



Additional observations on the enigmatic Permian plant *Buriadia* and implications on early coniferophyte evolution

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ABSTRACT

An extensive collection of compressed altered remains, including leafy shoots and ovules similar to specimens described as *Buriadia*, is reported from Lower Permian rocks on Mount Gran, Victoria Land, Antarctica. The specimens, preserved as a thin layer of aluminosilicate film in a fine-grained black shale, show a number of morphological features like those reported from the type species, *Buriadia heterophylla*. The leaves are highly polymorphic and appear to be helically arranged. The ovules are orthotropous and attached to leafy shoots by a short stalk; they do not appear to be organized into distinct zones along the axis. The ovules are obovate, with a conspicuous bifid apex and prominent chalazal disk. The combination of features in these Antarctic specimens indicates affinities with the putative Permian coniferophyte, *B. heterophylla*, originally described from India. The discovery of a presumed coniferophyte with erect terminal ovules from the Permian of Antarctica adds support to the hypothesis that there were at least two major groups of conifer-like plants present during the late Paleozoic. Differences in the ovulate parts of these plants suggest a unique evolutionary history for the late Paleozoic coniferophytes from the Southern Hemisphere.

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1. Introduction

Buriadia is an enigmatic gymnosperm that occurs at several Lower to Upper Permian Gondwanan localities and exhibits some unusual morphological features. The taxon has a wide distribution in India (Seward and Sahni, 1920; Maithy, 1969; Banerjee, 1973; Singh et al., 2000, 2003), and species have also been documented in South America (Rigby, 1972; Guerra-Sommer et al., 1980; Bernardes-de-Oliveira and Yoshida, 1981; Cazzulo-Klepzig and Guerra-Sommer, 1983; Jasper et al., 2005). Schopf (1968) reported *Buriadia* in Lower Permian rocks of Antarctica together with foliage of *Glossopteris*, *Gangamopteris*, and *Noeggerathiopsis*. The presence of multiple morphological features has been used to ally other taxa with *Buriadia*, including *Paraburiadia* (Zimina, 1983), *Birsinghia* (Pant et al., 1995) and *Walkomiella* (Surange and Singh, 1953).

Fossils from India described by Feistmantel (1879) and initially referred to *Voltzia heterophylla* Brongniart were later examined and reassigned to *Buriadia* by Seward and Sahni (1920). In their reinterpretation, it was determined that the lack of identifiable reproductive structures and the disposition of the bifid leaves on foliage shoots were unlike those of *Voltzia* and *Walchia*. The bifid

leaves, considered to be a diagnostic feature of the genus, are similar to taxa such as *Gomphostrobus* (Marion, 1890) and the smaller leaves of *Dicranophyllum* (Seward and Sahni, 1920). Almost 50 years later, the type material was reexamined and additional collections from the type locality in India were made (Pant and Nautiyal, 1966, 1967). The new specimens included larger shoot systems and numerous ovules, some of which provided previously unknown cuticular detail when macerated. Macerated wood revealed anatomical details such as tracheid wall patterns and ray configurations (Pant and Nautiyal, 1967). This new material helped to more fully characterize *Buriadia*, but the interpretation of ovule attachment would prove to be the most misleading and controversial aspect of the study, as the ovules were regarded as being attached to leaves by one of the slender bifid tips. According to this interpretation ovules were thought to be anatropous on stalks extending beyond the helically arranged leaves. The random arrangement of the stalked ovules suggested that *Buriadia* lacked an aggregated or cone-like structure typically associated with conifers. Based to a large degree on this interpretation, the evolution of the conifer cone was envisioned with *Buriadia* occupying a basal position in a transformational series (Pant and Nautiyal, 1967). Subsequent studies (e.g., Pant, 1977, 1982; Archangelsky and Cúneo, 1987) utilized this interpretation in discussions of conifer cone evolution. The investigation of Pant and Nautiyal (1967) alluded to the nature of conifer reproduction, phylogenetic affinities, and the pivotal position occupied by *Buriadia* (Pant and Nautiyal, 1967), but also suggested that the combination of characters in the fossils may in fact indicate

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that *Buriadia* was either an unusual conifer or a gymnosperm with obscure affinities.

These controversial aspects of *Buriadia* initiated a more recent study that focused on reexamining as much of the original material as possible (Singh et al., 2003). These authors determined that the ovules were not attached by one of the apical horns. They suggested that the ovules previously described as attached were only in close proximity to shoots and became compressed in positions suggesting organic attachment. Although Singh et al. (2003) greatly contributed to clarifying several important aspects of the reproductive biology of *Buriadia*, the new information has not diminished the importance of this organism in paleobotanical research, since without the controversy surrounding this enigmatic plant new discoveries may go unnoticed or remain undocumented until a later date.

The fossils described in this paper were collected over 40 years ago in Antarctica by Geoffrey (Toby) Rose and sent to Dr. James M. Schopf of the U.S. Geological Survey. Many of the specimens had been photographed and there were associated notes suggesting that Schopf was in the process of preparing a manuscript detailing ovules associated with shoots. These new specimens of *Buriadia* add new information about the ovulate parts of this enigmatic gymnosperm from an additional Gondwanan continent at a critical time in coniferophyte evolution.

2. Materials and methods

Specimens were collected from Mount Gran (B7 Unit), on the north side of Mackay Glacier at approximately 76° 58' S, 161° E, Prince Albert Mountains, Victoria Land, Antarctica (Mirsky et al., 1965). Mount Gran was initially reported by Robert Falcon Scott's Second Antarctic Expedition in 1912 (Mulligan et al., 1963), but at that time was not explored. The material was collected during the 1966–1967 austral field season by Geoffrey (Toby) Rose of the University of New South Wales, Australia, and initially consisted of eight hand specimens of highly metamorphosed black shale. Based on geologic and paleobotanical information, the deposits at Mount Gran are considered to be Lower Permian (Mulligan et al., 1963; Mirsky et al., 1965; Schopf, 1968); however, the precise stage still remains to be determined. The fossils occur within the Mount Bastion Formation which is made up of numerous coal layers suggesting that it was deposited under conditions of a high water table (Mirsky et al., 1965). Although the sample size is relatively small it has provided a wealth of new information that is useful in detailing several important aspects of this Gondwanan coniferophyte.

To maximize the data potential of the sample, additional surfaces were continually exposed along weak bedding planes and only the original samples containing larger shoots were left intact. As a result several hundred pieces were processed and examined. Initial preparations used to enhance surface detail and to acquire anatomical information from embedded and sectioned material relied on the assumption that the plant fossils were preserved as a thin layer of pyrite. Numerous acid preparations (hydrofluoric, nitric, sulfuric, hydrochloric) were applied to enhance detail but none proved effective. Submersion in concentrated hydrofluoric acid for several days eventually disaggregated some samples and isolated plant material that occurred as thin silvery pieces was recovered. These macerated pieces and larger samples were mounted on stubs and coated with gold for scanning electron microscope (SEM) analysis.

Surface details varied among the scanned samples and each specimen typically provided only a small amount of information. Both the thin silvery specimens and the larger samples were subjected to energy-dispersive X-ray spectroscopy (EDX) which provided information about the elemental and chemical composition. The results of these tests indicated the absence of both Fe and S, and the presence of Al, Si, O, and a small amount of C within the samples. As a result it was determined that the fossil plants from Mount Gran are not preserved as pyrite films but rather are made up of some type of aluminosilicate

film, which has presumably replaced the plant material. This type of secondary preservation is often believed to be associated with low- to intermediate-grade metamorphism (Butterfield et al., 2007). The formation at Mount Gran includes numerous Jurassic intrusives of the Ferrar Group (Mulligan et al., 1963; Elliot and Fleming, 2008) and these may represent the metamorphic event that altered the strata and subsequently the fossil material. As a result of this unusual preservation, many morphological and anatomical details are obscured or dramatically altered, making it difficult to fully characterize the exact nature of these Antarctic fossils.

