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The "New Approach to Corystospermales" and the Antarctic Fossil Record: A Critique

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Abstract. Much is now known about the Mesozoic pteridosperm order Corystospermales based on over seventy years of research. However, several concepts of corystosperm evolution have been proposed that avoid well-established phylogenetic methodology and arbitrarily discount evidence of the group from Antarctica. Here, we focus on the "New approach to Corystospermales" published by Artabe and Brea, which establishes a phylogeny for corystosperms based mainly on a restricted concept of anomalous wood anatomy in this group, and assumed relationships with cycads and medullosan pteridosperms. These authors also question evidence regarding attached corystospermalean organs from Antarctica. Based on a reconsideration of the Antarctic record, we reaffirm the evidence for a *Dicroidium* leaf in attachment to branches that also bear distinctive short shoots. *Umkomasia* cupulate organs occur on identical attached short shoots. We also emphasize that wood morphotaxa attributed to the corystosperms from Antarctica, including *Jeffersonioxylon* and *Kykloxylon*, indicate that anomalous secondary growth is not necessarily basic to the corystosperms. We conclude that a greater understanding of the corystosperms will require a consideration of all relevant evidence, and will not be advanced by single organ phylogenies based on fossils from one region.

Resumen. LA "NUEVA PROPUESTA PARA EL ORDEN CORYSTOSPERMALES" Y EL REGISTRO FÓSIL EN LA ANTÁRTIDA: UNA CRÍTICA. El orden Corystospermales, reconocido grupo de pteridospermas mesozoicas, ha sido profusamente estudiado durante los últimos setenta años. Sin embargo, varias teorías sobre la evolución de las corystospermas han sido propuestas sin considerar ni la metodología filogenética establecida ni el registro fósil del grupo en Antártida. En este trabajo nos remitimos a la "Nueva propuesta para el orden Corystospermales" publicado por Artabe y Brea, quienes establecen una filogenia para las corystospermas basada principalmente en una teoría restringida a la anatomía anómala de la madera en el grupo, y atribuyendoles una relación con las Cycadales y con las Medullosales. Estas autoras asimismo cuestionan la evidencia relacionada con la conexión de órganos vegetativos y reproductivos a ramas de las corystospermas. Sobre la base de una reconsideración del registro fósil para Antártida, confirmamos la evidencia de una hoja de *Dicroidium* en conexión a ramas que también portan braquiblastos. Las cúpulas de *Umkomasia* nacen en braquiblastos idénticos. También enfatizamos que las maderas-morfotaxa de Antártida atribuidas a las corystospermas, incluyendo *Jeffersonioxylon* y *Kykloxylon*, indican que el crecimiento secundario anómalo no es necesariamente un carácter básico para las corystospermas. Concluimos que para un mayor entendimiento de las corystospermas, se deberá considerar toda la evidencia fósil relevante, y no anticipar filogenias basadas en fósiles únicos provenientes de una sola región.

Key words. Antarctica. Corystospermales. *Dicroidium*. Gondwana. Phylogeny. South America. Triassic. Seed ferns.

Palabras clave. Antártida. Corystospermales. *Dicroidium*. Gondwana. Filogenia. América del Sur. Triásico. Helechos con semilla.

Introduction

Research over the last seventy years has established that the pteridosperm order Corystospermales was the dominant seed plant group over much of Gondwana during the Triassic Period (e.g., Petriella, 1981; Anderson and Anderson, 1985; Taylor, 1996). The best-known morphotaxa assigned to this group include several species of the cupulate, ovule-bearing structure *Umkomasia*, the pollen organ *Pteruchus*, and bifurcating fronds of *Dicroidium*, as originally proposed by Thomas (1933), based on material from South Africa. Several types of anatomically preserved wood have also been linked to the corystosperms, including species of *Antarcticoxylon* (Seward, 1914), *Cuneumxylon* (Artabe and Brea, 2003), *Jeffersonioxylon* (Del Fueyo *et al.*, 1995), *Kykloxylon* (Meyer Berthaud *et al.*, 1993), *Rhexoxylon* (Archangelsky and Brett, 1961), and *Tranquiloxylon* (Herbst and Lutz, 1995).

