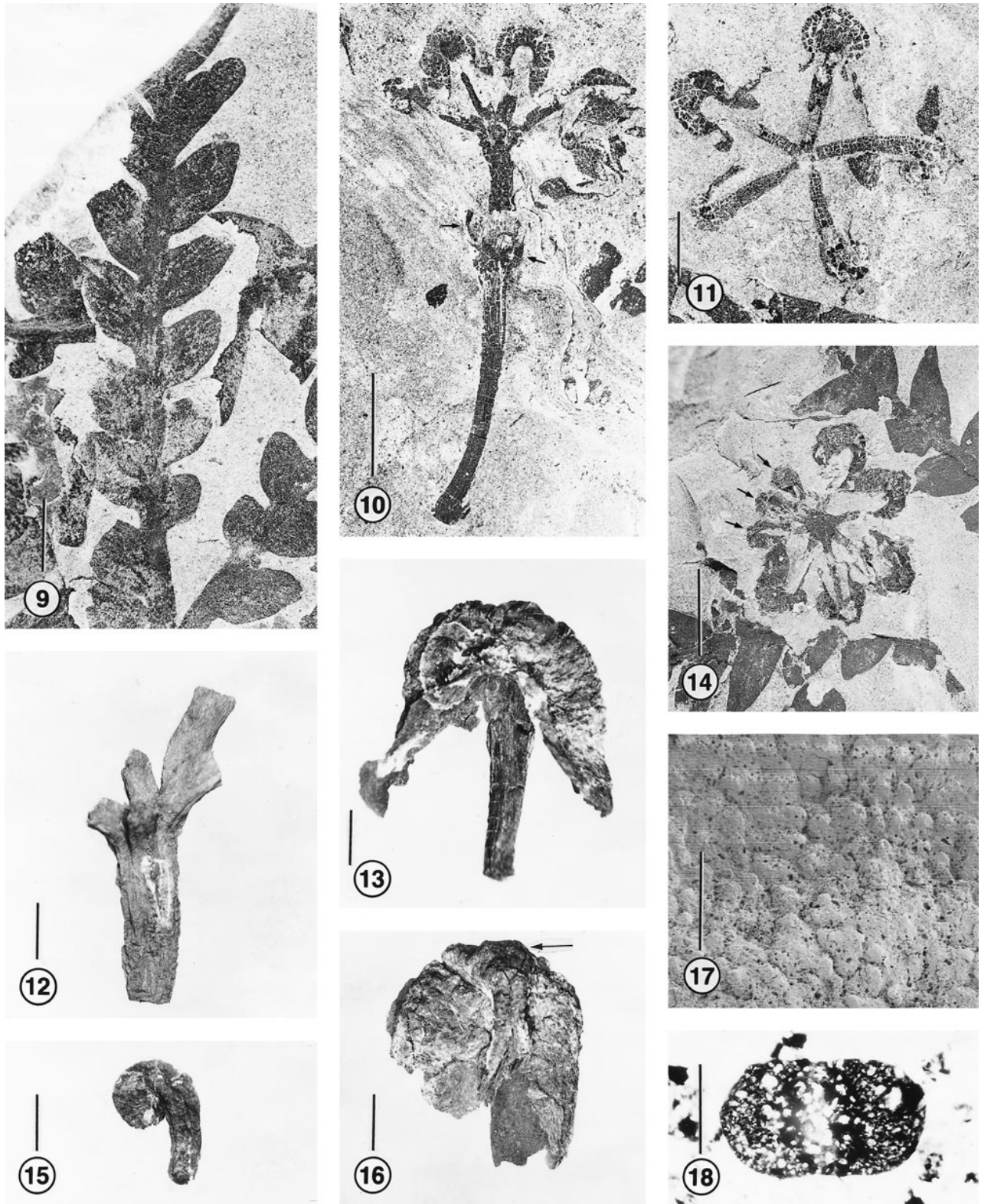
Vegetative branches—Isolated vegetative branches of the *Umkomasia uniramia*-*Dicroidium odontopteroides* plant are common at the "Alfie's Elbow" locality and are recognized by the presence of distinctive short shoots. The largest branch specimen is 23.0 cm long × 2.3 cm wide, but it was undoubtedly much longer as it shows no indication of narrowing toward either edge of the rock slab. One specimen (Fig. 3) consists of a section of branch 14.8 cm long × 1.4 cm wide bearing four alternate or distichously arranged, lateral short shoots up to 3.5 cm long, two of which bear cupulate organs distally. The stem apex also exhibits the short shoot growth habit, but no cupulate organs are visible. Several other stem sections show regions with extremely short internodes (short shoots) alternating with long shoot regions (Fig. 5). Larger branches and oriented logs occur at the Alfie's Elbow locality, but they cannot be definitively attributed to the new *U. uniramia*-*D. odontopteroides* plant due to the absence of the distinctive short shoots.

