

**A REVISION OF THE OVULIFEROUS  
FRUCTIFICATIONS OF GLOSSOPTERIDS  
FROM THE PERMIAN OF SOUTH AFRICA**

**VOLUME I**

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## DECLARATION

I, Rosemary Adendorff, declare that this thesis is my own, unaided work. It is being submitted for the Degree of Doctor of Philosophy in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.

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(Signature of candidate)

On this \_\_\_\_\_ day of \_\_\_\_\_ 2005



## ABSTRACT

A comprehensive re-assessment of the South African ovuliferous glossopterid fructifications was conducted. This involved the creation of a database of quantitative and descriptive information based on over 500 specimens from 14 localities in the northern and eastern Karoo Basin and the Bushveld Basin. Specimens belonging to four families, thirteen genera and 24 species were measured in detail, re-described, re-evaluated and in many cases, existing diagnoses were emended. In total, this revision effected the creation of four new genera, one new species and emendations to two families, seven genera and thirteen species. All taxa were photographed, and representative specimens were drawn and reconstructed. An illustrated key to the ovuliferous glossopterid fructifications was compiled as a guide to the identification of all known species from South Africa. The South African literature on glossopterid polysperms was reviewed, with reference to discoveries from other parts of Gondwana.

All the glossopterid ovuliferous fructifications examined were impression fossils, and a major component of the project was to re-evaluate the structure and morphology of the specimens from a taphonomic perspective. Although not widely taken into account in palaeobotanical studies, impression fossils are essentially moulds of the original plant, providing valuable three-dimensional information which is easily overlooked. This approach led to the discovery of several radical, new morphological types in well-known taxa. These discoveries could change the way glossopterid homologies are interpreted in the future. Additionally, these structures may help to resolve some of the conflicting reports regarding the presence of more than one set of cuticle per fructification, and sterile scales.

*Hirsutum intermittens* was found to have a peculiar dual wing structure, and was transferred to a new genus, *Bifariola*. In addition to the primary wing with its tapered base, extended apex and apically inclined striations, an additional, secondary wing was recognised in these fructifications, which has a structure similar to that of *Scutum* and *Gladiopomum*. *Hirsutum leslii* was found to possess a unique, hood-like wing which arched over the seed-bearing surface

of the fructification, partially enclosing the ovules, which were in many cases found still attached to the fructification. The species was deemed to be a junior synonym of *Elatra*. The semi-enclosed structure of *Elatra* raised questions regarding the pollination and seed dispersal mechanisms employed by members of this genus.

A review of the literature on *Arberia*, and examination of South African specimens, led to emendation of the genus to include the presence of a scale-like extension distal to the single seed attachment point at ultimate branch termini. Appreciation of the bifacial nature of some *Arberia* species, which bear lateral branches across one surface of a laminate primary axis has important implications for the recognition of homologies and establishment of evolutionary trends among members of the glossopterids. Existing ideas regarding the homologies and phylogeny of the glossopterids were refined and developed further. The glossopterid polysperms are considered to have evolved from a basal member of the Arberiaceae, with planation, fusion and reduction of lateral branches having given rise to fructifications of the Rigbyaceae and Dictyopteridiaceae. Members of the Lidgettoniaceae are thought to have been derived from members of the Dictyopteridiaceae. The hypothesised derivation of the glossopterid fertile structures from modified shoots rather than leaves, supports an affiliation with the cordaitaleans rather than the pteridosperms.

The biostratigraphic and biogeographical significance and application of the South African genera of glossopterid polysperms was briefly evaluated.

To my parents,

**Louis and Shirley Adendorff**

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## CHAPTER 1 INTRODUCTION

Ever since Brongniart (1828) described a strange entire-margined, tongue-shaped leaf form-genus from the Permian of India and Australia, the *Glossopteris* plant and its associated organs have been the source of controversy, intrigue and lively speculation among morphologists, taxonomists and phylogeneticists alike.

Glossopterid leaves are ubiquitous in Permian sediments throughout Gondwana, including India, Australia, South America, Antarctica and southern Africa, and played an important role in the development of the theory of continental drift (e.g. du Toit, 1937). They are universally recognised as the primary index fossil for Permian sediments of these southern continents. Not only were they wide-spread, they were the dominant plant type in these regions for some fifty million years of Earth's history. The glossopterids first appeared in Late Carboniferous or Early Permian times and ruled supreme until the end of the Permian, when they fell victim to the most catastrophic extinction event in the history of life on Earth (e.g. Rigby & Schopf, 1969; Raup & Sepkoski, 1982; Benton, 1995; Pant, 1996; Retallack, 1995; Retallack *et al.*, 1996; McLoughlin *et al.*, 1997; Erwin, 1994, 1999; Kerr, 1993, 2000). There have been reports of glossopterid leaves occurring in the Triassic sediments of Gondwana (e.g. Thomas, 1952; Ash, 1981; Pant & Pant, 1987; Holmes, 1992), and even from the Jurassic of Honduras and Mexico (*Mexiglossa*: Delevoryas & Person, 1975; Ash, 1981) which were never a part of the Gondwana continent. Although it is difficult to imagine that at least some stray members of this wide-ranging did not survive the Permian-Triassic extinction, reports of glossopterid leaves from strata younger than the Permian generally have not been accepted as conclusive (e.g. McLoughlin, 1993a), and may represent examples of convergent leaf morphologies. Past reports of *Glossopteris* from the Triassic of South Africa (e.g. Du Toit, 1927; Thomas, 1952; Anderson & Anderson, 1983a; Kovacs-Endrody, 1984) have referred to specimens of what Anderson & Anderson (1989; 2003) named *Gontriglossa verticillata*. These leaves, which have also been attributed to the northern hemisphere taxon *Sagenopteris* (Du Toit, 1927; Thomas, 1958), are superficially very similar to *Glossopteris*, but

differ in terms of cuticular structure and mode of attachment (Anderson & Anderson, 1989, 2003). A strong piece of evidence in support of the extinction of this plant group at the end of the Permian, is the absence of any reports of *Vertebraria*, the very distinctive and characteristic root material of the glossopterids, beyond the Permian-Triassic boundary. We are all waiting in anticipation for the recovery of glossopterid fructifications from Triassic and Jurassic strata before we can unequivocally extend the biostratigraphic and biogeographic range of this plant group.