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Despite a remarkable history of research that has shed considerable light on the morphology, anatomy, and paleoecology of the Corystospermales, it has proven difficult to establish a stable and generally agreed upon concept of phylogenetic relationships within this order. The systematic position of the Corystospermales within the seed plants also has been a source of considerable controversy. This is due, at least in part, to the lack of many whole plant reconstructions, along with difficulties in interpreting the morphology and potential homologies of corystospermalean reproductive organs in relation to those of other potentially relevant fossil and extant taxa (Taylor, 1996). These issues can also be considered within the broader context of the current role of morphological/paleobotanical data in higher-level phylogeny reconstruction in general, following the nearly complete takeover of this field by molecular approaches (e.g., Palmer *et al.*, 2004).

Despite the current dominance of molecular systematics, it should be obvious that a satisfactory account of character evolution, which is one of the main points of phylogenetic inference, must incorporate information from the fossil record in groups of great antiquity with large numbers of extinct higher taxa, such as the seed plants (Crane *et al.*, 2004). This is true even if the relationships among extant taxa seem to have been correctly resolved (Axsmith *et al.*, 1998). Although the exact manner in which morphological/paleobotanical and molecular approaches to seed plant phylogenetic reconstruction will ultimately be synthesized are still being debated, there is no question that the transparent evaluation of all potentially relevant characters, followed by the application of established tree-searching algorithms, will continue to be essential components. Therefore, the present period of uncertainty should not be construed as a reason to return to precladistic approaches, which often proceeded without an explicit methodology, and employed an arbitrary choice of characters supported mainly by intuited evolutionary scenarios.

Corystosperm evolution has been the subject of several recent studies reminiscent of the most problematical aspects of pre-cladistic research, such as the "mostly male hypothesis" of Frohlich (2000), and the "new approach to Corystospermales" of Artabe and Brea (2003). The few testable predictions of the mostly male hypothesis were based on an unconstrained series of dubious homology assessments and hypothetical transformations putatively linking corystosperms and angiosperms. These were conclusively refuted soon after their publication based on analyses of Antarctic corystosperm fossils (Axsmith *et al.*, 2000; Klavins *et al.*, 2002). We comment here on the paper of Artabe and Brea (2003), which we assert does not take into account or misinterprets important data on the corystosperms from Antarctica.

Materials and methods

The branch specimen with the attached *Dicroidium* leaf (Specimen number T12-1002) was previously described by Axsmith *et al.* (2000), and is deposited in the Paleobotany Division of the Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence, Kansas, USA. No special preparation was needed for study of this specimen. Detailed locality data can be found in the original description.