Submersion of the specimens in 100% ETOH proved to be the most promising procedure for detailing the features in this type of preservational mode. Images were acquired using a Leica DC500 digital camera and SEM micrographs were captured on a LEO 1550 with an EDAX silicon lithium detector. Images were processed with Adobe® Photoshop® CS Version 8.0 (©1999–2003, Adobe Systems Incorporated) and stored on archival compact disks. Specimens are housed in the Division of Paleobotany, Natural History Museum and Biodiversity Institute (PBKU), University of Kansas, Lawrence, Kansas under acquisition numbers PM 635–638, PM 5439–PM 5889 and ANT 4Rose (original field number designation).

3. Systematics

Division: Coniferophyta

Genus: *Buriadia* Seward and Sahni

Buriadia heterophylla Seward and Sahni emend. Singh, Rothwell, Mapes et Chandra

Diagnosis (emended): woody vegetative shoots with irregular branching, bearing helically arranged polymorphic, simple, bifid and multifid leaves. Leaves closely arranged on ultimate and penultimate branches, more distantly spaced on antipenultimate branches and absent from largest stems. Stem surface on apparently decorticated stems rugose with thick cuticle and round to tangentially oriented oval branch scars and longitudinally disposed subtle wavy ridges. Corticated stems with persistent bifid leaves. Leaves decurrent and broadly attached, with one to eight dichotomizing veins, each vein forming an adaxial ridge and terminating in an obtuse to narrowly acute point. Simple leaves 4–16 mm long and 0.2–2.2 mm wide, lanceolate to ovate-lanceolate to cordate; bifid leaves 4–13 mm long and 0.5–4.0 mm wide, obovate to lanceolate with short teeth or more deeply dissected with spreading tips; multifid leaves 5–25 mm long and 2.0–6.1 mm wide, deltoid-cuneate with serrate distal margin or more deeply dissected with multiple tips. Lateral leaf margins with unequally distributed trichomes that are more densely arranged near leaf bases. Leaves epistomatic; relatively smooth abaxial surface consisting of longitudinally elongated cells with smooth margins and transverse-oblique end walls. Adaxial surface papillate with irregularly oriented stomata in wide bands; smooth rectangular cells occur between bands and near lateral margins. Haplocheilic, monocyclic or incompletely monocyclic stomatal complexes round to oval and axially elongate with four to seven subsidiary cells; overarching papillae more-or-less developed on subsidiary cells. Dense wood of narrow tracheids with mostly uniseriate, circular-to-oval bordered pits with oval apertures on radial walls; uniseriate rays one to three cells high. Shoots with helically arranged leaves bearing randomly interspersed ovules. Ovules with 180° rotational symmetry up to 4.5 mm long and 3.5 mm wide with prominent bifid apex, longitudinal striations, and conspicuous basal disk. Ovule orientation orthotropous, attached to leafy shoot by simple slender stalk.

Buriadia heterophylla Seward and Sahni emend. Serbet et al. (Plates I–IV)

Diagnosis (emended): compressions of shoots of two kinds bearing helically arranged simple to multifid leaves; shoots without ovules

with densely packed acute-to-round-tipped bifid leaves occasionally appearing in whorls. Leaves with abaxial elongate epidermal cells and adaxial papillae. Leaf margin with small inconspicuous trichomes. Ovule bearing shoots with simple, bifid, and multifid leaves. Simple rounded leaves subtending orthotropous ovules with 180° rotational symmetry. Ovule with prominent apical integumentary extensions, longitudinally oriented striations, and a prominent basal disk. Ovule attached to an axis by a short stalk.

Locality: Mount Gran, north side of Mackay Glacier (76° 58' S, 161° E), Prince Albert Mountains, Victoria Land, Antarctica

Stratigraphy: Mount Bastion Formation

Age: Early Permian

3.1. Description

3.1.1. Leaves

The leaves of the Antarctic specimens are highly variable and demonstrate numerous morphologies. Almost all leaves display at least some degree of bifurcation at the distal end. We have divided the leaves into two groups: those that are simple and organized as a single laminar unit (Plate I, 1, 2, 7, 8), and those with multiple bifurcations demonstrating a complex laminar unit (Plate I, 3–6). The simplest leaves have a single bifid acute tip with a deep incision (Plate I, 1, 2), while others are somewhat rounded with a less pronounced incision (Plate I, 8; Plate III, 5, 6) and in at least two specimens the simple multifid leaves have virtually no apical incisions (Plate I, 7). This morphology is rare compared to the abundance of other kinds of leaves and these are also some of the only specimens that clearly show some pattern of venation (Plate I, 7, arrows). The complex laminar unit leaves are dichotomous (Plate I, 3, 4) or trichotomous (Plate I, 5, 6). These leaves are continuous towards the base and separated at approximately half their length. The tips of these complex laminar units can be bifid (Plate I, 3, 4, 5) or trifid (Plate I, 6). A single specimen shows a close association between simple cordate leaves and narrow elongate multifid leaves (Plate II, 7).

Details of the leaf surfaces were difficult to resolve, no doubt the result of taphonomic modification. In one specimen there was a complete absence of any kind of surface ornamentation; however, other leaves contained marginal trichomes (Plate I, 9). Based on earlier studies of *Buriadia heterophylla* cuticles (Pant and Nautiyal, 1967) and the distribution of various types of cells on the adaxial and abaxial surfaces, we have developed a composite description of the leaf surfaces from these Antarctic specimens. The abaxial surface is made up of relatively uniform elongate cells that are oriented parallel to the long axis of the leaf (Plate I, 10). Both the scanned material and specimens examined in reflected light showed no evidence of stomatal complexes. There are papillate structures on one specimen (Plate I, 11). We suspect that the absence of stomata on the specimens is the result of preservation; however, the complexes may also occur in rows like those reported for the Indian material (Pant and Nautiyal, 1967) and one of the scanned samples from Antarctica was from a different portion of a leaf.

3.1.2. Shoots

The collection includes stems with attached leaves referred to as shoots. These shoots are of various sizes with the longest being approximately 7 cm with densely packed leaves (Plate II, 4). As a result of this density, it is often difficult to obtain an accurate measurement of the width of larger stems. Smaller shoots that contain fewer leaves suggest stem diameters of about 2.5 mm. Based on the size of the smaller shoots we interpret that the larger stems perhaps range from 4 to 5 mm in diameter. Some shoots are composed entirely of elongate bifid leaves (Plate II, 1, 2, 4), but the density of leaves on many shoots may obscure some of the smaller multifid leaves, thus giving a biased view of overall shoot morphology. One of the specimens (Plate II, 3) has densely packed leaves and the tips of the leaves have shallow incisions, giving them the appearance of being rounded. Leaves appear to be helically arranged (Plate II, 4), but the absence of any anatomical detail and the compressed nature of the specimens make it difficult to determine the precise phyllotactic pattern.

The divergence angle of leaves appears to be variable, ranging from 45° to almost 90°. In some specimens leaf orientation gives the impression that the leaves were arranged in a whorl (Plate II, 6). Not all of the shoots, however, have a single stem with helically arranged leaves. Some have more than one leafy shoot or some shoots have attached ovules with subtending simple round-tipped leaves intermixed among the bifid leaves. This latter organization indicates a dual function for these shoots (see below).