The leaves of the glossopterids are the most abundant and common palaeosignature of this group, but over the past 180 years since they were first described, it seems that less progress has been made in the classification of these organs than might have been expected. A huge amount of literature has been written on *Glossopteris* leaves from around the world, but the taxonomic approaches that have been used to characterise species of this form-genus have varied considerably. There have been some brave attempts to simplify and unite glossopterid populations from across Gondwana (e.g. Arber, 1905), but ultimately, these classification systems have been fairly subjective. There has been a tendency either to shoe-horn morphotypes into relatively few species, or to create vast numbers of species which could probably be accounted for in terms of natural variation within individual species. Because most of the leaves occur as detached individuals within fossilised leaf mats, with very few being directly associated with or physically attached to fertile organs, it has been very difficult for workers to judge the boundaries of reasonable biological entities within this group.

The overwhelming abundance of leaves from such a vast portion of the world, the paucity of morphological characters available in *Glossopteris* leaves for taxonomic discrimination, and the apparent plasticity in size and form amongst leaves in any one population, has made many workers cautious about the validity of glossopterid taxonomy based on leaf morphology alone (e.g. Schopf, 1976; Chandra & Surange, 1979; Taylor, 1981; Anderson & Anderson, 1985; White, 1986; McLoughlin 1993b,c). Some researchers have had reservations about past taxonomic approaches to glossopterid leaves, questioning the rigour

of the methods employed, but have nonetheless been optimistic regarding the meaningful classification of *Glossopteris* species and their potential utility as biostratigraphic indices (e.g. Kovács-Endrödy, 1981, 1984, 1991; Jeyasingh, 1987; Singh, 2000).

Generally, in botanical studies it is the fertile structures of a plant group that tell us the most about its affinities and levels of diversity, and a central theme of debate and investigation in glossopterid research over the years has been the recognition and characterisation of the ovuliferous structures of *Glossopteris*. Although the typification of these organs has had its own set of contentious issues and causes of dissent, these structures offer us the best hope of placing the glossopterids in a consistent and useful taxonomic and phylogenetic context. This study will hopefully, in the process of reviewing and critically re-evaluating past ideas and interpretations, serve to advance our understanding of the structure and taxonomic position of the glossopterids from a South African perspective.

### **1.1. THE GLOSSOPTERIS PLANT: AN OVERVIEW**

In the past the informal term 'glossopterids' has been loosely applied to most gymnospermous leaves from the Permian of the Gondwana supercontinent, mainly on the basis of fairly superficial similarities in overall morphology. As a result, the term has been used for a large, heterogeneous group of plants including leaf types assignable to the form genera *Rubidgea*, *Euryphyllum*, *Gangamopteris*, *Glossopteris*, *Palaeovittaria*, *Rhabdotaenia*, *Pteronilssonina*, *Belemnopteris*, *Surangephyllum*, *Illexiodephyllum* and *Noeggerathiopsis* (e.g. Pant, 1982; Meyen, 1987; McLoughlin, 1993c). In line with the recommendations of Rigby (1978) and Maheshwari (1990), the glossopterids are taken here to include only members of the form genera *Gangamopteris*, *Palaeovittaria*, *Surangephyllum* and *Glossopteris*. These taxa share similar epidermal features (Srivastava, 1956) and are associated with, or have been found in organic connection to, glossopterid fructifications. *Gangamopteris* is a controversial generic designation which has been used by some authors for glossopterid leaves which lack a distinct 'midrib' and have interreticulations in

the parallel medio-longitudinal veins (e.g. Maheshwari, 1965a; Taylor, 1981; McLoughlin 1993c; Pigg & Taylor, 1993). Leaves with this venation type tend to be confined to Lower Permian sediments, which has promulgated use of the name in a biostratigraphic context. Many authors, however, have questioned the distinction between *Glossopteris* and *Gangamopteris*, and have suggested that they may represent the two poles of a morphological continuum (e.g. Etheridge, 1894; Rigby, 1967; Chandra, 1974; Gould & Delevoryas, 1977; Kovács-Endrődy, 1977). Seward (1910) considered retention of the two distinct genera a matter of convenience, to avoid confusion. Anderson & Anderson (1985) and McLoughlin (1993c), while acknowledging the existence of a morphological continuum between *Glossopteris* and *Gangamopteris*, noted that the bulk of leaves could easily be sorted into one or the other genus. Anderson & Anderson (1985) ultimately circumvented the issue by assigning all *Gangamopteris* leaves to *Ottokaria*, in line with their novel approach to glossopterid taxonomy (see section 4.1.2.5). Leaves that have been assigned to *Gangamopteris* in the past are here referred to as 'gangamopteroid forms' of *Glossopteris*.