Leaf bases on the short shoots are closely spaced, helically arranged, and slightly raised (Fig. 7). Each base is ~3.0 mm wide with the lateral margins extending out an additional 1.0–1.5 mm on each side, forming a prominent thickened ridge. Remains of these ridges can be identified on older shoots that have undergone considerable thickening and are useful for recognizing alternating regions of short shoot and long shoot growth (Fig. 5). In a few of the leaf bases, a row of four circular depressions can be discerned near the upper margin of the leaf base, which may represent vascular bundle scars. Due to poor preservation and the apparent presence of an abscission layer over the leaf base, it is uncertain whether this represents the complete vascular tissue arrangement.

Stem section with attached leaf—Among the most significant specimens in the new collection is a stem fragment (8.0 cm long × 1.6 cm wide) bearing a lateral short shoot identical to the specimens described above (Fig. 6). Attached to the opposite side of the stem and slightly distal to the short shoot is a 7.5 cm long, bifurcating leaf conforming to the common species *Dicroidium odontopteroides* (Figs. 6, 8–9). The short pinnule length/width ratio (1.2/1–1.5/1) along with the absence of a distinct



Figs. 3-8. *Umkomasia uniramia*-*Dicroidium odontopteroides* plant. **3.** Branching system showing four lateral short shoots. Bracket indicates shoot with attached cupulate organs. T12-990a. Scale bar = 2.0 cm. **4.** Detail of the counterpart of shoot bracketed in Fig. 3 with three distal cupulate organs. Note whorl of eight cupules (arrows) on leftmost organ. T12-990b. Scale bar = 1.0 cm. **5.** Branch showing long shoot growth proximally (bottom of figure) and short shoot growth distally. Arrow indicates transition. T12-1028a. Scale bar = 1.0 cm. **6.** Branch with lateral short shoot (bottom left of figure) and attached *Dicroidium odontopteroides* leaf (arrow). T12-1002. Scale bar = 1.0 cm. **7.** Detail of short shoot. Arrow indicates a leaf base. T12-1074. Scale bar = 5.0 mm. **8.** Detail of leaf attachment and proximal pinnules. T12-1002. Scale bar = 5.0 mm.



Figs. 9–18. *Umkomasia uniramia*–*Dicroidium odontopteroides* plant and associated pollen. **9.** Detail of distal region of attached leaf. T12–1002. Scale bar = 5.0 mm. **10.** Isolated cupulate organ in longitudinal view. Arrows indicate bracts. Bracts appear unpaired due to being oriented along a fracture in the rock matrix. T12–1019a. Scale bar = 1.0 cm. **11.** Top of cupulate organ showing cupule whorl. T12–1036a. Scale bar = 5.0 mm. **12.** Cupulate organ axis apex with attached cupule stalks. T12–1078. Scale bar = 2.0 mm. **13.** Opened cupule in front view. T12–1081. Scale bar = 2.0 mm. **14.** Whorl of eight cupules in top view. Arrows indicate three abortive cupules. T12–1049. Scale bar = 1.0 cm. **15.** Immature cupule in side view. T12–1080. Scale bar = 2.0 mm. **16.** Cupule in front view showing large central vein (arrow) on upper surface. T12–1082. Scale bar = 2.0 mm. **17.** SEM showing irregular (verrucose) cupule surface. T12–1076. Scale bar = 100.0 μm . **18.** Pollen grain extracted from associated *Pteruchus* sp. pollen sac. T12–1001b. Scale bar = 50.0 μm .

midvein (i.e., "odontopteroid" venation) make this leaf closely comparable to forms recognized by some workers as *D. odontopteroides* var. *moltense* (Retallack, 1977), or *D. odontopteroides* var. *orbiculoides* (Anderson and Anderson, 1983). The leaf petiole can be seen to curve toward the stem just above the point of attachment. That this leaf is actually attached and not merely overlapped by the stem is clear due to the continuous strands of tissue visible between the stem and leaf base (Fig. 8).

The absence of an axillary bud associated with the leaf is somewhat problematic. However, the axillary buds described from permineralized corystosperm stems from Fremouw Peak in Antarctica (Meyer-Berthaud, Taylor, and Taylor, 1993) are small relative to the leaf bases and could easily be obscured in a compression fossil. It is also possible that the stem is covering the bud as a result of flattening during compression, or that the bud is on the uncollected counter slab. Another possibility is that this species of corystosperm did not have axillary branching or that axillary buds are not associated with every leaf, as is the case in many extant and fossil plants. It may be possible to excavate through the leaf base area to reveal such a bud if present, but such an effort will not be undertaken as this could potentially destroy the specimen for relatively little gain. Furthermore, the *Dicroidium odontopteroides* leaves and the *Umkomasia uniramia* cupulate organs are, by far, the most common floral elements at the Alfie's Elbow locality. This association and relative abundance evidence alone would constitute compelling evidence that both structures were produced by the same plant even in the absence of the attached leaf specimen, especially considering that *U. uniramia* is the only corystosperm cupulate organ found to date at Alfie's Elbow.