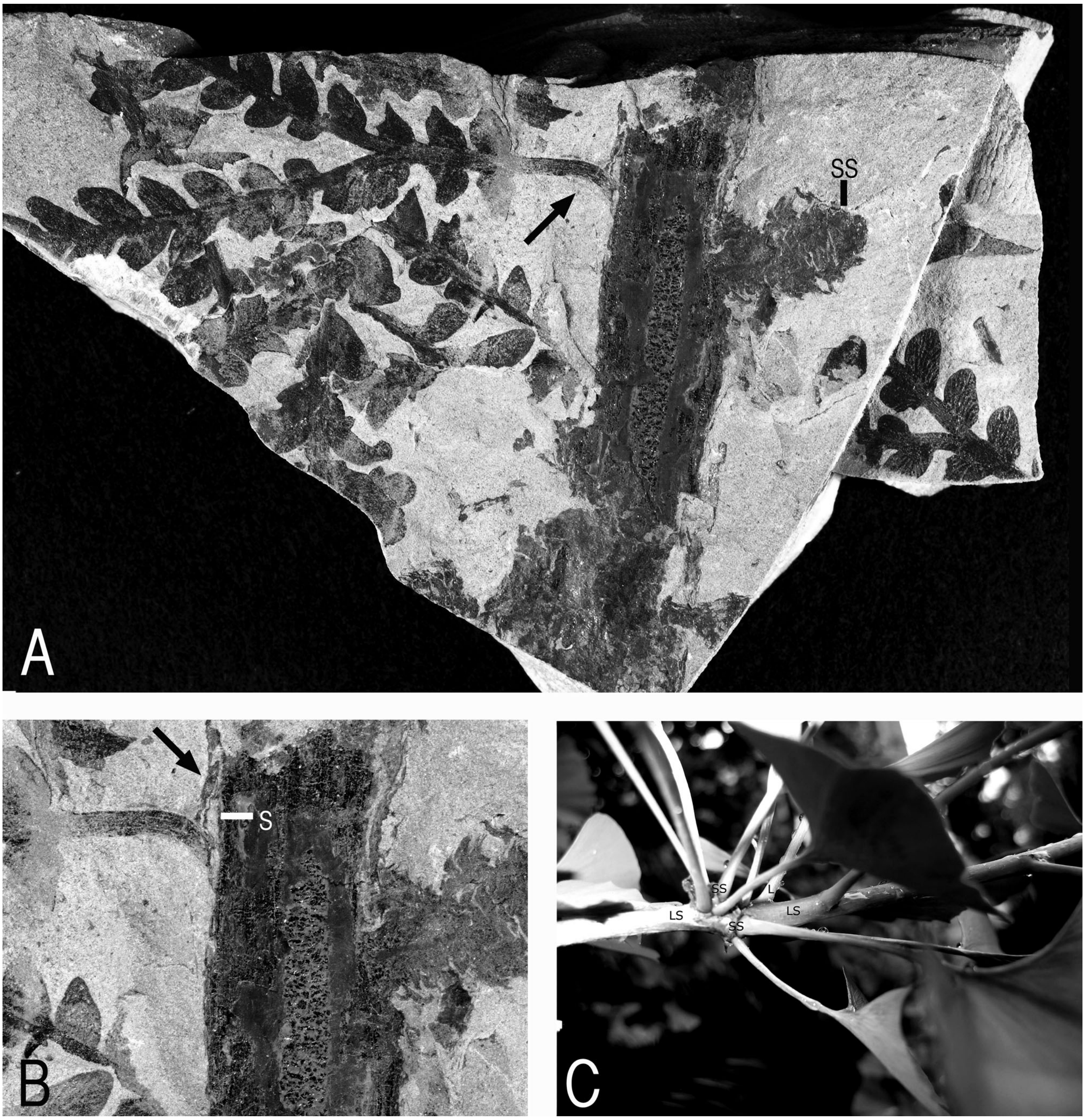
Discussion

Attachment evidence reaffirmed

Misinterpretations of the Antarctic corystosperm fossil record appear early in the Artabe and Brea (2003) paper. Within an introductory paragraph in which the Corystospermales are reaffirmed as a natural group based on classic association and cuticular evidence, the assertion is made that attached corystospermalean organs have not been found. This conclusion directly challenges previous research of ours regarding evidence for leaf and cupulate organ attachment to distinctive stems from Antarctica (Axsmith *et al.*, 2000).

The attachment evidence in question is based on impression/compression fossils collected from exposures of the upper Fremouw-lower Falla Formation on an unnamed ridge in the Shackleton Glacier area, central Transantarctic Mountains. The locality is informally called "Alfie's" site (Axsmith *et al.*, 2000). Branches bearing short shoots are common among the abundant *Dicroidium odontopteroides* (Morris) Gothn leaves, *Umkomasia uniramia* Axsmith *et al.* cupulate organs, and *Pteruchus* sp. pollen organs at this site. The short shoots of one specimen have groups of stalked cupules still attached to their apices. This and other shoot specimens show alternating regions of long and short shoot growth. Along with anatomical and paleoecological evidence for deciduousness (e.g., Meyer-Berthaud *et al.*, 1993; Taylor, 1996), these fossils indicate a growth habit and phenology for the *Umkomasia uniramia* / *Dicroidium* plant somewhat like that of extant *Ginkgo biloba* L..