Initially, the *Glossopteris* plant was thought to be small and herbaceous, mainly as a result of Zeiller's (1886) report of glossopterid leaves he purportedly found in direct attachment to a *Vertebraria* rhizome. Pant (1962) reviewed the evidence cited in favour of this theory, the most notable being the specimen figured by Dolianiti (1954). This impression fossil of *Glossopteris* leaves in apparent organic attachment to a section of *Vertebraria*, looks suspiciously like a *Vertebraria* axis bearing lateral roots, and closely associated with a single, fortuitously placed *Glossopteris* leaf. Increasingly, as evidence accumulated of *Glossopteris* leaves attached to woody axes rather than directly to *Vertebraria* axes, and as workers continued to find these leaves consistently associated with broad trunks of gymnospermous wood, the *Glossopteris* plant was reconstructed as a large tree (Schopf, 1970; Gould & Delevoryas, 1977; Retallack & Dilcher, 1981, 1988; Meyen, 1987; Bajpai & Tewari, 1990; Pigg & Taylor, 1993; Stewart & Rothwell, 1993; Pant 1999). Perhaps the most commonly reproduced reconstruction of the *Glossopteris* plant is that of Gould & Delevoryas (1977), who depicted a large, deciduous tree. Pant (1999),



from extrapolations of permineralized tree stumps, suggested that some *Glossopteris* trees may have reached heights of 30 to 40 m! Taylor *et al.* (1992) described an *in situ* permineralized *Glossopteris* forest in Antarctica, with young trees growing in dense stands. They considered it unlikely that this forest would have been able to support much in the way of an understorey, indicating that in some cases, *Glossopteris* dominated the flora in an arborescent form. However, bearing in mind the vast territory covered by these plants, some authors have continued to argue in favour of at least some species possibly having had a shrubby or herbaceous habit (White, 1978, 1986; Pant, 1999; Singh, 2000). Pant (1999) suggested that some forms of *Glossopteris*-bearing plants may even have been woody climbers.

Gymnospermous wood attributed to the *Glossopteris* plant has commonly been referred to *Araucarioxylon* Kraus and *Dadoxylon* Endlicher (e.g. Kräusel *et al.*, 1961-1962; Maheshwari, 1972; Bajpai & Singh, 1986; Pant & Singh, 1987). These are essentially form genera which may represent the wood of a variety of plant groups. Bamford (1999) discussed the historical problems surrounding the genus *Dadoxylon*, with its very broad diagnosis and numerous, conflicting emendations. Additionally, the genus is nomenclaturally invalid according to the Botanical Code of Nomenclature (Philippe, 1993). Bamford (1999) considered *Dadoxylon* to be useful only as a 'catch-all for woods with araucarian tracheid pitting and pith, which do not fit into the described woods with characteristic or distinctive pith types'. *Araucarioxylon* also has a confused taxonomic history, but its main distinguishing features are the presence of secondary xylem with araucarian tracheid pitting, and the absence of features such as ray border cells, clustered pits or resin canals (Bamford, 1999). Bamford & Philippe (2001) recommended the synonymisation of *Araucarioxylon* with *Agathoxylon*.

Bamford (1999, 2004) recorded the presence of three wood genera from Permian strata of the Karoo Basin, viz. *Agathoxylon*, *Australoxylon* and *Prototaxoxylon*, each of which may include examples that are glossopterid in origin. According to Weaver *et al.* (1997), *Australoxylon* has bordered radial tracheid pits (less than 15 µm in diameter) which are araucarian, abeitoid or arranged in groups of up to five, and may be separated by bars of Sanio.

Tracheids are quadrangular in transverse section and may have tangential pits. Bamford (1999) considered the clustering of the pits to be the most important diagnostic character of this genus, which appears to have been restricted to the Permian. Various members of the genus *Prototaxoxylon* have a broader temporal distribution, ranging from the Carboniferous into the Mesozoic, and are characterised by the following features: secondary xylem of gymnosperm wood, with spiral thickenings on the tracheid walls, 1-2 seriate, araucarian bordered pits on the radial walls of the tracheids, taxodioid cross-field pits, and narrow rays (Bamford 1999). In South Africa, however, only two species have been recorded and they are from the Upper Ecca and Lower Beaufort. Unfortunately the precise location and age of the type species, *Prototaxoxylon africanum* Kräusel and Dolianiti (based on *Spiroxylon africanum* Walton), is unknown. It would appear that the wood has a more restricted temporal distribution than that of the glossopterids, yet *Prototaxoxylon africanum* and *Prototaxoxylon uniseriale* may well prove to have been glossopterid in origin.

Conspicuous growth rings have been found in glossopterid wood, branches and *Vertebraria* roots, favouring theories of a seasonal growth periodicity in these plants (e.g. Taylor *et al.*, 1992; Francis *et al.*, 1993; Weaver *et al.*, 1997). The deciduous nature of *Glossopteris* has also been inferred from the occurrence of abundant, isolated leaf impressions in so-called 'autumnal bank' deposits (Plumstead, 1958b; Schopf, 1976; Surange & Chandra, 1978; White, 1986; Pigg & Taylor, 1993), and the occurrence of numerous leaf impressions in the autumn-winter, but not summer-spring deposits in varved sediments (Retallack, 1980; Taylor, 1981). As Pigg & Trivett (1994) noted however, there is no direct evidence of deciduousness in permineralized *Glossopteris* leaves.