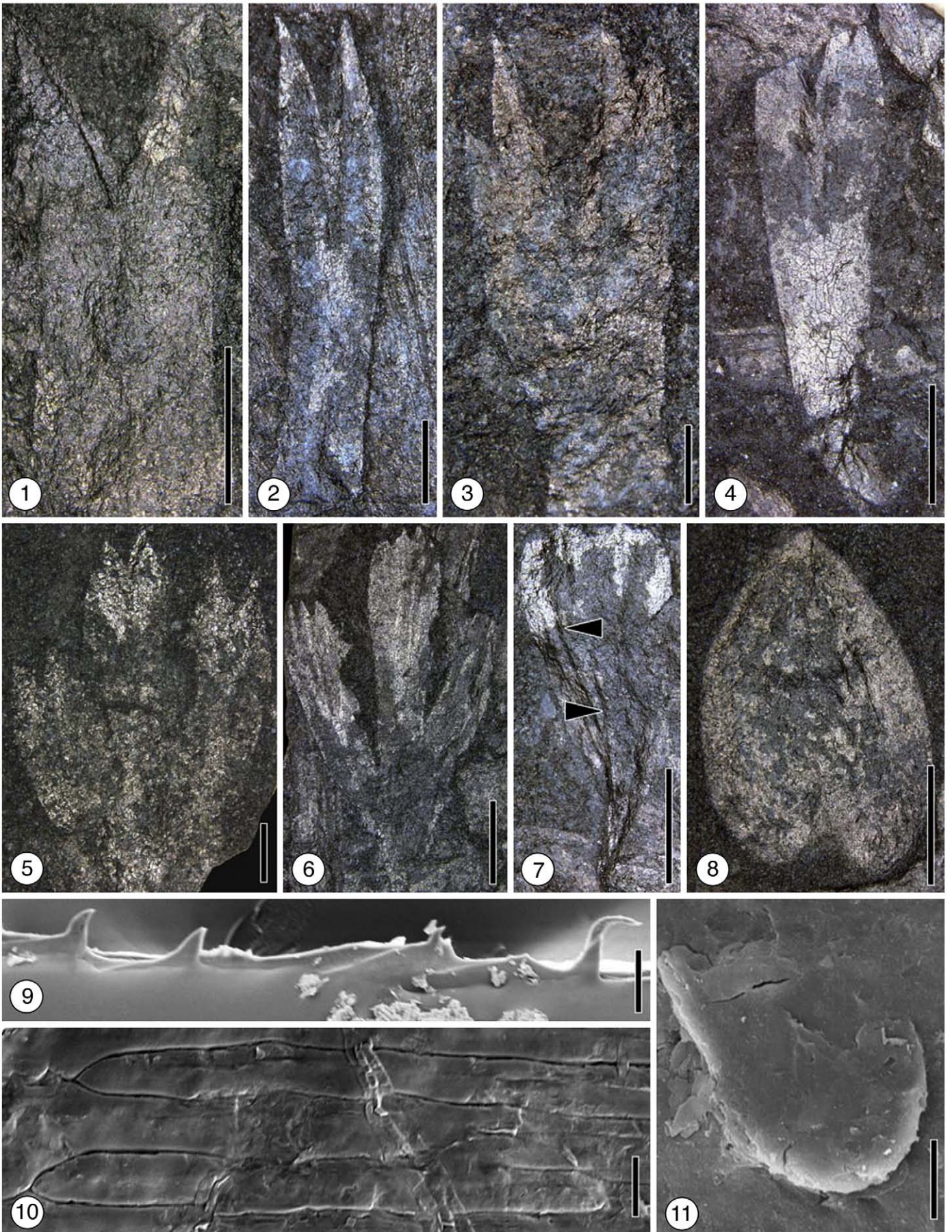
3.1.3. Shoots with ovules

The most informative specimens are those in which ovule orientation is obvious and attachment to the stem is unequivocal. Shoots with ovules contain multiple leaf types, including long bifid leaves (Plate IV, 1, upper left portion of shoot), short bifid leaves (Plate IV, 1, below ovule), and simple rounded bifid leaves (Plate III, 5, 6). Leaf arrangement on these shoots is interpreted as helical, but like the shoots lacking ovules, it is difficult to determine the precise phyllotactic spiral because of the density of leaves.

Attached ovules are orthotropous and possess a bifid tip (Plate III, 1, 2, 6; Plate IV, 2), well-defined border around the margin (Plate III, 2), prominent basal disk (Plate III, 1, 4), and slender stalk (Plate IV, 2, 4, 5, at arrows). These ovules range from 3.0 to 4.0 mm long and 1.5 to 2.0 mm wide, and share all of the features found among the isolated ovules in the sample (see below). The angle of divergence (~30°) between the base of the ovule and stem is relatively consistent and can provide an additional piece of evidence when determining whether ovules were actually attached to a shoot or simply closely associated and addressed during preservation. Plate IV, 1–3 shows the part and counterpart of a specimen with two closely associated ovules, with one of the ovules being attached to the stem by a small stalk. This specimen is also depicted as a line drawing to more clearly demonstrate the position and attachment of the ovule (Fig. 1A–C). It is also interesting to find that several Mt. Gran specimens show a close association between simple leaves, multifid leaves, and ovules (Plate II, 7; Plate III, 5, 6).

Plate I. Vegetative remains of *Buriadia heterophylla* from Antarctica showing leaf morphology and variability.

1. Bifid leaf with a deep apical incision and broad base. PM 637 (ANT 4Rose #51). Scale = 1 mm.
2. Long narrow bifid leaf. PM 5439 (ANT 4Rose #26). Scale = 2 mm.
3. A broad based bifid leaf with two primary segments, each with a bifurcate tip. PM 5454. Scale = 1 mm.
4. A narrow bifid leaf with two primary segments, each with a shallow apical incision. PM 5458. Scale = 2 mm.
5. A trifid leaf with three primary segments, each with a bifurcate apex. PM 5461 (ANT 4Rose #128). Scale = 1 mm.
6. A trifid leaf with three primary segments, each with multifid apices. PM 5440 (ANT 4Rose #44). Scale = 2 mm.
7. Multifid leaf with shallow incisions. Arrows indicate position of vascular bundles. PM 5441 (ANT 4Rose #75). Scale = 3 mm.
8. Simple cordate leaf. PM 5442 (ANT 4Rose #113). Scale = 3 mm.
9. Margin of leaf showing several small trichomes. PM 5443. Scale = 20 µm.
10. Leaf surface showing elongate epidermal cells with tapering end walls. PM 5443. Scale = 20 µm.
11. Detail of papilla on surface of a leaf. PM 5443. Scale = 2 µm.



