Ovule-bearing reproductive organs of the glossopterid seed ferns from the Late Permian of the Beardmore Glacier region, Antarctica

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Abstract   The Glossopteridales are an extinct group of seed ferns that dominated Gondwana during the Permian. The strap-shaped leaves of *Glossopteris* are widespread and provided early evidence of continental drift, but reproductive organs of this group have remained enigmatic since they were first described in the 1950s. Based on compression-impression fossils, there are at least two basic types of ovulate (seed-bearing) organs. In one form, numerous ovules are borne on the surface of a leaf-like megasporophyll (e.g., *Plumsteadia, Dictyopteridium*), while the second type consists of stalked, apparently uniovulate cupules borne on a branching system (e.g., *Lidgettonia*). More than 30 genera of seed-bearing organs have been described, many based on compressions or, more commonly, impression fossils, in which it is often impossible to discern the three-dimensional morphology or attachment of these structures. Both morphological types have now been found in permineralized peat from Skaar Ridge, central Transantarctic Mountains (CTM), and provide some of the first anatomical detail of the diversity of reproductive organs of *Glossopteris*. The multiovulate organ is small (6 mm wide), with ovules borne on the upper (adaxial) surface; the uniovulate structure consists of four stalked cupules, each containing a single ovule about 2 mm long. These two forms provide important information about the diversity of the glossopterids and their status as a natural group of seed plants.

Introduction

The glossopterid seed ferns (pteridosperms) have occupied both a prominent and perplexing position in the history of paleobotany, prominent because the spathulate *Glossopteris* leaves with complex venation represented some of the earliest evidence for the existence of the supercontinent Gondwana and subsequent movement of continental plates, and perplexing because the phylogenetic position of the group has continued to remain equivocal. While *Glossopteris* has been used as an index fossil for the Permian, it has also been described from the Early Triassic of India (Pant and Pant, 1987; Shah, 2000) and from the Fremouw Formation in Antarctica (McManus et al., 2002), which has previously been considered to be Triassic (Collinson et al., 2006). McLoughlin (1993) noted that while some glossopterid reproductive organs may be used in biostratigraphy, leaves and other vegetative organs are not useful for correlation due to problems in delimiting species, especially among impression floras. Permineralized leaves have been described from Antarctica (Pigg, 1990) and Australia (Gould and Delevoryas, 1977; Pigg and McLoughlin, 1997), along with evidence of their attachment to the parent plant (Pigg and Taylor, 1993). The distinctive roots of the *Glossopteris* plant, *Vertebraria* (e.g., Neish et al., 1993), can be identified in both compression-impression and permineralized specimens. *Glossopteris* remains have been found in a number of types of depositional environments in Antarctica (Cúneo et al., 1993).

The ovule-bearing structures of the glossopterids continue to be poorly understood; many are known only from impression fossils, making interpretation of three-dimensional morphology difficult. Numerous taxa have been erected based on size, shape, number of ovules (often only ovule scars), and various other features (see, e.g., Surange and Chandra, 1975; Pant, 1977; Rigby, 1978; McLoughlin, 1990a, 1990b). Attachment of reproductive organs to the parent plant is based on impression specimens only and is controversial.

All glossopterid ovulate reproductive organs suggest a basic morphological organization in which a vegetative leaf subtends a structure that bears ovules or seeds. Historically, this seed-bearing unit has been termed a megasporophyll, cupule, or other, less specific morphological entities (e.g., fertiliger, capitulum, cladode); the latter terms are no longer in use. The reproductive structure is generally regarded as an axillary shoot that has become reduced and flattened evolutionarily (e.g., Doyle, 2006), much like the secondary shoot of the cordaites (Schopf, 1976). In some cases, this structure appears to be adnate to a typical *Glossopteris* leaf, although this is difficult to confirm based only on impressions. Gould and Delevoryas (1977) provided the first description of a structurally preserved, seed-bearing organ from the Bowen Basin, Australia. It showed definitively that the ovules were borne on a leaflike megasporophyll, thus confirming the assignment of these plants to the pteridosperms. Another permineralized megasporophyll (Figs. 1, 2) was described from the Permian of Antarctica (Taylor and Taylor, 1992); it provided additional evidence that the ovulate organ was a megasporophyll, and showed that the seeds were borne on the adaxial (upper) surface of the megasporophyll (Fig. 2), based on the orientation of the vascular bundles. The presence of bisaccate, striate pollen