Pigg & Taylor (1993) and Pigg & Trivett (1994) reviewed and discussed the rare examples of branch impressions that have been found with attached glossopterid leaves, and the even rarer and anatomically informative examples of permineralized axes with attached leaves. These latter specimens provided the first irrefutable evidence for the link between wood of the *Araucarioxylon* type (= *Agathoxylon* Hartig. of Bamford & Philippe, 2001) and *Glossopteris*. The body of evidence available indicates that *Glossopteris* leaves were alternate or

borne in tight helices simulating whorls (e.g. Etheridge, 1894; Thomas, 1952; Schopf, 1967; Pant, 1977; White, 1978, 1986). There have also been suggestions of a short shoot - long shoot arrangement, not unlike that seen in many conifers and in *Ginkgo* trees (Rigby, 1967; Pant & Singh, 1974; Plumstead, 1975; Pigg & Trivett, 1994; Holmes, 1995; Pant, 1999).

The underground parts of the *Glossopteris* plant are universally considered to be the aerenchymatous roots assigned to the form-genus *Vertebraria* Royle 1833. These axes are consistently found in association with glossopterid leaves across Gondwana. Gould (1975) demonstrated the presence of pycnoxylic wood in permineralized *Vertebraria* roots which was the same as that found in trunks of *Araucarioxylon arberi*. This was later confirmed by Neish *et al.* (1993). In cross section the roots have a central core of exarch primary xylem, surrounded by several radiating wedges of secondary wood. Between the wedges are empty spaces, representing what would have been large air channels in the living plant. These aerenchymatous tissues are thought to have been an adaptation to growth under very wet soil conditions. *Vertebraria* axes with diameters of 150 mm have been found, lending credence to the theory that at least some species of *Glossopteris* were large trees (Schopf, 1976; Pant, 1977).

With its characteristic midrib comprising several parallel veins and single order of lateral, bifurcating and anastomosing veins, the *Glossopteris* leaf has not provided researchers with a wealth of taxonomic features for the easy identification of species. Features which have been used in the past to delimit species, have included leaf shape, shape of apex, shape of base, petiole morphology, appearance and persistence of the midrib, and perhaps most importantly, various features relating to the venation, such as mesh shape, mesh size, angle of the venation to the midrib, number of anastomoses from midrib to margin, marginal vein density and the nature of the vein course from midrib to margin (e.g. Kovács-Endrödy, 1976, 1977, 1979, 1981, 1991; Surange & Chandra, 1978; Chandra & Surange, 1979; Pant & Pant, 1987; McLoughlin, 1990a; Singh 2000). Gould & Delevoryas (1977) described the first examples of permineralized *Glossopteris* leaves ever examined, and proved what had

already been deduced from impression fossils, i.e. that the midrib comprises a medio-longitudinal aggregation of closely spaced, parallel veins and is therefore not a true midvein as seen in other groups such as ferns and angiosperms. In some cases the midrib is enhanced by the presence of a well-developed hypodermis, particularly on the abaxial side of the leaf.

Cuticular studies (e.g. Srivastava, 1956; Surange & Srivastava, 1956; Pant, 1958; Pant & Gupta, 1968, 1971; Pant & Singh, 1971, 1974; Chandra, 1974; Maheshwari & Tewari, 1992; Pant & Pant, 1987;) and the examination of anatomical features of permineralized leaves (e.g. Pigg, 1990; Pigg & Taylor, 1990; Pigg & McLoughlin, 1992; Pigg & Trivett, 1994; McManus et al., 2002), have added a new dimension to the recognition of diversity in *Glossopteris* leaves. However, authors still appear to be uncertain as to how these features reflect or relate to diversity at the generic and species levels. Surange & Srivastava (1956) and Maheshwari & Tewari (1992) concluded that cuticular features of *Glossopteris* leaves may not reflect the same taxonomic patterns as gross leaf morphology, and the former authors eventually delimited species of *Glossopteris*, *Palaeovittaria* and *Gangamopteris* into six groups equivalent to genera, on the basis of cuticular features alone. There appears to be a high degree of intergradational variation in glossopterid cuticles, which may restrict the taxonomic utility of this feature.

According to Taylor (1996), studies of permineralized *Glossopteris* leaf material have revealed an unexpected diversity in leaf anatomy (e.g. Pigg, 1990; Pigg & Taylor, 1990, 1993). At least three types of anatomy are now known, with two of the types each being consistently associated with a particular mesh shape. As discussed by Pigg & McLoughlin (1997), further sampling of permineralised leaf material is required before the diversity of anatomical types can be adequately compared to the diversity of gross morphological features observed from impression fossils.

Although the first fertile structures demonstrated to be in physical organic connection with *Glossopteris* leaves were initially described as bisexual (Plumstead, 1952, 1956a, 1958a), it is now universally accepted that the

*Glossopteris* plant produced separate ovulate and pollen-bearing organs. The ovuliferous glossopterid fructifications displayed an interesting array of morphological variants, as will be discussed during the course of this thesis. The pollen-bearing structures, however, were apparently not as diverse.

Proposed pollen-bearing organs of the glossopterids have been recognised as such on the basis of strong associative evidence, and the fact that they have an overall appearance and arrangement very similar to members of the Lidgettoniaceae, a widely recognised family of ovulate glossopterid fructifications. Clusters of microsporangia were borne on thin pedicels arising from the basal portion of a reduced, scale leaf. The filamentous pedicels had multiple terminal branches, each bearing an elongate-oval to falcate microsporangium, with fine longitudinal striations/ridges. The venation of the scale leaves in these organs is very similar to that seen in glossopterid leaves, re-enforcing their affiliations to the group. Holmes (1995) illustrated forms which appear to be transitional, in size and general morphology, between typical *Glossopteris* leaves and reduced scale leaves.