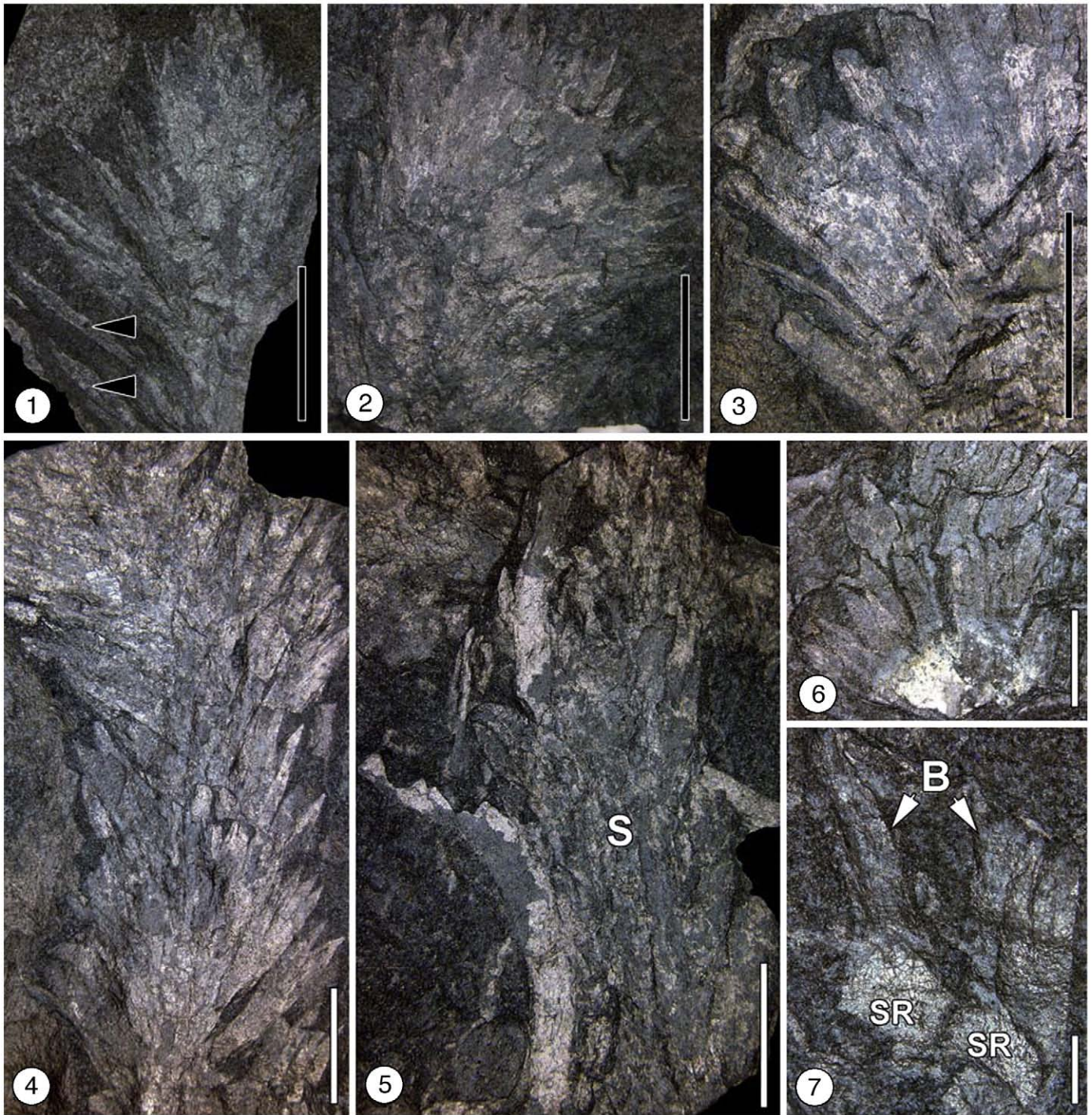


Plate II. Vegetative remains of *Buriadia heterophylla*.

1. Apical portion of a shoot with narrow bifid leaves. Lower leaves (arrows) could be interpreted as simple lanceolate leaves if folded longitudinally and partially buried in sediment. PM 5444 (ANT 4Rose #20). Scale = 5 mm.
2. Portion of a shoot showing numerous bifid leaves. PM 5445 (ANT 4Rose #17). Scale = 5 mm.
3. Portion of a shoot consisting of bifid leaves with shallow incisions suggesting they had rounded tips. PM 5446 (ANT 4Rose #103). Scale = 1 cm.
4. Shoot system with numerous helically arranged bifid leaves. PM 5447 (ANT 4Rose #27). Scale = 5 mm.
5. Stem (S) with persistent bifid leaves. PM 5448 (ANT 4Rose #39). Scale = 5 mm.
6. Cluster of obliquely compressed bifid leaves that demonstrate a "whorled" appearance. PM 5449 (ANT 4Rose #67). Scale = 5 mm.
7. Bifid (B) and simple, rounded leaves (SR). PM 5450 (ANT 4Rose #101). Scale = 1 mm.

3.1.4. Ovules

Over 200 isolated ovules were examined and the morphological features are relatively consistent with those of the attached specimens. Ovule size ranges from 3.0 to 4.0 mm long and 1.5 to 2.5 mm

wide. Typically ovules measure 3.0 mm long and 2.0 mm wide and are characterized by 180° rotational symmetry (Plate III, 1, 2) (Rothwell, 1986). The prominent bifid apex is up to 2 mm long (Plate III, 2) and contains no conspicuous trichomes. The ovule body is obovate and the

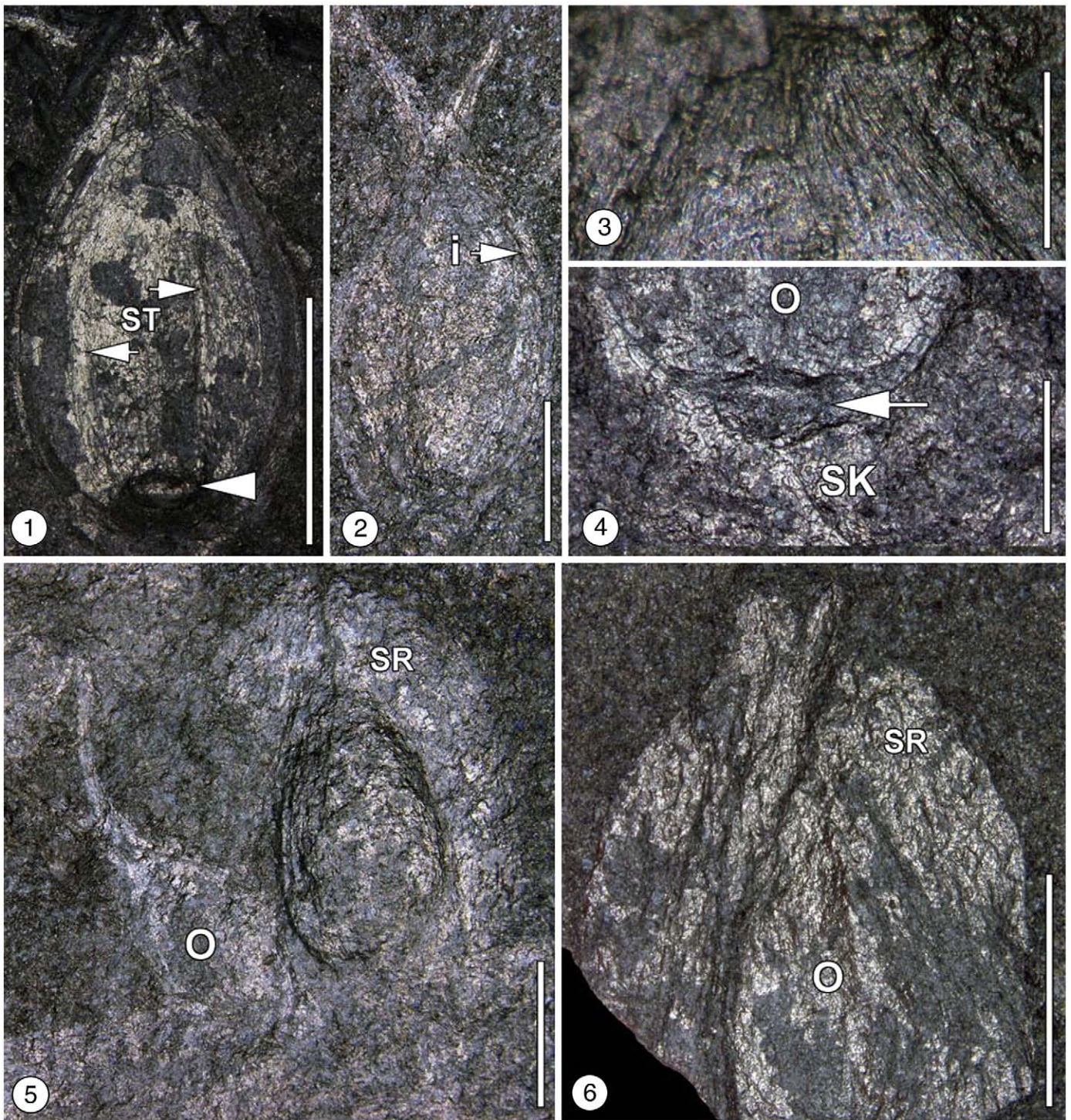


Plate III. Seeds of *Buriadia heterophylla*.