Another significant specimen from the Alfie's site, which is refigured here (figure 1.A), consists of a section of long shoot, bearing an attached *Dicroidium odontopteroides* leaf. Also attached to this shoot is a



F**igure 1.A-B.** Attached *Dicroidium odontopteroides* leaf. Alfie's site, Antarctica. Specimen number T12-1002 / *hoja de* Dicroidium odontopteroides *en conexión a la rama. Localidad fosilífera Alfie, Antártida. Ejemplar número T12-1002.* **A,** view of entire branch section with lateral short shoot (SS) and attached ***D. odontopteroides*** leaf. Arrow indicates severe bend in leaf petiole X1.0 / *aspecto de la rama con un braquiblasto (SS) lateral y hojas de* **Dicroidium odontopteroides** *en conexión. La flecha indica una marcada curvatura en el pecíolo de la hoja.* **B,** Detail of the ***D. odontopteroides*** leaf attachment point in figure 1.A. Arrow indicates branch margin. Note that the line of sediment (S) occurs within this margin, not between the petiole and branch X1.6 / *detalle del punto de inserción de la hoja de* **Dicroidium odontopteroides** *señalado en A. La flecha indica el margen de la rama. Nótese que la línea de sedimento(S) se encuentra dentro de este margen y no entre el pecíolo de la hoja y la rama.* **C,** Branch of a living ***Ginkgo biloba*** specimen from the University of South Alabama campus showing a long shoot (LS) with attached leaves of the current season in close proximity to short shoots (SS) growing out from last season's section of the long shoot X0.5 / *rama de la especie actual* **Ginkgo biloba***, tomada de los terrenos de la Universidad del Sur de Alabama, mostrando ramas de crecimiento indefinido (LS) con hojas de la reciente temporada en conexión y en las cercanías de braquiblastos originados durante la estación anterior en las ramas de crecimiento indefinido.*

short shoot identical to those bearing the *Umkomasia uniramia* organs on the fertile specimen mentioned above. Therefore, taken together, these specimens provided the first attachment evidence that *Umkomasia* and *Dicroidium* were parts of the same plant. However, Artabe and Brea challenge this conclusion based on the following interpretations of the supporting figures:

"The supposed attachment of the *Dicroidium* leaf to the axis reported by Axsmith *et al*. (2000) could be questioned because the single attached leaf has a seam of sediment between the petiole and the axis. Its orientation is opposite that of the associated short shoots, in contradiction to the rule that all leaves and shoots grow toward the light. Furthermore the short shoots with their abundant leaf bases have not a single leaf attached (Artabe and Brea, 2003, p. 209)".

We submit that this assessment is based on a superficial examination of the supporting figures. The first point, that there is a "seam of sediment" between the leaf petiole and the stem, is incorrect. We have refigured the leaf attachment detail here (figure 1.B), which is similar to the one in our original paper (Axsmith *et al*., 2000, fig. 16). In the current figure, we have added an arrow to emphasize the position of the stem margin just distal to the leaf attachment area. It is obvious from this that the "seam of sediment" occurs on the stem itself, not between the petiole and the stem. If one carefully follows the position of the stem margin, beginning at the point indicated by the arrow and moving down toward the leaf, it is clear that the leaf petiole base directly contacts the stem margin. In addition, the tissue of the leaf petiole can be seen to merge directly into that of the stem margin with no break or indication of overlap, clearly indicating attachment. A similar elongate line of sediment occurring within the stem margin can be seen on the opposite side of the stem immediately adjacent to the short shoot (figure. 1.A), proving that such overlapping lines of sediment are common.

We find the second point in the Artabe and Brea (2003) critique of the leaf attachment evidence particularly confusing, but we will attempt to rectify what we believe is the primary misconception. The authors claim that the leaf and short shoot are not oriented the same way relative to the main stem, as they should be if both were growing toward the light. This may be referring to the fact that the short shoot diverges from the stem at an angle (about 65°), whereas the leaf is oriented nearly perpendicular to the main stem. However, it should be obvious that the skewed orientation of the blade portion of the leaf is due to its having been bent backwards during deposition. We have added an arrow to figure 1A to indicate the position of a severe bend in the leaf petiole near the attachment point in support of this interpretation. Of particular note is the fact that other detached *Dicroidium* leaves at this site, and elsewhere, do not have such a strongly bent petiole, which provides additional evidence that this leaf was attached to the stem and bent during or shortly after deposition. The original orientation of the leaf can be determined from the proximal petiolar region (i.e. below the bend), which emerges from the stem at about 45° relative to the distal end of the long shoot. This indicates that the short shoot and leaf were oriented in the same way in life in that they both diverge from the stem with only ~ 20° difference in divergence angle. We assume that Artabe and Brea (2003) are not referring to the left vs. right orientation of the short shoot and leaf, respectively, as this is a necessary consequence of helical phyllotaxis exaggerated by compression.