Perhaps the first record of these pollen-bearing structures was made by Dana (1849). He referred to two specimens collected in Antarctica (drawings pl. 12, figs 7 & 8a) as scales with 'a cluster of granules'. Du Toit (1932) referred similar specimens from the upper Permian of South Africa to the new genus *Eretmonia*. *Eretmonia* is abundant in the fossiliferous beds of the Estcourt Formation of Natal, and is consistently found in association with the ovuliferous glossopterid fructification *Lidgettonia*. Typically, *Eretmonia* bears one to two pairs of pedicellate microsporangial clusters in opposite ranks in the base of a rhombohedral scale leaf. The scale leaf varies considerably in size and shape (Lacey *et al.*, 1975). Initially Du Toit (1932) did not recognise the pedicellate nature of the microsporangial clusters. His diagnosis was later emended by Surange & Maheshwari (1970) to include details of attachment of the microsporangia to the scale leaf. Lacey *et al.* (1975) emended the diagnosis further, incorporating additional information on leaf scale venation and microsporangium morphology.

Surange & Maheshwari (1970) and Surange & Chandra (1974c,d; 1975) described the only other well-characterised pollen-bearing structure confidently associated with *Glossopteris*, viz. *Glossotheca*. This pollen-bearing fructification is very similar to *Eretmonia*, but the pollen-sac clusters are borne on pedicels that share a common, central stalk. The scale leaf also tends to be larger and more linear in *Glossotheca*, there are three pairs of sporangial clusters, and the clusters are larger than those of *Eretmonia* (Lacey *et al.*, 1975).

*Eretmonia* scale leaves are commonly thought to have been borne in fairly loose cones. White (1978) published examples of what appear to be specimens of *Eretmonia* aggregated into strobili, which she referred to the form genus *Squamella*. Nishida *et al.* (2002) recently reported permineralized sporangiate scales from the Upper Permian of Australia which were 'borne distally in shoots with basally attached tight helices of sterile scale-like leaves'.

Another fertile organ that some authors have attributed to the glossopterids is *Kendostrobus*, first described by Surange & Chandra (1974d). This cone-like structure bears groups of pollen sacs that are helically arranged on an axis. There is no convincing evidence to suggest that this fertile structure is glossopterid.

Isolated pollen sacs of the type found attached to *Eretmonia* were first described by Arber (1905) from Australia, and were later assigned the form-genus *Arberiella* by Pant & Nautiyal (1960). *Arberiella* has also been reported from Antarctica (Cridland, 1963; Schopf, 1970), South Africa (Lacey, *et al.*, 1975; Anderson & Anderson, 1985), India (Pant & Nautiyal, 1960; Surange & Chandra, 1974c,d; 1975) and South America (Lundqvist, 1919). *Arberiella* pollen sacs have a very distinctive appearance: each sac is elliptical to reniform or falcate, with fine, longitudinal striations that bifurcate and anastomose. Several authors have described pollen extracted directly from *Arberiella* pollen-sacs. Pant (1958) and Pant & Nautiyal (1960) extracted striate, bisaccate, *Protohaploxypinus* pollen from *Arberiella* pollen-sacs from Africa and India. Gould & Delevoryas (1977) figured permineralized specimens containing striate, bisaccate pollen grains, and in a fascinating paper by Lindström *et al.* (1997),

pollen grains that would otherwise be assignable to four different form-genera and five form-species, were extracted from a single *Arberiella* pollen sac!

The ovuliferous fructifications of the glossopterids apparently reflect a diversity that is far more easily recognisable than that seen in the pollen-bearing structures or leaf material of this group. Following Brongniart's (1828) description of *Glossopteris* foliage, there was a long hiatus during which the fertile structures of the glossopterids remained unknown. Although various reports of strange, isolated fertile structures associated with *Glossopteris* leaves were tantalising, they only fuelled speculation (e.g. Bunbury, 1861; Feistmantel, 1881; Zeiller, 1886; Arber, 1905; White, 1908).

Then, during the 1940's Mr Stephanus Le Roux, an amateur palaeobotanist and resident of the small industrial and mining town of Vereeniging near Johannesburg, discovered a rich Gondwanan palaeoflora at the quarries of the Vereeniging Brick and Tile Co. He found several puzzling fertile structures that he proposed were the elusive fructifications of the *Glossopteris* plant. He approached Dr Edna Plumstead of the University of Witwatersrand with his theory, but failed to convince her. Nonetheless, he continued intensive exploration of the site, and managed to assemble a large collection of various fructifications preserved in direct, organic attachment to *Glossopteris* leaves (Anderson and Anderson, 1985). Plumstead finally conceded that these were indeed the fructifications of *Glossopteris*, and subsequently published her famous series of papers describing these polysperms (1952, 1956a,b, 1958a). Immediately, her interpretations were the subject of international interest and debate, and examples of glossopterid fructifications started appearing from all over Gondwana.

The body of knowledge on the ovuliferous structures of the glossopterids has grown steadily over the years, with over 30 genera currently recognised. These have been reviewed in several key works, e.g. Surange & Chandra (1975), Schopf (1976), Pant (1977), Rigby (1978), Anderson & Anderson (1985), McLoughlin (1990b; 1993a). This accrual of information has not been a harmonious affair, and researchers have developed radically contrasting views

on even the basic morphology of these organs. As a result, limited agreement has been reached on the homologies of the fructifications, and the phylogeny of the entire group is a perennial subject for debate. Much of this discord has stemmed from conflicting interpretations of the variously preserved fossils from across Gondwana.