1. Compressed ovule showing longitudinally oriented striations (ST, arrows) and prominent basal disk (arrowhead). PM 5451 (ANT 4Rose #10). Scale = 2 mm.
2. Ovule with bifid apex. Note the continuity of the integument (i) with the bifid tip. PM 5452 (ANT 4Rose #61). Scale = 1 mm.
3. Apical portion of ovule showing elongate cellular pattern that may represent the impression of endotestal or nucellar cells. PM 5453 (ANT 4Rose #92). Scale = 200 μ m.
4. Detail of basal portion of ovule (O) showing small stalk (SK) attached to the shoot axis (base of stalk). Arrow indicates the position of the basal disk illustrated in 1. PM 5457 (ANT 4Rose #80). Scale = 1 mm.
5. Bifid ovule (O) with associated simple cordate bifid leaf (SR) similar to the ones in [Plate II](#), 7. The central depression in the leaf is consistent with the length and width of isolated ovules suggesting a possible relationship. PM 5459 (ANT 4Rose #86). Scale = 2 mm.
6. Specimen consisting of an ovule (O) overlain by a simple cordate bifid leaf (SR). PM 5460. Scale = 2 mm.

integument consists of at least two distinct layers. The outer zone is interpreted as the sclerotesta (175 µm thick) and is constructed of elongate cells that are oriented parallel to the long axis of the seed (Plate III, 1). These cells extend apically to form the bifid apex and also make up the basal region of the ovule where it attaches to the stem. Internal to the sclerotesta at the apex of ovules is a layer of elongate cells that may represent the impression of endotestal or nucellar cells (Plate III, 3). Several of the ovules possess longitudinal bands (Plate III, 1) that may indicate regions of the integument that were vascularized. Due to the preservation mode of these fossils, however, secondary wall thickenings or other histological features indicating the presence of vascular tissue were difficult to identify. A prominent feature of some ovules is a basal disk (Plate III, 1, 4, arrow) that may represent the region of attachment to the stalk (see discussion for stalk affinities), or some remnant of the ovule base where the vascularization was prominent.

Larger stems and wood associated with *Buriadia*. There are several large branches among the Mt. Gran samples, but most have been metamorphosed into thin silvery sheets and thus lack important morphological and anatomical details. One of these is about 1 cm wide and 2.5 cm long (Plate II, 5). Along one surface are long, narrow, bifid leaves similar to those found on the shoots. Wood fragments are also present in the matrix and show tracheid pitting and uniseriate rays up to 5 cells high. There are not enough diagnostic features preserved that can be used to relate the wood with confidence to any particular morphotaxon other than the common Permian taxon “*Dadoxylon/Araucarioxylon*” (see Philippe, 1993 for nomenclatural information on these wood morphotaxa).

4. Discussion

4.1. Comparison with other late Paleozoic coniferophytes

Despite the higher frequency of leaf variability in the Antarctic fossils, the general features of the leafy shoots, ovules, and associated wood fragments are virtually identical to *Buriadia heterophylla* initially described from India (Pant and Nautiyal, 1967; Singh et al., 2003). The only Permian coniferophytic taxon that bears any resemblance to *Buriadia* is *Paraburiadia menneri* (Zimina, 1983) from the Upper Permian of Primorye (Angaraland). The size, bifid apex, and orthotropous orientation of the ovules are comparable to *Buriadia*, but the attachment of the ovules is uncertain in the case of *Paraburiadia*. Two diagrams in the paper indicate that the ovules were attached either at the apex of a leaf or within the axil of a leaf. Both of these interpretations are difficult to assess using figured specimens and additional information on this poorly defined taxon is needed before accurate comparisons can be made.

Several coniferophyte taxa from Argentina have comparable morphology to *Buriadia*, although the organization of the fertile regions appears to be more complex when compared to that of *Buriadia*. For example, in the cones of *Ferugliocladus*, *Ugartecladus*, and *Genoites*, ovules are associated with basal bracts arranged on a central axis (Cúneo, 1985; Archangelsky and Cúneo, 1987). The

ovules of *Genoites patagonica* are subtended by a bifid leaf and the ovules of both *Ugartecladus* and *Genoites* lack a bifid tip. Unlike these Argentinean coniferophytes, the fertile units of *Buriadia heterophylla* show no specific organization and no more than two or possibly three fertile units have been observed attached to a leafy shoot. *Buriadia* has also been described from the Permian of Brazil, i.e., *B. mendesii* and *B. heterophylla*, but none of these descriptions provide details on the position or organization of the ovules (Bernardes-de-Oliveira and Yoshida, 1981; Guerra-Sommer and Bortoluzzi, 1982).

Prior to the present study *Buriadia* was known only from India and South America at paleolatitudes of 45°–60° S. The discovery of *Buriadia heterophylla* in the Early Permian of Antarctica not only increases our understanding of the geographic distribution of this plant, but also indicates the existence of this organism at a higher paleolatitude (~70°–75° S) than previously documented. Although the mode of preservation and the sample size of the Antarctic material continues to limit our understanding of many aspects of *B. heterophylla*, there are several important new features that are now recognized and these are critical to interpreting this interesting Permian coniferophyte.