grains in the pollen chambers (Fig. 3) confirmed the glossopterid affinities. Nishida et al. (2007) have recently confirmed that the ovules in the Bowen Basin specimens were borne on the anatomically adaxial surface of the megasporophyll. The exact relationship between the megasporophyll and the subtending leaf, however, has yet to be determined, and is an important piece of the puzzle that is needed to accurately homologize the ovule-bearing structures with other seed plants.

An examination of the more than 30 ovulate organ morphogenera that have been named to date suggests that there are two basic types, as previously suggested by Surange and Chandra (1975). The multiovulate type consists of a flattened, leaf-like megasporophyll, e.g., *Plumsteadia* (Rigby, 1962; McLoughlin, 1990a) and the cupulate type consists of a branching structure, e.g., *Denkania* (Surange and Chandra, 1973) or *Lidgettonia* (Thomas, 1958). Both structures are subtended by a vegetative leaf and presumed to represent ovulate organs, although ovules are often not preserved. The multiovulate types often show only scars where the ovules would be attached (e.g., McLoughlin, 1990b). In impression fossils with no cuticle preserved (e.g., Anderson and Anderson, 1985), it is often difficult to determine whether structures represent ovules or ovule scars. The preliminary description of an ovule-bearing structure in this paper represents the first to provide anatomical details of the cupulate type of reproductive organ.

Material and methods

The specimen (#13677) is from a silicified peat in the Upper Buckley Formation, Skaar Ridge, Beardmore Glacier region, CTM (84° 49' 15.8" S, 163° 20' 18.9" E, Buckley Island Quadrangle, Barrett and Elliot, 1973; Taylor et al., 1989) and is considered Late Permian, based on floral content and palynology (Farabee et al., 1991). Acetate peels were made of the surface after etching in hydrofluoric acid (Galtier and Phillips, 1999); peels were mounted on slides for light microscopy and digital photography. All materials are housed in the KU Natural History Museum, Division of Paleobotany (http://paleobotany.bio.ku.edu/PaleoCollections.htm).

Results

The new cupulate organ consists of four small, uni-ovulate cupules that appear to be arranged in a C-shaped pattern. Each cupule is approximately 3 mm long and 1 mm in diameter (Figs. 4, 5) and contains a single ovule; the cupule extends distally beyond the level of the micropyle. Ovules are sessile, orthotropous, and approximately 2 mm long. The multilayered integument has short wings at the apex, and bilaterally symmetrical ovules (1.2–2.0 mm wide in the primary plane). These features distinguish this ovule from the similar-sized, obovoid ovules of *Chaonostoma* (Klavins et al., 2001) previously described from this same locality. The cupules are attached to the distal end of an axial system; each axis undergoes two dichotomies resulting in a total of four uniovulate cupules

in each unit (Fig. 5). One dichotomy, resulting in two terminal cupules, is shown in Figure 5. The most proximal end of the cupule axis has a C-shaped vascular strand. This cupulate structure, like the megasporophyll previously described from Skaar Ridge, is not preserved attached to the parent plant or in relationship to a vegetative leaf, and thus the homologies of the fertile organ continue to remain imprecise.
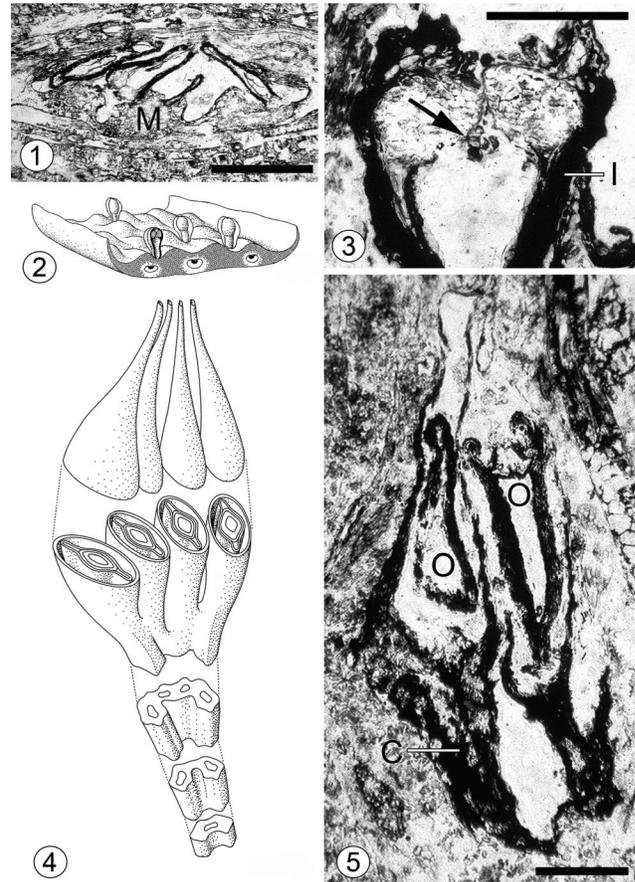