## **1.2. GLOSSOPTERIS IN SOUTH AFRICA**

During Permian times, the landscape of what is today South Africa, was dominated by a huge inland sea in which a thick sequence of sediments called the Karoo Supergroup accumulated. This Karoo Basin spanned most of the country from the Early Carboniferous to the Early Jurassic, and has provided us with vast exposures of continuous Permo-Triassic sequences that are unique in the world. This geological setting has presented palaeobotanists with a broad scope for the exploration of Gondwanan Permian floras. The *Glossopteris* flora is particularly well represented in the northern and eastern parts of the Karoo Basin, in the middle to upper Ecca and Lower Beaufort groups.

No permineralized *Glossopteris* is known from South Africa, and cuticle is rare, so we rely on impression/ compression fossils in our studies of the Permian floras. Numerous important localities have been discovered over the years, such as the fossiliferous deposits at Vereeniging, Hammanskraal, Mooi River and Lawley. The abundance and diversity of the fossils extracted from these sites has contributed greatly to the understanding of the Gondwanan floras, and to our knowledge of *Glossopteris* in particular. Intensive collection from these sites by palaeontologists over the years has resulted in South Africa hosting the largest collection in the world of glossopterid fertile organs attached to *Glossopteris* leaves.

*Glossopteris* has played a particularly important role in the science of palaeobotany in South Africa. Anderson & Anderson (1985, 1997) reviewed the rich palaeobotanical history of South Africa, with some of the earliest collections of *Glossopteris* having been made in the late 1800's and early 1900's by George Stow, David Draper and Thomas Leslie, all medical doctors with an



interest in plant fossils. The earliest publications on South African *Glossopteris* were by Seward (1897, 1898, 1903, 1904, 1907) and Leslie (1904, 1921) with some important later additions by du Toit (1927, 1932).

Thomas (1921), based at Cambridge University, published the first glossopterid fertile structure to be recovered from South Africa. Originally called *Ottokaria leslii* by Thomas (1921) and later renamed *Hirsutum leslii* (Anderson & Anderson, 1985), this fascinating taxon has been the subject of some of the most interesting discoveries in this study (see *Elatra leslii*, sections 3.2.3 and 7.3). Plumstead's (1952, 1956a,b, 1958a) famous papers describing the first attached glossopterid fertile structures to be recognised have already been discussed. These papers, and her continued involvement in glossopterid studies (e.g. Plumstead, 1958b, 1962a,b, 1969), placed South Africa firmly in the centre of the international controversy and debate that still dominates studies of Permian Gondwanan floras. The first recorded member of the Lidgettoniaceae in Gondwana also hailed from South Africa. Thomas (1958) described this fructification, which he called *Lidgettonia*, from the Upper Permian Lidgetton locality.

Studies on South African *Glossopteris* gathered momentum in the 1970's and early 1980's, with the work of Lacey (1974, 1978), Lacey *et al.* (1975), Benecke (1976), Le Roux (1976), Anderson (1977), Le Roux & Anderson (1977), Kovács-Endrödy (1976, 1977, 1979, 1981, 1984), Smithies (1978) and Rayner & Coventry (1985), culminating in the publication of a broad synthesis of South African palaeobotanical knowledge of the time by Anderson & Anderson (1985).

Since Anderson & Anderson (1985) produced their mammoth prodromus, work on the glossopterids and the *Glossopteris* flora of South Africa has been sporadic. Kovács-Endrödy (1991) soldiered on with the noble cause of *Glossopteris* leaf taxonomy, Aitken (1994) made inroads into the palynology of the Permian, Bamford (1999) has contributed to our knowledge of the fossil woods from the Permian of South Africa, and papers by Anderson & Anderson (1997), Anderson (1999) and Anderson *et al.* (1999) have emphasised the role the South African floras play in a global context. In recent years van Dijk (1998),

van Dijk & Geertsema (1999) and Geertsema *et al.* (2002) have considerably advanced our knowledge of the insects associated with the glossopterids.

The papers of Adendorff *et al.* (2002, 2003) represent the first in an envisaged series of publications on the South African glossopterids and associated floral elements, and will hopefully create renewed interest in glossopterid research in this country.

Although few people in South Africa are aware that the *Glossopteris* plant ever existed, they rely each day on the energy harnessed from the sun by these trees. *Glossopteris* trees thrived 280 million years ago in the great swamp forests of what are today the provinces of Gauteng and Kwa-Zulu Natal. A slow process involving the burial, gradual compression, heating and chemical alteration of dense mats of accumulated organic material derived primarily from the *Glossopteris* plant eventually resulted in the formation, over millions of years, of the huge coal reserves present in South Africa today (e.g. Falcon, 1986).

The South African Department of Energy released the following astounding figures (as of 2001), reflecting the enormous impact that coal has on the everyday lives of South Africans. Over 90% of our electricity is produced from coal, and South Africa produces an incredible two thirds of Africa's entire electricity supply. Sasol is the world's largest producer of synfuels from coal, which form the major components of South African petroleum, and the many by-products of this process are in themselves a multi-billion Rand industry. Six percent of the world's total coal reserves are to be found in South Africa, and we are the sixth largest coal producer, contributing 5% of the world's total coal supply. We are the second greatest exporter of coal after Australia, and this is South Africa's third largest source of foreign exchange, after gold and platinum. All this is thanks to *Glossopteris*!