Cupulate organs—The new collection includes a single branching system bearing attached cupulate organs, along with hundreds of isolated specimens. The attached organs occur in groups of at least three near the apices of two of the lateral short shoots on the branching system described above (Figs. 3, 4). The cupulate organs appear to arise from the axils of the uppermost leaf bases, although this is uncertain due to poor preservation of the short shoot surface. The axes of the individual cupulate organs are unbranched and up to 2.0 cm long \times 2.0 mm wide with slightly expanded bases. Attached in variable positions along the upper quarter of the axes are two oppositely arranged, narrow bracts, each up to 4.0 mm long. Each axis bears a whorl of five to eight cupules just below the apex. The cupules are ovoid, \sim 4.1 mm long \times 4.0 mm wide, and are borne on stalks (Fig. 4). These attached cupules appear to be unopened, but the interiors are filled with an amorphous coaly substance making it impossible to discern the presence of ovules or ovule attachment scars. Nevertheless, these cupules were undoubtedly the ovule-producing organs as they are identical to *Umkomasia* cupules from other localities that are known to have produced ovules based on the occurrence of in situ specimens (e.g., Thomas, 1933). As in other *Umkomasia* species, a small circular to slightly elongate opening occurs at the distal end of undehisced cupule laminae.

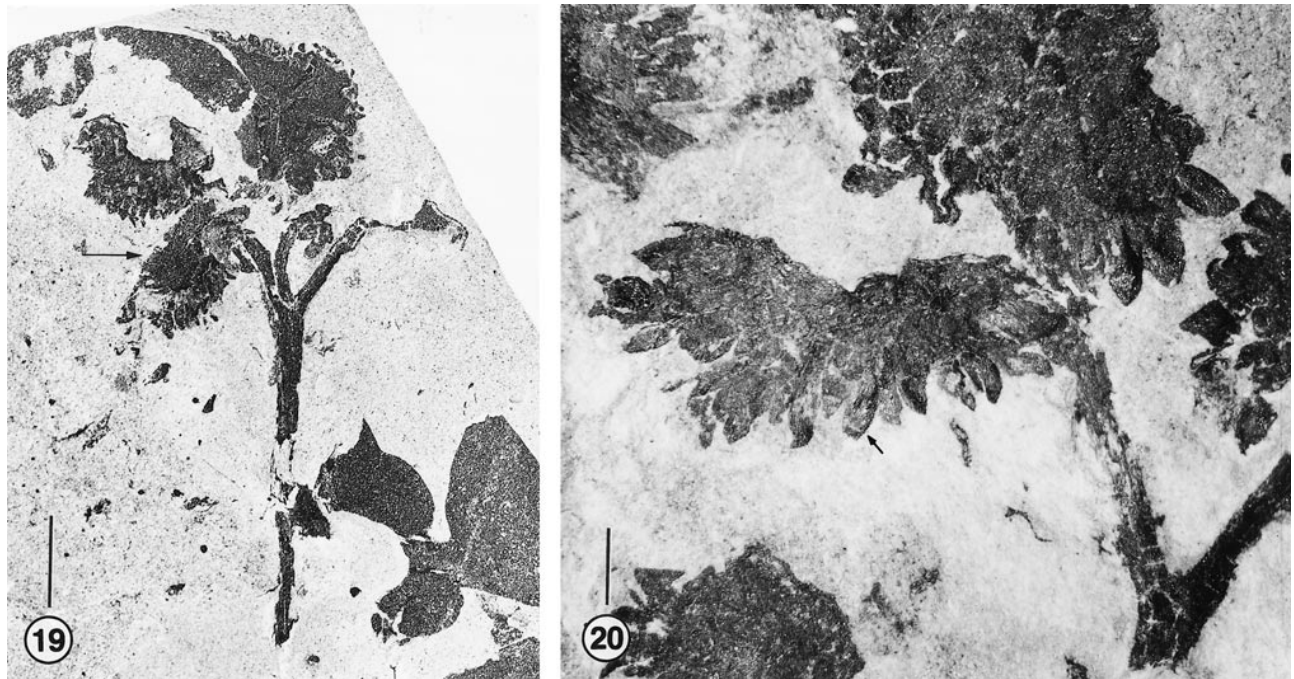
Isolated cupulate organs are common at the new lo-

cality. These specimens appear to represent mature, abscised organs based on their larger size relative to the attached specimens, thickened bases, and dehisced cupules (Figs. 10, 11, 14). The axis of the largest isolated specimen was at least 7.5 cm long. Typically five cupules are present on mature specimens. In rare instances (Fig. 14), up to eight cupules are present, but the additional ones are small and probably represented aborted individuals. The individual cupules are up to 1.3 cm in diameter. The cupule stalks expand somewhat near the point of cupule attachment and continue as a thickening over the upper surface of the cupule. This thickening is most obvious on specimens in a somewhat advanced state of deterioration based on their shriveled appearance (Fig. 16).

Some of the cupulate organs are preserved with their axes perpendicular to the bedding plane clearly revealing the probable whorled cupule arrangement from above (Figs. 11, 14). A whorled cupule arrangement is also suggested by an axis with attached cupule stalks that was recovered by bulk maceration on which the cupule stalks can be seen to arise from the same level (Fig. 12). Further evidence for a whorled arrangement is that on most specimens, all of the cupules on a single axis appear to be at the same developmental stage. On the few specimens with both large and small cupules (Fig. 14), a whorled arrangement is still likely as two discrete size classes are present, whereas a pseudowhorled arrangement would more likely be represented by a gradual transition from small to large cupules. Nevertheless, a pseudowhorled cupule arrangement cannot be entirely ruled out, but seems unlikely based on the available evidence. On several specimens a short section of the main axis of the cupulate organ protrudes slightly above the level of the cupule stalk bases indicating a subapical cupule attachment (Fig. 10). Apparently this apex became inactive after producing the cupule whorl, as no specimens indicating continued apical growth or additional cupule whorl formation have been found.