The final point of Artabe and Brea's (2003) critique of the Antarctic attachment evidence is also difficult to understand. They appear to be suggesting that the attachment evidence is somehow challenged by the lack of leaves attached to the short shoots. They also emphasize earlier in their paper that there is only one attached leaf, but this certainly does not negate the evidence for attachment presented above. Although there is good evidence that *Dicroidium* leaves in Antarctica were seasonally deciduous (Meyer-Berthaud *et al*., 1993; Taylor, 1996), this does not preclude finding specimens with leaves still attached. We assert that the Alfie's specimen simply represents a fortuitous example of a leaf that remained attached a bit longer than is typical and survived fossilization intact.

We are especially uncertain as to why Artabe and Brea (2003) believe that the lack of leaves on the short shoot is problematical considering the general absence of attached leaves anywhere else in the corystosperm fossil record. It is also possible that these short shoots produced only reproductive organs. There may have been other leaves attached to this stem, as the surrounding matrix is full of leaf remains, some of which are oriented in such a way as to be consistent with being attached. However, this fossil is a flattened, highly coalified compression that, fortuitously, split through the stem at just the right position to show the attachment point of the one leaf in question. This is no way precludes the possibility that other leaves are attached.

Fundamental misinterpretations of this attachment evidence similar to those of Artabe and Brea (2003) have been promoted by several other workers. For example, Holmes and Anderson (2005, p. 2) argue that, "By analogy with extant plants bearing long and short shoot morphology (e.g. *Ginkgo biloba*) it would be unlikely in the extreme for a plant with this growth morphology to bear a leaf on the long shoot section of a stem subsequent to the formation of well-developed short shoots". At 1.75 cm, the short shoot is hardly "well-developed". Furthermore, this comment mistakenly assumes that the short shoot and leaf were growing from the same year's section of long shoot. Clearly, based on the orientation of the short shoot and leaf, the apical meristem of the main long shoot was toward the bottom of the original figure (we have re-oriented the two figures here with the distal end up; figures 1.A, 1.B). In this case, the attached leaf represents the most proximal leaf on the current season's long shoot. The short shoot probably began growing out during the previous season due to early loss of its associated leaf. The proximity of a long shoot leaf from one season to a previous season's short shoot is not problematical, as it is a common feature of extant *Ginkgo biloba.* Figure 1.C illustrates this morphology from a *Ginkgo biloba* branch growing in southern Alabama, which shows the proximal leaves on this year's long shoot in close proximity to short shoots growing out of last year's section of the same long shoot. The transition from one season's growth to another would not necessarily be obvious on the fossil, especially if this species did not produce prominent bud scales. It is also likely that the stem is split through interior tissues, which would obscure evidence of such seasonal transitions. Although the short shoot on the fossil is relatively well developed compared with the modern *Ginkgo* in figure 1.C, it must be realized that the fossil trees may have achieved greater growth rates during a single season due to the continuous available light at these high paleolatitudes. For example, Cúneo *et al.* (2003) demonstrated considerable seasonal growth in the wood of a slightly older *Dicroidium* forest from another locality in the Central Transantarctic Mountains. A suggested reconstruction of a branch from the Alfie's corystosperm is presented in figure 2.

Anderson and Anderson (2003) also question our Antarctic corystosperm attachment evidence based on their belief that the Alfie's locality stem is too robust to bear leaves compared to modern *Ginkgo biloba* stems of the season. It is not clear to us why the Alfie's locality stem is considered robust, as it is only 1.6 cm wide at the point of leaf attachment. We have observed leaf-bearing stems of *Ginkgo biloba* specimens on the University of South Alabama campus of comparable width at the most proximal region of the current season's growth.