### **1.3. A RE-EVALUATION OF SOUTH AFRICAN GLOSSOPTERID FRUCTIFICATIONS**

The current study has focussed on the fertile glossopterid structures that have been collected in South Africa over the years. It has been 20 years since these glossopterid fructifications were examined in any detail (Anderson & Anderson, 1985), and initially the only aim of this project was to review and update their taxonomy, and to provide detailed descriptions of all the known taxa. However, it soon became apparent that for such an undertaking to be successful, the basic nature of the fossils themselves had to be thoroughly re-evaluated. There were many conflicting views in the literature on what impression fossils actually represented, and as a result there was confusion and a general lack of consensus regarding the morphology of the plant organs they represented.

Perhaps the single most rewarding aspect of this entire study has been the dawning realisation and appreciation of the wealth of information that impression fossils can provide. Because of the importance of these revelations in the visualisation and reconstruction of the three-dimensional structure of the original fructifications, an entire chapter (Ch. 3) has been devoted to this topic. These concepts had a direct bearing on all the descriptions and taxonomic decisions comprising the bulk of the document and needed to be clarified early on in the work. An appreciation of the true nature of impression fossils also provided some insights into some of the puzzling taxonomic decisions that have been made in the past, and led to some interesting ideas regarding the homologies of the various features of the glossopterid fructifications.

This study has drawn on specimens housed at all major repositories of glossopterid material in the country, and has involved the careful measurement, documentation and reconstruction of all the species of glossopterid ovuliferous fructifications that were encountered. All four of the families of glossopterid polysperms recognised in this work (see section 4.1.2, p. 125) are represented in the South African palaeobotanical collections, providing the ideal forum for an investigation of this nature. The suprageneric classification of the glossopterids has been a source of contention in the literature, mainly because the

morphology of their fertile structures is not fully understood, and because anatomical information about these organs is so scarce. The different systems that have been suggested by authors over the years are discussed in section 4.1. The system of naming of the different species of glossopterid fructifications is also addressed, in section 4.1.2.5.

A basic key to the identification of all the glossopterid ovuliferous fructifications described in this study is presented in section 4.2 (p. 131). A table of key end-notes summarising the diagnostic features of each species (with an accompanying line-drawing reconstruction), has been included with the aim of facilitating easy and rapid identification of all the South African taxa. This section serves as a summary of the information presented in the main body of the thesis, the compendium of South African taxa spanning Chapters 5 to 8. Although this treatise only encompasses South African ovuliferous glossopterid fructifications, where possible, comparisons have been made with glossopterid fructifications from other parts of Gondwana. In addition, some historical background has been included on the origins of the various genera and species.

A fairly exhaustive database of morphological features and morphometric information was generated, with the examination of over 500 fructifications from 14 localities in the northern and eastern Karoo Basin and the Bushveld Basin of South Africa. There are very few examples in the literature of morphometric analyses of the fertile structures of glossopterids. Lacey *et al.* (1975), on the basis of numerous measurements of *Eretmonia* pollen-bearing structures, plotted a very interesting scatter chart illustrating the degree of diversity in scale leaf morphology in this taxon. McLoughlin (1990a) used scatter plots of key characteristics to assess the intraspecific morphological variation of two Australian fructifications, *Ottokaria inglisensis* and *Dictyopteridium walkomii*. He concluded that the delimitation of glossopterid ovuliferous fructification species should involve the recognition of subtle difference in stalk, receptacle and wing morphology, and the structure of the seed scars and attached seeds. He emphasised that taxonomic decisions based on comparisons of dimensional statistics, should involve large collections as opposed to a few individuals. In

most cases, such studies are not possible, due to the paucity of available specimens, but the South African collections are fairly unusual in housing relatively large numbers of some taxa, which present an ideal opportunity for morphometric analysis. The data accrued during the course of this study was particularly useful in that it introduced a high degree of consistency as far as comparisons between different taxa were concerned. Only very basic statistical analyses were conducted, establishing size ranges, averages and standard deviations for each quantitative character, but together with the more visual input from scatter diagrams, this information was invaluable when assessing and comparing similar taxa.

Polysperms attached to *Palaeovittaria*, as described by Anderson & Anderson (1985), were excluded from the study because of the poor preservation of the available specimens. Detail of these purported fructifications is limited to vague and inconclusive secondary imprints. The obtuse, possibly fertile organ *Vannus gondwanensis* which was first described by Plumstead (1962c), and which was considered by Anderson & Anderson (1985) to represent the pollen-bearing organ of *Ottokaria*, was also omitted from this study because of a lack of evidence of its fertile nature.

Almost all of the taxa examined required some re-characterisation, particularly with regard to the relationship between the wing and marginal seed scars of the receptacle. Many of the diagnoses of the glossopterid fructifications have been emended here as a result of the careful re-evaluation of their basic morphology. Thirteen genera and 24 species are recognised in this revision, and each one is reviewed and described in Chapters 5 to 8. The taxonomic changes which have been recommended in these chapters are summarised in Table 1.3.1.

During the course of this broad reassessment of the morphology and taxonomy of the glossopterid fructifications, certain patterns emerged which have helped me to formulate my own opinions regarding the homologies of the structures comprising the glossopterid fructifications, and the implications these have for the phylogenetic relationships between glossopterids and other major plant groups. These are considered in the discussion (section 9.2, p. 340).