In nearly all of the isolated specimens, the cupule lamina is entirely split longitudinally along the lower surface so as to form two flaps connected to the midrib (Fig. 13). This feature is consistent and appears to represent the actual dehiscence mechanism of the cupules rather than a preservational artifact caused by compression. This interpretation is supported by the unopened condition of the small cupules on the attached cupulate organs (Fig. 4) and the single immature specimen recovered by bulk maceration (Fig. 15). The cupule exterior is distinctly irregular ["verrucose" in Thomas's (1933) terminology] (Fig. 17). The cupule interior is smooth. Interestingly, no seeds have yet been found within any of the cupules or dispersed in the sediment. This is somewhat surprising because the cupules are quite common at the new locality, and dispersed and in situ seeds are known from many *Umkomasia* species at other localities (Thomas, 1933).

Associated pollen organs—Several fragments of a pollen organ circumscribed by the genus *Pteruchus* occur at the new Antarctic locality (Figs. 19, 20). Because these specimens are not connected to the distinctive short shoot-bearing branches, it cannot be conclusively demonstrated that they were produced by the same plant as the cupulate organs and leaves described above. For this



Figs. 19–20. Associated *Pteruchus* pollen organs. **19.** Pollen organ fragment. Arrow indicates an individual microsporophyll in slightly oblique, lateral view. T12–1035. Scale bar = 5.0 mm. **20.** Detail of microsporophyll in front view. Arrow indicates a single abaxial pollen sac. T12–1001a. Scale bar = 2.0 mm.

reason, we will refrain from naming this organ as a new species of *Pteruchus* until attachment evidence is found. However, these are the only corystospermaceous pollen organs found so far at the Alfie's Elbow locality and are therefore likely to be those of the *Umkomasia uniramia*–*Dicroidium odontopteroides* plant.

This description is based on the four most complete pollen organs. The main axis was up to 3.0 cm long \times 1.5 mm wide with at least ten unbranched microsporophylls with narrow stalks up to 6.0 mm long, suboppositely to alternately arranged on an otherwise naked axis. The microsporophyll laminae are ovate, up to 7.5 mm long \times 7.3 mm wide, with entire margins and a slightly irregular adaxial surface (Fig. 19). Venation of the lamina is somewhat obscured but includes a central vein and at least one order of more weakly developed, pinnate lateral veins. At least 80 pollen sacs, each up to 2.5 mm long, are attached in crowded rows on the abaxial lamina surface (Fig. 20). Within the pollen sacs are poorly preserved pollen grains that range from 72 to 116 μm in diameter with relatively large, laterally situated sacchi with prominent endoreticulations (Fig. 18). These grains correspond most closely to the dispersed pollen genus *Alisporites*, but are too poorly preserved for determination to the species level.

DISCUSSION

Considered together, the distinctive short shoot-bearing branch specimens with attached *Umkomasia* cupulate organs and *Dicroidium* leaves described here provide the first definitive evidence based on attachment that these organs were produced by the same plant. This alone is not surprising as it has been suspected since the original

description of the corystosperms by Thomas (1933) that these organs belong together based on well-established locality associations and general cuticular similarity. The most significant and unexpected aspect of the new assemblage comes from the demonstration that the new *U. uniramia* cupulate organs, which are unlike those known from any other locality, were produced by the same plant that bore leaves conforming to the stratigraphically and geographically widespread and common species *D. odontopteroides*. This indicates that the *D. odontopteroides* leaf type was produced by more than one species of corystosperm based on reproductive organs as discussed below.

Based on relative locality abundances in the Molteno Formation of South Africa, Retallack and Dilcher (1988) proposed that *Umkomasia granulata* cupulate organs and *Dicroidium odontopteroides* leaves were produced by the same plant. If this reconstruction is correct, it would indicate, along with the reconstruction of *U. uniramia* provided here, that at least two different species of corystosperm produced the *D. odontopteroides* leaf morphology. *Umkomasia granulata* differs significantly from *U. uniramia* in having two branch orders, opposite cupule arrangement, papillae on the outer cupule surface, and a hairy inner cupule surface (Thomas, 1933). The Antarctic *U. uniramia* cupules are actually more similar to those of *U. verrucosa* (Thomas, 1933) from the Molteno Formation in having a smooth interior, an irregular (verrucose) outer surface, and a similar dehiscence mechanism.

The conclusion that the South African and Antarctic *Dicroidium odontopteroides* leaves were produced by different corystosperm species is also supported by the associated pollen organs. Townrow (1962) and Retallack

and Dilcher (1988) have suggested that *Pteruchus johnstonii* is the pollen organ of the Molteno Formation *D. odontopteroides*-producing plant based on association and relative locality abundances. The new Antarctic *Pteruchus* pollen organs described here, which were probably produced by the *U. uniramia*-*D. odontopteroides* plant as discussed above, differ considerably from *P. johnstonii* in having larger pollen grains (average: 91 μm vs. 63 μm in diameter), and an unlobed microsporophyll with many more pollen sacs (≥ 80 vs. ≥ 30) per microsporophyll. In fact, the new Antarctic *Pteruchus* differs from any previously described species in this combination of characters.