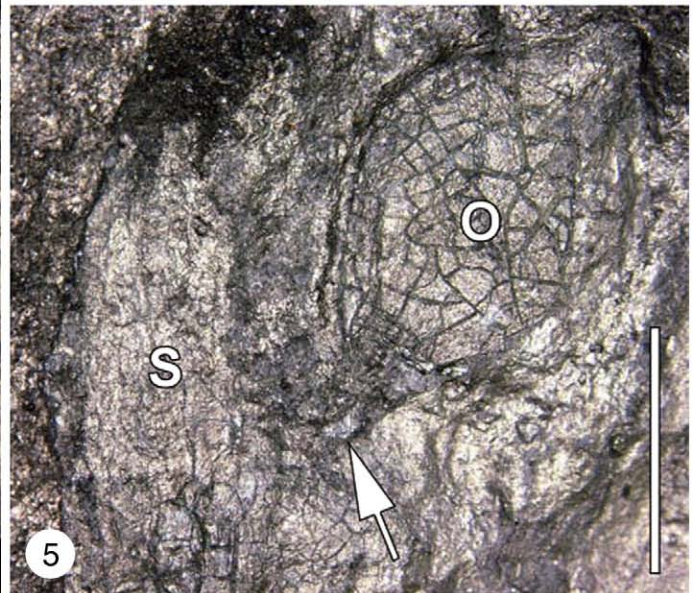
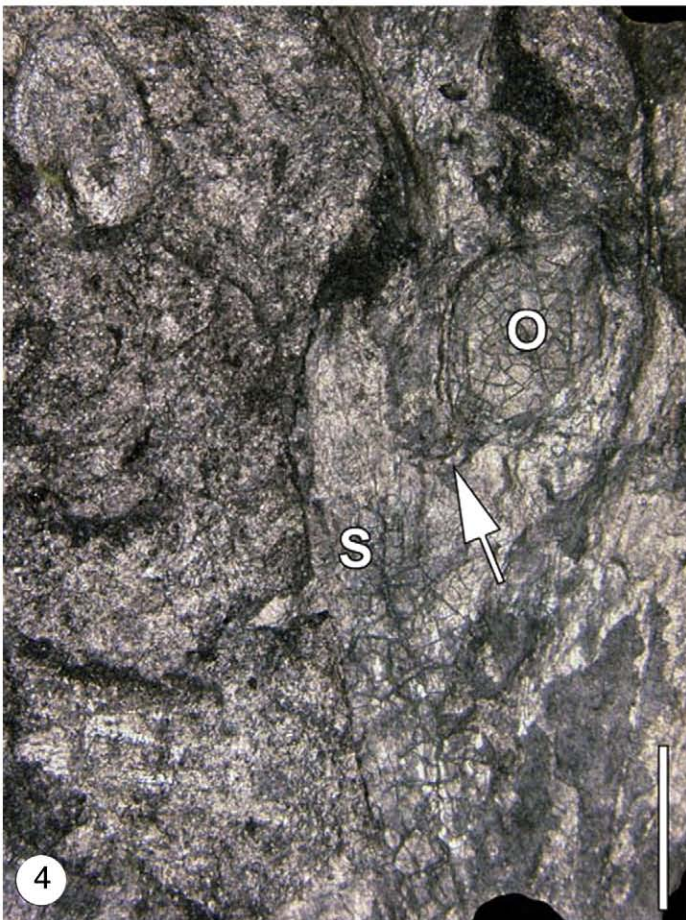
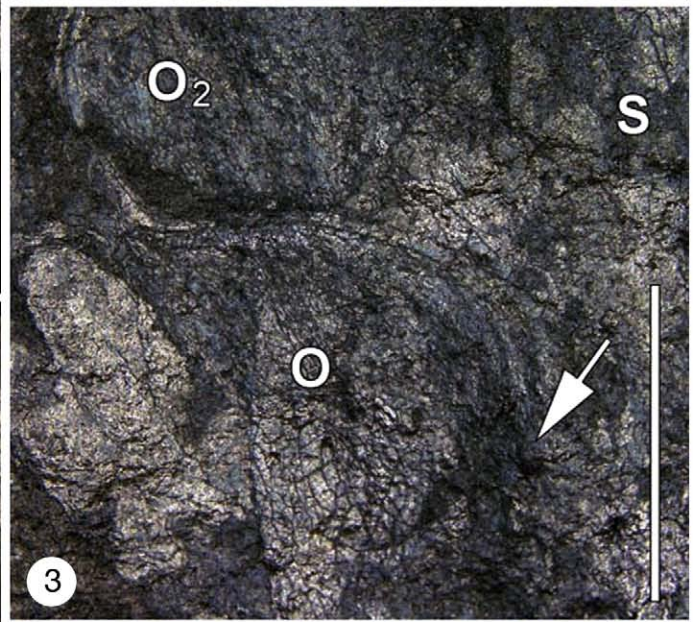
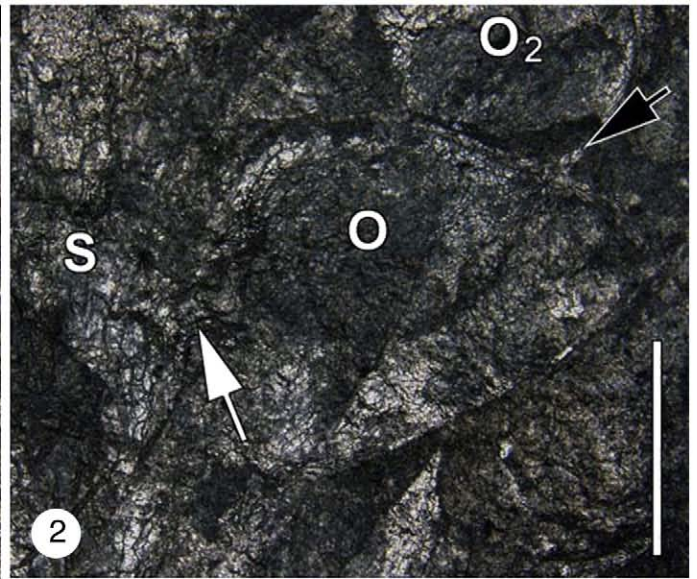
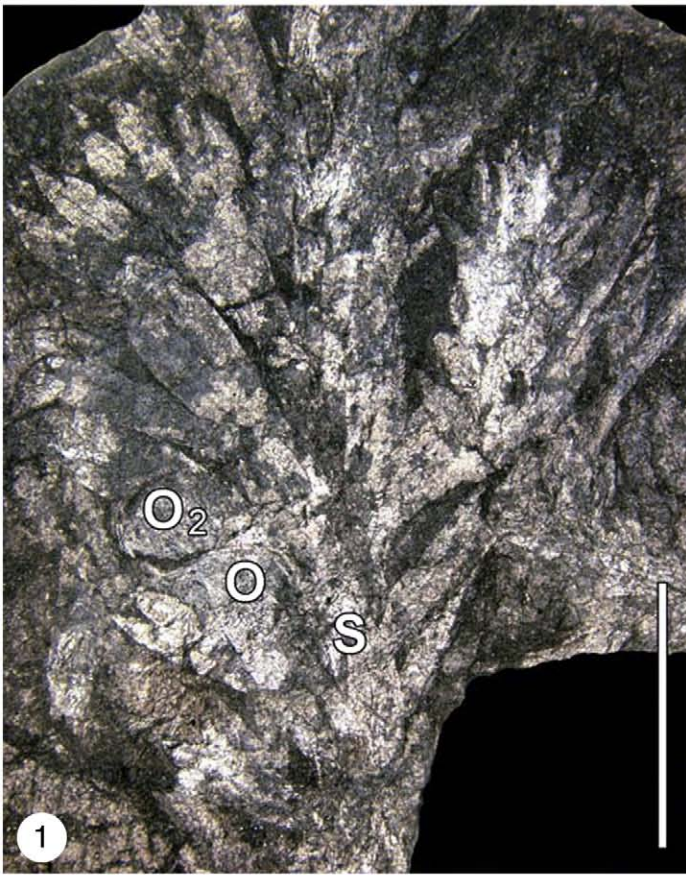
4.2. Vegetative remains

Leaf morphology in the new species shows a greater morphological diversity than previously reported for other species of *Buriadia*. Leaves of the type species from India are already known to be variable, ranging from simple to multifid morphologies. In the Antarctic specimens, however, the multifid leaves show even higher levels of plasticity including incisions of various degrees on the same leaf. This morphological pattern is very unusual when compared to most coniferophytes which typically exhibit one or two basic leaf types. Although the Antarctic *Buriadia* has a greater diversity of leaf types than previously described, this does not warrant the establishment of a new species; the causes of this variability are discussed below.

The consistency of leaf variability in *Buriadia* throughout its geographic and stratigraphic range and within different paleoclimatic regimes may suggest that these leaf morphologies can be attributed to variation within a single species. The significance of this leaf plasticity in the biology of the plant, however, remains unexplained. One possible explanation is that these differences merely reflect stages of leaf development along an axis. A number of seed ferns, e.g., the Jurassic seed fern *Archangelskya* show considerable morphological variation from the proximal to the distal portion of the frond (Rees and Cleal, 1993). Another possible explanation for the range of leaf shape in *Buriadia* may be related to whether the leaves were produced on sterile or fertile shoots. The differences in leaf morphology may also reflect some type of environmental response. Barbacka and van Konijnenburg-van Cittert (1998) suggested that differences in leaf morphology in the pteridosperm foliage taxa *Komlopteris* and *Ctenozamites* represent sun versus shade leaves. Their hypothesis is supported by differences in the cuticular anatomy of the different leaf types. Pant and Nautiyal (1967) also used cuticular anatomy as a basis

Plate IV. Attached seeds of *Buriadia heterophylla*.