Based on these considerations, we reaffirm our original assertion that the *Dicroidium* leaf from the Alfie's locality is attached to the same branch that bears short shoots with *Umkomasia* cupules (Axsmith *et al.*, 2000). The criticisms offered to date are based on misinterpretations of the fossil's size and morphology, and incorrect assertions regarding short shoot growth in extant *Ginkgo biloba.* They also do not take into consideration possible differences in phenology between the temperate *Gingko biloba* and a fossil plant from a polar habitat. Even in the absence of the direct attachment evidence, the consistent association of the distinctive, short shoot-bearing branches, *Dicroidium odontopteroides* foliage, and *Umkomasia uniramia* cupulate organs at the Alfie's locality is itself compelling evidence that all of these organs were parts of the same parent plant. Holmes and Anderson (2005) admit that this association is suggestive of affiliation, but argue that other leaf taxa are present in the assemblage that could be from the same plant as the cupules. This view overlooks the fact that the *Dicroidium odontopteroides* leaves and *Umkomasia uniramia* cupulate organs are extremely common at the Alfie's site and occur together in great numbers on the same slabs, whereas the other leaf taxa (e.g., *Heidiphyllum* and *Taeniopteris*) are exceedingly rare in these layers. Interestingly, Anderson (1978) was the first to argue that *Heidiphyllum* is the leaf of the conifer that produced *Telemachus* seed cones. Regardless of one's final position on the attachment evidence, it is clear that the *D. odontopteroides* leaf is a morphospecies in the strictest sense, and can no longer be considered a proxy for a particular biological species of parent plant. This underscores the importance of whole plant reconstructions, and demonstrates the inherent problems with phylogeny reconstructions based on single organs, especially when dealing with the corystosperms.

Phylogenetic challenges

Despite the general realization that plant phylogenetic reconstruction must consider all available evidence and follow established methodologies, Artabe and Brea (2003) propose a close phylogenetic relationship between the corystosperms, cycads, and medullosans based almost entirely on wood anatomy. In so doing, they propose a hypothetical evolutionary series of wood morphotaxa based on this unsubstantiated phylogenetic hypothesis, which ignores equally plausible alternatives based on Antarctic fossils.

The suggested demise of the anthophyte hypothesis has, for now, largely dampened attempts at large-scale cladistic analyses of the seed plants that incorporate fossil data (Donoghue and Doyle, 2000). Nevertheless, several such studies have been published, and these remain the only assessments of relationship for extinct seed plant taxa available that incorporate a broad array of characters and explicit phylogenetic methodologies (e.g. Crane, 1985; Rothwell and Serbet, 1994; Nixon *et al.*, 1994; Doyle, 1996). Although a detailed discussion of these analyses and their reliability compared to molecular phylogenies is beyond the scope of this paper (see, e.g., Axsmith *et al.*, 1998), there is little support for a close relationship between the corystosperms and cycads or medullosans in any of these analyses. This was

Figure 2. Stylized reconstruction of branch bearing ***Dicroidium odontopteroides***-type fronds and short shoots with attached *Umkomasia uniramia* cupules, based on plants from the "Alfie's" locality, Antarctica / *reconstrucción de una rama con hojas del tipo* **Dicroidium odontopteroides** *y con braquiblastos portando cúpulas de* Umkomasia uniramia, *basada en las plantas de la localidad fosilífera Alfie en Antártida.*

true even before new evidence based on Antarctic fossils was included (Axsmith *et al*., 2000; Klavins *et al*., 2002).

Artabe and Brea (2003) briefly discuss the prevailing theories of corystosperm systematics, but ignore most of the characters painstakingly revealed by over seventy years of research on this group, and the legacy of analysis of these characters established by previous phylogenetic studies. Instead, they link the corystosperms with cycads and medullosan pteridosperms based mainly on wood features. In particular, they rely most on the shared presence of "… deviations from the typical pattern of secondary growth and the development of anomalous secondary growth" in various members of these groups (Artabe and Brea, 2003, p. 218). Such similarities between the anomalous *Rhexoxylon* wood attributed to the corystosperms and that of cycads and medullosans have been noted before (e.g., Archangelsky and Brett, 1961). Cycad-like petiole vasculature has also been described in *Dicroidium* leaves from Antarctica (Pigg, 1990). However, in many groups, anomalous stem anatomy has been correlated with habit and environment rather than with systematics. For example, in the Bignoniaceae, liane taxa exhibit anomalous wood growth, while tree taxa do not (Gasson and Dobbins, 1991). Although *Rhexoxylon* appears to consistently exhibit anomalous growth, the taxon is not present or is very rare in a number of sites where *Dicroidium* foliage is dominant (e.g., Antarctica and South Africa; see Taylor, 1996). Therefore, using this vegetative growth pattern as the sole basis for a phylogeny or evolutionary scenario does not take into account the complete variation within the corystosperms.