Biostratigraphic and paleoecological implications—

The realization that the *Dicroidium odontopteroides* leaf was not produced by a unique species of corystosperm plant may have important implications for current Gondwanan biostratigraphic and paleoecological reconstructions. For example, Retallack (1977) identified a series of biostratigraphic zones in the Triassic of Australia based on a hypothetical evolutionary scenario of *Dicroidium* leaf species, and included a *Dicroidium odontopteroides* zone. Retallack recognized this zone in other regions of Gondwana as well, including Antarctica (Lashly Formation), New Zealand (Tank Gully Formation), and South Africa (Molteno Formation). A basic assumption of such biostratigraphic correlations, which we challenge here, is that the *Dicroidium odontopteroides* leaves from these different localities were produced by the same plant species.

The use of *Dicroidium* leaf species in a systematic and paleoecological context finds its most extreme expression in Anderson and Anderson's (1983) paleodeme concept. Based on variations in leaf morphology at a given locality, these workers suggest the recognition of actual biological populations of *Dicroidium* and have identified what they consider subspecies and hybrids based on variations in leaf morphology. Furthermore these workers have delimited putative ecozones including mature and immature *Dicroidium* riparian forests and woodlands based on the occurrence of particular leaf species in assemblages from the Molteno Formation of South Africa (Anderson, Anderson, and Cruickshank, 1998). Based on our findings, we suggest that real progress in understanding Gondwanan plant biostratigraphy and paleoecology will only be possible after more reliable reconstructions of corystosperm species, including both reproductive and vegetative organs, are complete. Our demonstration that the common leaf species *D. odontopteroides* was produced by more than one species of corystosperm based on reproductive organs indicates that all corystosperm-based systematic, biostratigraphic, and paleoecological concepts that treat *Dicroidium* leaf morphospecies as proxies for biological species of entire plants should be considered suspect.

Morphological implications—The relatively well-articulated specimens described here provide new data regarding the overall growth habit of the corystosperms. Previously, Petriella (1978) suggested that the *Dicroidium* plant was an unbranched, medium-sized tree with an apical crown of closely spaced fronds like that of a

tree fern. Archangelsky's (1968) suggestion that the permineralized stem genus *Rhexoxylon* was produced by the corystosperms based on associated fossils from the Ishigualasto Formation of Argentina indicates a liane-like morphology. However, abundant *Dicroidium* leaves in shales surrounding large in situ trunks lacking liane-like anatomy from the Gordon Valley locality of Antarctica suggest that these corystosperms were large trees (Taylor, 1996). Furthermore, the anatomy of the undisputed corystosperm stem genus *Kykloxylon* shows lateral branches and no obvious liane-like features (Meyer-Berthaud, Taylor, and Taylor, 1993). Apparently, the corystosperms were a diverse group that may have exhibited several different growth habits. Consequently, characterization of these plants must be based on painstaking species-by-species reconstructions.

The presence of lateral short shoots and alternating long and short shoot growth, a probable deciduous habit, along with the presence of elongate ovulate organs with distally oriented ovulate structures attached at the short shoot apices indicates a growth habit for the *Umkomasia uniramia*-*Dicroidium odontopteroides* plant similar to that of extant *Ginkgo biloba*. This similarity would find additional support if the larger branches at the new locality also belong to the *U. uniramia*-*D. odontopteroides* plant as this would indicate an arborescent habit. However, no close phylogenetic relationship between *Ginkgo* and the corystosperms is implied. The presence of short shoots may actually be a more general feature of the corystosperms based on Retallack and Dilcher's (1988) report of short shoot growth on small stems of *Rhexoxylon tetrapteridoides*, which they claim is the stem type of the *U. granulata*-*D. odontopteroides* plant. However, the *Rhexoxylon* stems from South Africa occur in Early Jurassic deposits in which other corystosperm fossils have not been found (Anderson and Anderson, 1983). Anderson and Anderson (1983, Pl. 88, fig. 2) illustrate a group of closely spaced *D. odontopteroides* leaves suggestive of an arrangement on a short shoot, although the actual leaf attachment is not visible. Despite these intriguing specimens, the demonstration in this paper of short shoots on the *U. uniramia*-*D. odontopteroides* plant from Antarctica is the only unequivocal example of this growth habit in the corystosperms.