1. Low magnification image of holotype indicating position of orthotropous ovule (O) attached by a slender stalk to a leafy shoot (S). A second ovule (O₂) is indicated above the first ovule. PM 5455 (ANT 4Rose #64, part). Scale = 5 mm.
2. Counterpart of specimen from 1 showing an orthotropous ovule (O) with a bifid apex (black arrow) and the attachment by a slender stalk (white arrow) to a leafy shoot (S). The second ovule (O₂) shown in 1 is also indicated. PM 5455 (ANT 4Rose #64). Scale = 2 mm.
3. High magnification of specimen from 1 indicating the position of the orthotropous bifid ovule (O) in relation to the leafy shoot (S). Area of attachment is indicated by arrow. The second ovule (O₂) shown in 1 is also indicated. PM 5455 (ANT 4Rose #64). Scale = 2 mm.
4. Low magnification image of orthotropous ovule (O) with micropylar region at upper right. Note the conspicuous, slightly curved stalk (arrow) attached to a stem (S). PM 5456 (ANT 4Rose #98). Scale = 2 mm.
5. Higher magnification of specimen from 4 showing an orthotropous ovule (O) attached to a stem (S) by a slightly curved stalk (arrow). PM 5456 (ANT 4Rose #98). Scale = 2 mm.



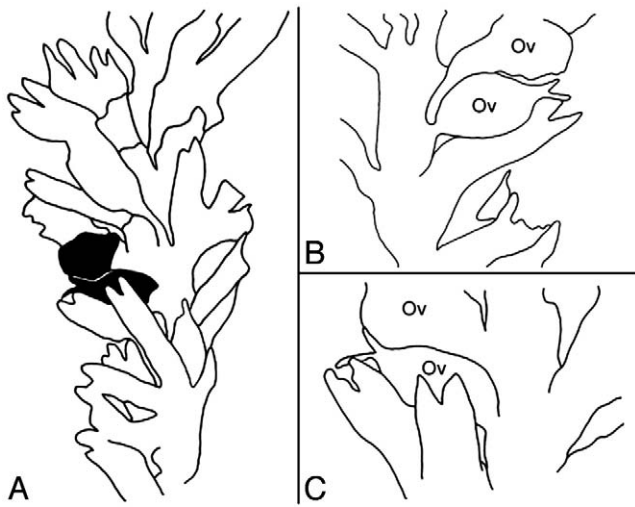


Fig. 1. A–C. Camera lucida drawings of *Buriadia heterophylla*. (A) Leafy shoot with position of two ovules (shaded areas). (B) Counterpart of A showing two ovules (Ov). (C) Detail of shaded ovules (Ov) in A.

for suggesting that differences in leaves on *Buriadia heterophylla* were attributed to some type of arrested growth caused by seasonal variation.

It is tempting to suggest that the leaves in *Buriadia* represent some transitional stage in the evolution of late Paleozoic coniferophytes. While this idea may have some merit, we are unaware of any living or fossil examples of coniferophytes in which leaf variability is as extensive as that reported in *Buriadia*. Until larger specimens of *Buriadia* are discovered, the biological significance of the leaf variability pattern in this plant will continue to remain conjectural.

Isolated wood fragments occur interspersed among the *Buriadia*, *Gangamopteris*, and *Glossopteris* fossils from Mt. Gran, and these specimens show features (e.g., circular bordered pits, various types of rays) that are characteristic of late Paleozoic wood morphotaxa. Pycnoxylic wood fragments associated with *Buriadia heterophylla* from India (Pant and Nautiyal, 1967) share several general features with the wood found in Antarctica. Both wood types have simple uniseriate with occasional biseriate pitting on the radial walls of the tracheids. Rays are generally uniseriate and up to three cells high; some of the fragments of wood from the Mt. Gran site have rays up to five cells high.

4.3. Ovule position

The arrangement and organization of the ovule in *Buriadia* has been discussed for more than 40 years (Singh et al., 2003 and references therein) and these discussions have obviously impacted phylogenetic assessments relating to conifer evolution. The most significant feature of the Antarctic *Buriadia* specimens is the

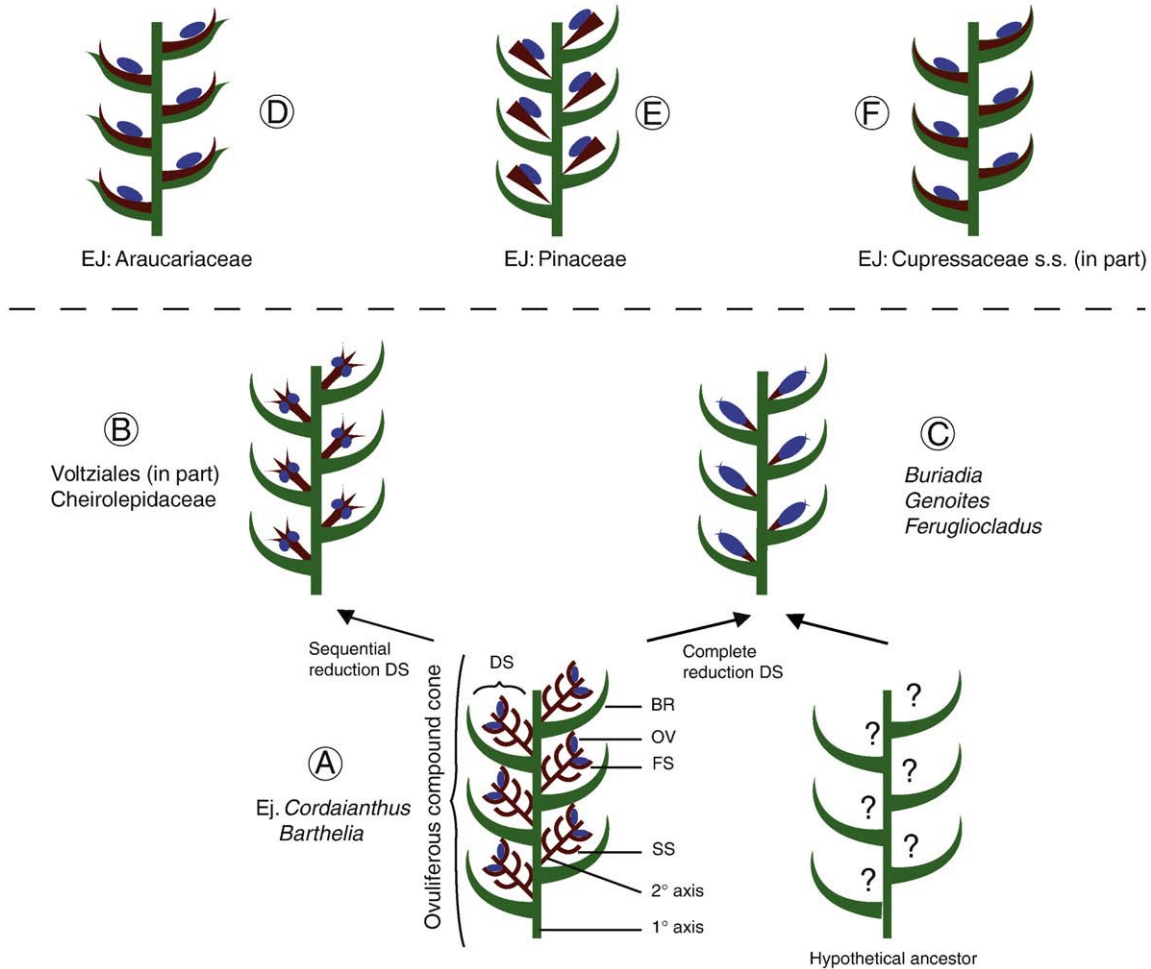


Fig. 2. Homology hypotheses for selected Paleozoic, Mesozoic and living conifer seed cones. Note the two principal hypotheses for the origin of Late Paleozoic simple cones (C) are represented. Structures interpreted as derived from the primary axis and bracts of the primitive seed cone are represented in green, structures classically related with the ancestral dwarf shoot are represented in purple and ovules are represented in blue. Br: bract. Ov: ovule. FS: fertile Scale. SS: sterile scale. DS: dwarf shoot.

demonstration of the orthotropous position of the ovules and their attachment to a small stalk that arises from the stem of a leafy shoot. This orientation differs from the original interpretation of Pant and Nautiyal (1967), who believed that the ovules were anatropous, a conclusion negated by Singh et al. (2003) after re-examination of the type material.