Based on the hypothesis that anomalous secondary xylem was derived from a cycad or medullosan-like ancestor and is, therefore, primitive in the corystosperms, Artabe and Brea (2003) propose that an early phyletic split produced two parallel groups termed the "cuneumyloid" and "rhexoxyloid" lineages. Although this scheme applies specifically to southwestern Gondwanan forms, the supposition that anomalous wood is primitive in the corystosperms must apply broadly, unless one is willing to entertain the unlikely prospect that *Umkomasia* and *Pteruchus* organs evolved independently in corystosperms from different areas of Gondwana.

No justification for the exclusive emphasis on wood structure in corystosperm systematics is provided by Artabe and Brea (2003), nor is there a discussion of the implications of this scheme for the evolution of the reproductive structures. This is a crucial issue, because we see no convincing points of comparison between the corystospermalean *Umkomasia* and *Pteruchus* reproductive organs and those of medullosans and cycads. In fact, recent studies of *Umkomasia* based on Antarctic fossils (Axsmith *et al*., 2000; Klavins *et al*., 2002), which show abaxial ovule attachment to the cupule surface and the open, multiovulate nature of some of the cupules, may suggest even greater similarity to the ovulate organs of the Peltaspermales than previously realized.

Even if one accepts the emphasis on wood anatomy at face value, the phylogenetic scheme proposed by Artabe and Brea (2003) ignores alternative scenarios based on other wood types linked to the corystosperms, particularly those from Antarctica. For example, *Kykloxyon* wood has been described in detail from permineralized Antarctic peat and, based on petiole anatomy, was produced by the same plant as the associated *Dicroidium* leaves and reproductive structures (Pigg, 1990; Meyer-Berthaud *et al*., 1993; Yao *et al*., 1995; Klavins *et al*., 2002). Artabe and Brea (2003) state that this wood is too poorly understood to include in their phylogenetic scheme, but the most relevant character, the lack of evidence for anomalous cambial activity, is extraordinarily well documented. This raises the distinct possibility that the presence of a continuous cylinder of secondary xylem is the basic condition in corystosperms. Furthermore, large trunks of *Jeffersonioxylon* found in situ in the Middle Triassic of the Gordon Valley of Antarctica are associated with *Dicroidium* leaves, and these also lack anomalous secondary growth (Del Fueyo *et al*., 1995; Cúneo *et al*., 2003). In fact, *Jeffersonioxylon* wood has many "coniferalean" features, as does that of *Kykloxylon* and the Late Paleozoic glossopterid pteridosperms (Taylor, 1996). In addition to calling the primitive status of anomalous secondary growth in the corystosperms into question, this fact underscores the mosaic evolutionary nature of wood anatomy, and therefore precludes an exclusive reliance on wood characters in phylogenetic studies.

Finally, Artabe and Brea (2003) ignore evidence from Antarctic corystosperms in their claim that there is no evidence for axillary branching in the Corystospermales. Presumably, this claim was made to provide some additional support for a close phylogenetic relationship between corystosperms and cycads. However, axillary branches have been demonstrated unequivocally on *Kykloxylon* stems, based on permineralized specimens from Antarctica (Meyer-Berthaud *et al*., 1993).

Conclusions

In summary, we contend that there is little new in Artabe and Brea's (2003) "New approach to Corystospermales". Rather, it represents a return to methodologically unsound, outmoded evolutionary schemes based on a limited set of arbitrarily chosen characters. Furthermore, it distorts or ignores substantial evidence regarding corystosperms gleaned from years of research on Antarctic corystosperms, much of which is based on anatomically preserved material. A robust understanding of the anatomy, biogeography, biostratigraphy, morphology, and systematics of the corystosperms will be realized only after a consideration of all relevant evidence based on the best reconstructions possible from throughout the geographic and stratigraphic range of this group. This will continue to be a painstaking process, but shortcuts will only lead to erroneous conclusions and further weaken the status of paleobotanical approaches to understanding the evolutionary history of seed plants.

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