The new Antarctic collection also provides important insight into the controversial issue of the homologies of the corystosperm cupulate organ. Thomas (1933) noted that the lateral axes of *Umkomasia* appear to be arranged in a single plane and, therefore, resemble the pinnae of a compound sporophyll. However, because these lateral axes are frequently situated in the axils of bracts, they more likely correspond to branches. In this interpretation, the entire *Umkomasia* cupulate organ is a branching system, and each cupule represents an individual megasporophyll. Thomas (1933) also reasoned that the *Pteruchus* pollen organ is similarly organized in that the ultimate flattened structures bearing the pollen sacs are individual microsporophylls borne on a branch. Townrow (1962) challenged this interpretation of *Pteruchus* and proposed that the flattened nature of the organ, along with the dorsoventral differentiation of the cuticle, indicates that the entire organ is a single compound sporophyll. Based on this interpretation, the pollen-sac-bearing structures

(“heads” in Townrow’s terminology) are pinnules rather than individual sporophylls, and the “bracts” occurring near the base of some specimens are sterile pinnules. Crane (1985) accepted this interpretation of *Pteruchus* and suggested that the cupule-bearing structures are also compound sporophylls because they too have dorsiventrally differentiated cuticles and lateral axes oriented in a single plane. According to this interpretation, the individual cupules represent pinnules rather than complete megasporophylls. The compound sporophyll interpretation of *Umkomasia* was rejected by Holmes (1987) in a description of *U. distans* specimens from the Basin Creek Formation of Australia in which the lateral axes are alternately and spirally arranged on the main axis, and are sometimes subtended by small bracts indicating that they are branches. Furthermore, Yao, Taylor, and Taylor (1995) demonstrated conclusively that the *Pteruchus* pollen organ is a branch bearing simple microsporophylls based on anatomically preserved specimens from Antarctica. This finding demonstrated that the dorsiventrally differentiated cuticle and flattened appearance of *Pteruchus* are not reliable indicators of either the structure or actual homologies of this organ. Therefore, these same features can no longer be considered as evidence in support of the compound megasporophyll hypothesis of the *Umkomasia* cupulate organ.

Considered together, the findings discussed above appear to support Thomas’s (1933) original interpretation of the *Umkomasia* cupulate organ as a branching system as opposed to Townrow’s (1962) compound megasporophyll interpretation. Using these arguments, Nixon et al. (1994) coded the cupulate organ as a branching system in their comprehensive seed plant phylogeny. Despite convincing evidence that the main axis of the cupulate organ is a branch, however, the homology of the cupules themselves was still not conclusively demonstrated. As noted by Doyle (1996, p. 29) in his discussion of character coding for the corytosperms, “Nixon et al. (1994) showed that the ovulate structures of corytosperms, previously interpreted as bipinnate sporophylls with cupules corresponding to pinnules, are actually branch systems, with the ‘pinnae’ arranged spirally. However, it is not so clear whether the pinnae are in turn branches, with the cupules representing paddle-like megasporophylls (coded by Nixon et al. as ‘peltate-enclosed’), analogous to the simple microsporophylls, or sporophylls with the cupules representing leaflets . . .” Doyle’s (1996) proposal can therefore be thought of as a combination of the branching system and compound megasporophyll interpretations.

The unusual architecture of the new Antarctic *Umkomasia uniramia* organs described here provides insight into the controversial question of cupule homologies. As discussed above, it is now clear that the main axis of *Umkomasia* is a branch rather than a compound sporophyll rachis. Therefore, the single primary axis of the new species described here must also correspond to a branch assuming that the short shoot upon which these axes are borne (Figs. 3, 4) is part of the vegetative structure of the plant and is not homologous with the main axis of the multibranched *Umkomasia* species. This is the most likely interpretation because the short shoot is indeterminate as indicated by branch specimens displaying alternating regions of short and long shoot growth as dis-

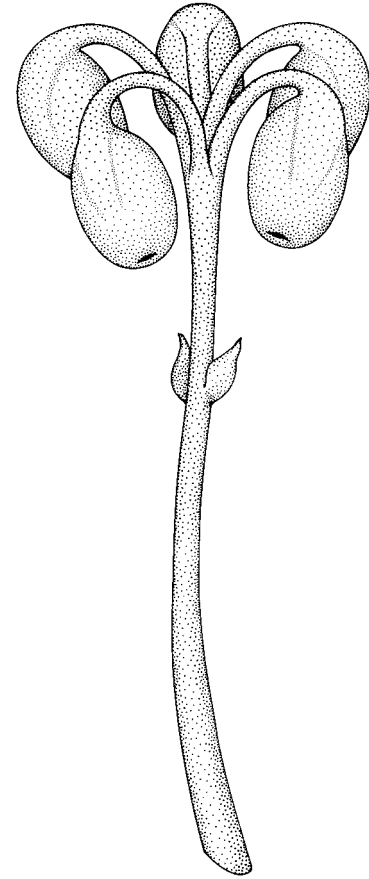


Fig. 21. Suggested reconstruction of an *Umkomasia uniramia* cupulate organ.

cussed above (Fig. 5), whereas *Umkomasia* organs were apparently determinate and abscised as a unit at maturity. Therefore, the entire structure consisting of a single axis with an apical whorl of cupules in *U. uniramia* is homologous with the entire multibranched forms rather than just one of the lateral axes. This interpretation is further supported by the lack of abscised short shoots either with or without attached cupulate organs at the Alfie’s Elbow locality. If the axillary position of the cupulate organ axis on the short shoot can be verified by better preserved specimens, this would further support the proposal of branch homology for the *U. uniramia* axis. Because the cupules of *U. uniramia* exhibit a whorled arrangement, each cupule must correspond to an individual lateral appendage of a branch (i.e., a leaf or branch) rather than a unit of a single leaf (pinnule or leaflet) as required by the compound megasporophyll hypothesis (Fig. 21). We further suggest that the individual cupules are modified leaves rather than branches, due to their leaf-like morphology consisting of a petiole-like stalk with an expanded laminar distal region that forms the cupule proper and lack of evidence for subtending leaves or bracts. If this interpretation is correct, it is likely that any enclosed ovules were borne on the abaxial sporophyll surface as the cupule itself appears to be formed by a downward (abaxial) infolding of the lamina.