The Antarctic material indicates that the stalk arises slightly above the axil of a leaf and not directly within it (Fig. 1B). It is difficult to ascertain if this position is the result of a preservational anomaly or a reflection of the growth architecture of *Buriadia*. Without valuable anatomical evidence demonstrating the symmetry of the vascular tissue within the stalk, two interpretations of this basal structure are presented. If the stalk represents a modified leaf, then this would suggest that the ovule was attached to a sporophyll. Evidence to support this interpretation includes: (1) the extension of the integument from the basal attachment point of the ovule to the apical bifid tips (Florin, 1950), (2) the absence of vegetative scales on the stalk, and (3) bilateral symmetry of the vascular strand within the stalk. If the stalk represents a reduced branching system, however, then the ovule would be considered attached to a highly reduced shoot. Evidence to support this interpretation includes: (1) helically arranged scale-like structures on the stalk, (2) typical radial symmetry of the stalk, (3) the presence of a seed-scale, (4) origin of the stalk in the axil of a leaf, and (5) radial symmetry of the vascular strand within the stalk. Either combination of features from each of the above hypotheses ultimately constitutes a fertile unit and represents the early evolution of a cone-scale complex. Each of the above scenarios still supports the possibility of a hypothetical ancestor giving rise to a Gondwanan clade of coniferophytes (Fig. 2). In the final analysis the relatively poor preservation of the Antarctic fossils does not provide a clear cut and unambiguous solution to the question of the affinities of the structure on which bears the seeds. The fossils do, however, provide additional information about this genus which has widely been discussed with regard to coniferophyte evolution.

In general morphology, the *Buriadia* ovules from Mt. Gran are nearly identical to those described in association with the Indian specimens of *Buriadia heterophylla*. One pronounced difference is the presence of a basal disk in the Antarctic ovules. While this structure is conspicuous in our specimens, we are uncertain whether this character was not reported, not preserved, or simply not present in other ovules that have been described.

4.4. Taxonomic considerations

The suite of characters used to define *Buriadia* has been variably used in establishing a taxonomic hierarchy for the group. For example, Meyen (1968) suggested that *Buriadia* should be classified in its own family or possibly order, while Pant et al. (1995) suggested that *Buriadia* should be assigned to the Burialiales. Even though ovule position and orientation are now more accurately defined, the systematic position of this plant remains problematic. In this context we are concerned that sometimes incompletely understood fossils can be included in higher-level classifications and these taxa ultimately obscure the significance of a particular group by overstating its importance in relationship to other forms.

4.5. Evolutionary implications

The orthotropous orientation and attachment of the Antarctic *Buriadia* ovules to a simple stalk represents an important discovery in the continuing discussion of conifer evolution. It greatly strengthens the ideas advanced by Archangelsky and Cúneo (1987), who suggested two evolutionary scenarios for this character combination (ovule position and orientation) in their analysis of the Gondwanan

family Ferugliocladaeae. We propose that their evolutionary interpretation of the Ferugliocladaeae can also be extended to include *Buriadia* (Fig. 2C). One of the hypotheses advanced by Archangelsky and Cúneo (1987) is that the stalked, erect ovules in *Ferugliocladus* represent an extremely reduced dwarf shoot in which all of the scale leaves have been lost. This hypothesis is based on the assumption that conifers are monophyletic and related to the Cordaitales, a concept that follows the original evolutionary transformational series postulated by Florin (1949, 1957). The axillary position of the stalked ovule in *Ferugliocladus* has been used by Rothwell and Mapes (2001) as evidence to support Florin's hypothesis (Florin, 1954). If this concept of positional homology is accurate, then the ovulate structures of *Buriadia*, *Genoites* (Cúneo, 1985), and *Ferugliocladus* (Archangelsky and Cúneo, 1987) must be considered homologous with a compound cone structure (Fig. 2A–C). If this evolutionary scenario has validity, then the geologic timing of the reduction process needs to be fully examined. The classic reduction theory of the dwarf shoot is thought to have occurred during the late Paleozoic and early Mesozoic (Florin, 1951). Evidence supporting this transition includes several coniferophytic cones that demonstrate intermediate stages in the reduction of the dwarf shoot, e.g., in the Voltziaceae and Cheirolepidiaceae (Watson, 1988; Rothwell et al., 2005).

The second hypothesis of Archangelsky and Cúneo (1987) interprets the stalked ovules as axillary, not subtended by any scale-like structure, and with the tissue covering the nucellus as being integumentary in origin (Fig. 2C–F); in this scenario the stalked seeds would not be homologous with a dwarf shoot. Lending support to this interpretation is the fact that the bifid tip of the ovule in *Buriadia heterophylla* from Antarctica is integumentary in origin rather than representing a remnant of a scale or other component of a primitive dwarf-shoot system. One of the problems in accepting this second hypothesis, however, is the absence of any obvious ancestral group (Archangelsky and Cúneo, 1987) from which these Gondwana coniferophytes may have evolved (Fig. 2). Further compounding the problem of conifer origins in Gondwana, and one that is rarely considered, is the absence of any reliable evidence of cordaitalean seed-bearing organs from the Southern Hemisphere. We suggest that the co-occurrence of a number of late Paleozoic coniferophytes, e.g., *Voltzia* and *Aethophyllum*, that show complete reduction of what has been interpreted as a dwarf shoot, with others such as *Buriadia* that show stalked ovules with no evidence of scales, may indicate that there were at least two distinct lineages present at this time.

Meyen (1997) also discussed this issue and suggested that the late Paleozoic conifers could be divided in two principal groups: ones that bore he termed compound polysperms (= compound cones) and another group with solitary seeds produced on non-specialized shoots identical to vegetative shoots. This latter group, however, could also be extended to conifers with specialized ovulate organs that still show a simple (or non-compound) organization (e.g., *Ferugliocladus*). The discovery of attached *Buriadia* ovules from Antarctica adds additional support the hypothesis of Archangelsky and Cúneo (1987) that the evolution of the conifer seed cone may be more complex than is generally interpreted using the single model of Florin (1951). Moreover, when one examines the diversity of coniferophytes present as early as the late Paleozoic, it is equally appropriate to challenge the assumption that all modern coniferophytes can be traced to a single ancestor (Fig. 2A).

4.6. Future directions

What then are the next steps in more accurately evaluating early conifer evolution? One continuing question that remains unresolved relates to the evolutionary relationships between fossil coniferophytes and modern families (Fig. 2). Most ideas on this subject

dismiss *Buriadia*-like fossils, since the organization of the seed-producing organs is interpreted as not fitting the compound cone-homologue model (e.g., Miller, 1999). The dwarf-shoot hypothesis of the evolution of the modern conifer cone-scale complex (Fig. 2A–B, D–F) has great merit. We also believe, however, that plants like *Buriadia* provide strong evidence for more than a single model for conifer seed-cone evolution as reflected in the fossil record (see also Escapa et al., 2008). One method that may help to resolve this issue is increased attention to Gondwanan conifers and especially to obtaining additional phylogenetic information based on whole-plant reconstructions. This process will require two components: (1) discovery of new localities from different stratigraphic levels and geographic regions, and (2) detailed analyses that focus on defining complete plants at a single locality. For example, despite the fact that *Buriadia* is known from three continents, there is absolutely nothing known about the pollen-producing organs of this group, nor any detailed information about other plants in the ecosystem, or the paleoecological setting in which these plants grew. It would also be interesting to construct the phylogenetic hierarchy of pre-cordaitalean ancestors to discover how their morphologies have changed over time and to establish unequivocal monophyletic relationships of this ancestral group. Addressing these issues will have a major impact on increasing our understanding during these critical times in conifer-coniferophyte evolution.

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