Figure 1. Cross section of multiovulate megasporophyll (M) with several ovules attached to adaxial surface. One ovule (just left of M) has broken off and is reversed, with its micropyle pointing back towards the megasporophyll. Two ovules (above M and, right) are still attached (see Taylor and Taylor, 1992 for further explanation); Scale bar = 2 mm. **Figure 2**. Suggested reconstruction of megasporophyll in Figure 1 (redrawn from Taylor and Taylor, 1992). **Figure 3**. Longitudinal section through the micropylar end of a dispersed ovule of the same type as Fig. 1, showing pollen grain (arrow) and poorly preserved integument (I); Scale bar = 1 mm. **Figure 4**. Suggested reconstruction of cupulate organ in Fig. 5. **Figure 5**. Section of cupulate reproductive organ with two terminal branches, each with a single, uniovulate cupule (one on left marked C). O = ovule. The cupule on the left extends above the seed (see two thin lines above). Note connection of two cupules at the base (= point of dichotomy). Scale bar = 1 mm.

Discussion

The permineralized specimens from Antarctica confirm the existence of two morphological types of ovule-bearing reproductive organs in the glossopterid seed ferns, an idea which was initially proposed based on compression-impression remains only (see, e.g., Surange and Chandra, 1975). They also provide the first definitive evidence of ovules borne within cupules, since the impression taxa described to date have no cellular details preserved. One type consists of a flattened leaf bearing a few to many seeds on the adaxial surface, the multi-ovulate type (e.g., Gould and Delevoryas, 1977; Taylor and Taylor, 1992; Nishida et al., 2007), and the second type encompasses uniovulate cupules borne terminally on elongate stalks, which themselves are part of a branching system (cupulate type). Both morphotypes contain orthotropous ovules and integumentary structures vary among taxa.

Compression-impression material suggests that both types of ovulate structures were borne in some relation to a vegetative leaf, either along the petiole on the upper (adaxial) surface of the leaf or in an axillary position. Only a very few specimens have been described that show glossopterid ovulate organs compressed laterally, so that the relation of the megasporophyll and the subtending vegetative leaf can be seen clearly. One of these, described by Pant and Singh (1974), shows a stalk terminated by an enlarged, flattened megasporophyll bearing numerous ovules on the surface. The stalk is attached in the axil of a typical vegetative leaf of *G. taenioides* with the ovules facing the stem (i.e., apparently on the adaxial surface of the megasporophyll). Based on this and other observations, Pant hypothesized in several publications (e.g., Pant and Singh, 1974; Pant, 1977) that all the multi-ovulate types bore their ovules on the adaxial (upper) surface of the megasporophyll, which was then attached to the stem in the axil of a vegetative leaf. Holmes (1973) also illustrated a specimen of *Austroglossa walkomii* with an attached axillary stalk bearing a megasporophyll and ovules. The specimen is somewhat crushed and may be twisted, but he hypothesized, based on this fossil, that the ovules were borne on the abaxial (lower) surface of the megasporophyll. In this scenario, the ovules would face the vegetative leaf and be appressed to it. Anatomical studies have now clearly demonstrated (Taylor and Taylor, 1992; Nishida et al., 2007) that the ovules were attached to the adaxial (upper) surface of the megasporophyll, based on the orientation of the vascular bundles in the structure.