Phylogenetic implications—The historical difficulties

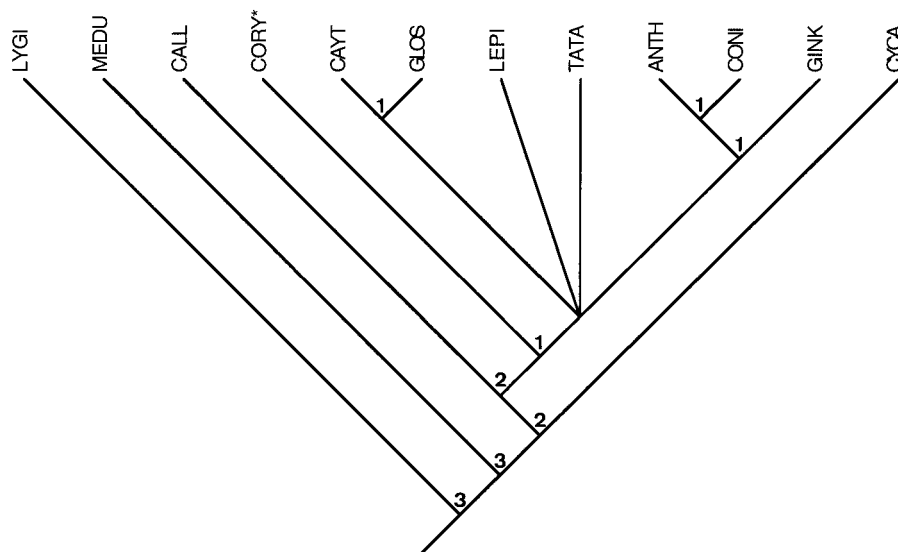


Fig. 22. Simplified strict consensus seed plant cladogram based on a modification of the Nixon et al. (1994) data set. LYGI = *Lyginopteris*, MEDU = *Medullosa*, CALL = *Callistophyton*, CORY = corystosperms, CAYT = *Caytonia*, GLOS = *Glossopteris*, LEPI = *Lepidopteris*, TATA = *Tatarina*, ANTH = anthophytes, CONI = conifers, GINK = *Ginkgo*, CYCA = cycads. Numbers are decay values of subtending nodes.

in deciphering the structure of the corystosperms and other Mesozoic pteridosperms, along with the lack of reliable specific reconstructions, are reflected in the unstable position of these plants within and between various comprehensive seed plant phylogenies (e.g., Crane, 1985; Rothwell and Serbet, 1994; Nixon et al., 1994; Doyle, 1996). In several published trees (e.g., Rothwell and Serbet, 1994) the corystosperms are part of a monophyletic group including *Callistophyton*, *Caytonia*, the glossopterids, and *Peltaspermum*. In many of Doyle's (1996) trees, the corystosperms occur in various arrangements with the peltasperms in a "hennigian comb" arrangement basal either to the "coniferopsid" (conifers plus *Ginkgoales* and Cordaitales) or "glossophyte" (traditional anthophytes of most previous analyses plus glossopterids and *Caytonia*) clades. In many of Nixon et al.'s (1994) trees, the corystosperms resolve close to the peltasperms either below the *Ginkgo* clade or subtending the "anthophyte" clade.

In order to assess the potential phylogenetic implications of the new corystosperm material from Antarctica, we recoded several characters in the Nixon et al. (1994) and Doyle (1996) analyses based on the new findings reported here. These studies were chosen for reanalysis because they include the most recent available data on seed plant morphological characters. We did not include the Rothwell and Serbet (1994) analysis because the corystosperms were coded under the assumption that *Petriella* (Taylor, Del Fueyo, and Taylor, 1994) is a corystosperm and would therefore have required major revision. In each of the reanalyses, *Umkomasia uniramia* was included as a single terminal, i.e., as an exemplar of the entire order Corystospermales. Anatomical characters were assumed to be like those found in permineralized forms previously described from Antarctica (Taylor, 1996) and were therefore not modified from the original matrices. Character numbers 4, 29, and 31 in the Doyle (1996) matrix were recoded to reflect the presence of

short shoots (1), simple ovule-bearing structures (1), and abaxial ovule attachment to the lamina (1), respectively. In the reanalysis of the Nixon et al. (1994) study, character numbers 2, 62, and 67 were recoded as short shoots present (1), megastrobili simple (0), and ovule position foliar (1), respectively. The revised data sets were analyzed with the PAUP* (Swofford, in press) program under the same search options as reported in the original studies. The theoretical and methodological difficulties with this approach to phylogenetic reconstruction are great, as discussed below, but are unavoidable until more is known about these plants and more improvements in parsimony algorithms are developed.

Analysis of the modified Doyle (1996) matrix resulted in 119 most parsimonious trees, whereas the original analysis produced 123 trees. The consistency index (CI) of both analyses is 0.49. The smaller number of trees found in the reanalysis is due to the loss of four examples in which the Paleozoic pteridosperm *Callistophyton*, the peltasperms *Autunia* and *Peltaspermum*, and the corystosperms form a clade that is the sister group to the coniferophytes. Other than this result, the new character codings had little effect and failed to provide much additional resolution regarding the phylogenetic position of the corystosperms.

Results of the Nixon et al. (1994) reanalysis were more dramatic in that the occurrence of 834 most parsimonious trees in the original study was reduced to 96. The CI of 0.38 was unchanged from the original analysis. In all of the trees obtained, the corystosperms occur just above *Callistophyton* and as the sister taxon to a large clade including all of the "anthophytes," the Mesozoic seed fern *Caytonia*, the conifers, the Paleozoic glossopterids, *Ginkgo*, *Lepidopteris*, and *Tatarina* (Fig. 22). The relatively basal position of the corystosperms in these trees indicates that the cupule in an unlikely homologue of either the angiosperm carpel or second integument. This result is also incongruent with stratigraphic data in that

the corystosperms, which are unknown in the fossil record before the Triassic, resolve below the Permian glossopterids. However, Archangelsky's (1996) suggestion that the Carboniferous-Permian pteridosperm *Botrychiopsis* provides a plausible ancestral morphology for the corystosperms may be relevant in this context.

Although the reanalysis of the Nixon et al. (1994) phylogeny resulted in greater resolution of the corystosperms, these results, along with those of all comprehensive seed plant phylogenies, must be assessed with extreme caution. As Nixon et al. (1994) have stressed, such studies require difficult estimates of homology across a wide range of taxa exhibiting highly divergent structures. Although molecular phylogenies are sometimes considered superior in not requiring such morphology-based homology assessments, the large number of extinct forms separating major groups in ancient clades like the seed plants, as well as subsequent evolutionary change in surviving lineages, renders molecular phylogenies practically useless for accurately reconstructing character evolution. Another serious problem with comprehensive seed plant phylogenies discussed by Nixon et al. (1994) is that higher fossil taxa are often represented as "synthetic" forms rather than distinct, reconstructed terminal species. This practice can seriously compromise the results of phylogenetic analyses in that global parsimony is relaxed. Although Nixon et al. (1994) attempted to reduce the negative effects of synthetic taxa by including many single species as terminals, most of the fossil terminals, including the corystosperms, are still mostly synthetic constructs. It will not be possible to include a single corystosperm species in a phylogenetic analysis as a terminal without numerous missing and assumed character states until more attached and anatomically preserved structures are discovered. Even if this is accomplished, it will still be necessary to relate them to the other particular species of permineralized and compressed organs already described (Taylor, 1996). Although this will be difficult, recent work on conifers from the Triassic of Antarctica suggest that such correlation of parts between permineralized and compression floras in Antarctica may already be feasible (Axsmith, Taylor, and Taylor, 1998).

The results of the Nixon et al. (1994) data set reanalysis must also be considered with caution because so little is yet known regarding the homologies of the ovulate structures in other critical "pteridosperms" such as the Caytoniales and Peltaspermales. Although the ovule attachment in these taxa was coded as "peltate-enclosed" in the Nixon et al. (1994) study, there is considerable evidence indicating that the ovule-enclosing structures of these forms are not homologous based on major structural differences. For example, the peltasperm ovulate structure is peltate, and the unenclosed ovules are borne on the lower surface (Naugolnykh and Kerp, 1996). In the Caytoniales, the cupule appears to be formed by a tip-to-stalk folding of a nonpeltate lamina, such that the cupule opening is surrounded by both lamina and stalk tissue (Nixon et al., 1994). A similar structural organization occurs in the cupule of *Petriellaea* from the Triassic of Antarctica (Taylor, Del Fueyo, and Taylor, 1994). The corystosperm cupule organization differs significantly in that it is formed by a downward infolding of the lamina as described above. Furthermore, the opening of the unde-

hisced cupule is formed entirely by lamina tissue with no contribution from the stalk. In this character, the *Umkomasia* cupule is most similar to that of the enigmatic pteridosperm *Ktalenia circularis* from the Cretaceous of Argentina (Taylor and Archangelsky, 1985). This interpretation is reflected in our recoding of ovule attachment in the corystosperms as foliar (1). The single central vein running over the upper surface of the corystosperm cupule is also unknown in other forms. Furthermore, it is uncertain whether the entire ovulate organ of the Peltaspermales and Caytoniales is a single compound megasporophyll or a branching system with simple megasporophylls as shown here to be likely for *Umkomasia*. A better understanding of these so-called Mesozoic pteridosperms, as well as the Late Paleozoic glossopterids, is obviously required before a more robust understanding of seed plant phylogeny and character evolution can be obtained. Although anatomically preserved fossils generally provide the most unambiguous information, the new Antarctic specimens described here demonstrate that the potential of compression fossils to elucidate the structure and systematics of these intriguing plants is far from being exhausted.

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