Several authors have reconstructed the glossopterid megasporophyll with the ovules attached to the abaxial (lower) surface of the megasporophyll (e.g., Schopf, 1976; Retallack and Dilcher, 1981) and these reconstructions have been widely copied. These interpretations, however, have relied heavily on theoretical considerations necessary to evolve the angiosperm carpel from the glossopterid megasporophyll (e.g., Doyle, 2006). Information from compressed fossils does suggest that the ovules probably faced the surface of the subtending *Glossopteris* leaf (e.g., McLoughlin, 1990a), that is, they faced abaxially, but the permineralized structures from Antarctica and Australia illustrate that anatomically, the ovules were borne on the adaxial surface of the megasporophyll. This result would imply that either the peduncle of the megasporophyll was twisted at the base, or perhaps the vascular bundles twisted, either in the stem or in the peduncle, a situation known to occur in cycad leaves (Le Goc, 1914; Hermsen et al., 2007).

Glossopterid reconstructions and phylogenetic relationships

In attempting to elucidate the phylogenetic position of the Glossopteridales, many authors have considered the group as a single terminal clade in phylogenetic analyses (e.g., Nixon et al., 1994; Doyle, 2006; Hilton and Bateman, 2006). To date, there is no whole-plant reconstruction of a *Glossopteris* plant based on organic attachment or anatomical evidence, so the '*Glossopteris*' plant used in phylogenetic analyses has been a composite of morphotaxa based on dispersed organs, which masks the potential diversity in the group. A number of impression-compression leaf specimens have been described attached to axes (see references in Pigg and Taylor, 1993). Taylor and Taylor (1992) attributed the small megasporophyll from Antarctica to the same plant that bore *G. schopfii* (Pigg, 1990) leaves, based on similar anatomy of the vascular bundles. Pigg and Taylor (1993) described leaves of *G. skaarensis*, also from the Antarctic permineralized peat, attached to woody stems assigned to the morphotaxon *Araucarioxylon*. Pigg and Nishida (2006) reconstructed three 'whole plants' of *Glossopteris* based on permineralized specimens, one with *G. homevalensis* leaves from Australia, and two based on *G. schopfii* and *G. skaarensis* leaves from Antarctica; these leaf species also occur in Australia. Immature ovulate organs have been found attached to axes with *G. homevalensis* leaves, but these cannot be related to the mature ovulate structure from the Homevale locality (Pigg and Nishida, 2006; Nishida et al., 2007). With the exception of the ovulate organ of Taylor and Taylor (1992) and the immature structure, all reconstructions to date consist of vegetative parts only. Any attribution of reproductive organs has been based on common occurrence at the same locality, and pollen organs have not been described from these sites. Despite a leaf morphotype that is relatively uniform throughout Gondwana in the Permian, the reproductive organs, in particular the ovule-bearing parts of the plant that bore *Glossopteris* leaves, are both morphologically and anatomically diverse. It should come as no surprise, therefore, that the glossopterids represent a heterogeneous group of Late Paleozoic seed plants, and, like the so-called seed ferns in the Mesozoic, constitute a major challenge in understanding gymnosperm phylogeny.

Summary

The glossopterid seed ferns dominated Gondwana during the Permian, which was an important period of transition in seed plant evolution from more archaic Paleozoic forms to those appearing in the Mesozoic. Two types of anatomically preserved ovule-bearing organs of the Glossopteridales occur in a permineralized peat deposit on Skaar Ridge in the central Transantarctic Mountains. Although multiovulate reproductive structures have been found previously in peat from the Bowen Basin of Australia and from Skaar Ridge, this report represents the first anatomical detail of the cupulate type of reproductive organ, as well as the first definitive evidence of ovules found within the cupules. The confirmation of two distinct types of seed-bearing organs in the glossopterids indicates that the group is more diverse than the single leaf morphotype, *Glossopteris*, would suggest. Anatomically preserved glossopterid reproductive organs are crucial in furthering our knowledge of the relationships within this group, and in understanding their phylogenetic position in relation to the other seed plants.

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