South Africa has a long tradition of biostratigraphic studies of the Karoo Supergroup based on fossil vertebrates, dating back to the early nineteenth hundreds. Over the years the biozonation of the Beaufort Group in particular has been, and continues to be, modified and refined (see Rubidge, 1995), and has become a powerful tool in the characterisation of sediments of the Karoo Basin. However, work on the fossil plants of the Karoo Supergroup has lagged far behind in terms of their application towards solving biostratigraphic problems. With the many difficulties that have been encountered in glossopterid leaf taxonomy, the glossopterid fructifications are generally regarded as being far more useful index fossils within the Permian of Gondwana. Although they are relatively rare, they do appear to reflect useful chronological trends. McLoughlin's (1993a) thorough treatise on the biostratigraphic application of the glossopterid fructifications from all of Gondwana provided us with a complete review of all the biostratigraphic information that has been gleaned from ovuliferous glossopterid fructifications to date. Care was taken during the course of this study to include information about the stratigraphic occurrences of the fructifications whenever possible. This topic is briefly dealt with in the discussion, including a short evaluation of the potential utility of each South African genus as an index taxon.

This thesis is primarily a taxonomic work, but whilst closely examining the ovuliferous fructifications of the South African glossopterids over the past few years, I have acquired a deeper understanding and appreciation of the plant group as a whole. The unexpected findings discussed in the sections dealing with the morphology of the different families (Chapter 3) have provided a tantalising incentive to explore this plant group still further. It seems that the more we look at the glossopterids, the more diverse and fascinating they become.

Table 1.3.1. Summary of the taxonomic revisions and name changes proposed during the course of this study.

| ACCEPTED NAME                        | ACCEPTED FAMILY    | PREVIOUS DESIGNATION                                                                                           | FAMILY EMEND. | GENUS NEW | GENUS EMEND. | SPECIES NEW | SPECIES EMEND. | NOM. CORR. |
|--------------------------------------|--------------------|----------------------------------------------------------------------------------------------------------------|---------------|-----------|--------------|-------------|----------------|------------|
| <i>Rigbya arberioides</i> †          | Rigbyaceae         | -                                                                                                              | +             | -         | +            | -           | +              | -          |
| <i>insertae sedis</i> §              | Rigbyaceae         | Arberiaceae; <i>Arberia allweyensis</i>                                                                        | +             | ?         | -            | ?           | -              | -          |
| <i>Arberia madagascariensis</i> †    | Arberiaceae        | -                                                                                                              | +             | -         | +            | -           | +              | -          |
| <i>Arberia hlobanensis</i> †         | Arberiaceae        | -                                                                                                              | +             | -         | +            | -           | +              | -          |
| <i>Vereenia leeuukuilensis</i> †     | Arberiaceae        | <i>Arberia leeuukuilensis</i> (Anderson & Anderson, 1985)                                                      | +             | +         | -            | -           | +              | comb. nov. |
| <i>Bifariola intermittens</i> †      | Dictyopteridiaceae | <i>Hirsutum intermittens</i> (Anderson & Anderson, 1985)                                                       | -             | +         | -            | -           | +              | comb. nov. |
| <i>Estcourtia conspicua</i> †        | Dictyopteridiaceae | <i>Scutum conspicuum</i> (Lacey <i>et al.</i> , 1975); <i>Estcourtia vandijkii</i> (Anderson & Anderson, 1985) | -             | -         | +            | -           | +              | +          |
| <i>Elatra leslii</i> †               | Dictyopteridiaceae | <i>Hirsutum leslii</i> (Smithies, in Anderson & Anderson, 1985)                                                | -             | -         | +            | -           | +              | comb. nov. |
| <i>Ottokaria transvaalensis</i> †    | Dictyopteridiaceae | -                                                                                                              | -             | -         | +            | -           | -              | -          |
| <i>Ottokaria hamanskraalensis</i> †  | Dictyopteridiaceae | -                                                                                                              | -             | -         | +            | -           | +              | -          |
| <i>Ottokaria buriadica</i> †         | Dictyopteridiaceae | -                                                                                                              | -             | -         | +            | -           | -              | -          |
| <i>Scutum leslii</i> †               | Dictyopteridiaceae | <i>Scutum leslium</i> (Plumstead, 1952); <i>Scutum rubidgeum</i> (Anderson & Anderson, 1985)                   | -             | -         | +            | -           | +              | +          |
| <i>Gladiopomum dutoitides</i> *      | Dictyopteridiaceae | <i>Hirsutum dutoitides</i> (Plumstead 1958)                                                                    | -             | +         | -            | -           | +              | -          |
| <i>Gladiopomum acadarensense</i> *   | Dictyopteridiaceae | <i>Hirsutum acadarensense</i> (Anderson & Anderson, 1985)                                                      | -             | +         | -            | -           | +              | -          |
| <i>Gladiopomum elongatum</i> *       | Dictyopteridiaceae | -                                                                                                              | -             | +         | -            | +           | -              | -          |
| <i>Plumsteadia lerouxii</i> †        | Dictyopteridiaceae | <i>Lanceolatus lerouxii</i> (Plumstead, 1952)                                                                  | -             | -         | +            | -           | +              | comb. nov. |
| <i>Plumsteadia gibbosa</i> †         | Dictyopteridiaceae | -                                                                                                              | -             | -         | +            | -           | +              | -          |
| <i>Gonophylloides strictum</i> †     | Dictyopteridiaceae | -                                                                                                              | -             | -         | +            | -           | +              | -          |
| <i>Gonophylloides waltonii</i> †     | Dictyopteridiaceae | -                                                                                                              | -             | -         | +            | -           | +              | -          |
| <i>Dictyopteridium natalensis</i> †  | Dictyopteridiaceae | <i>Plumsteadia natalensis</i> (Lacey <i>et al.</i> , 1975)                                                     | -             | -         | -            | -           | +              | comb. nov. |
| <i>Dictyopteridium flabellatum</i> † | Dictyopteridiaceae | -                                                                                                              | -             | -         | -            | -           | +              | -          |
| <i>Lidgettonia africana</i> †        | Lidgettoniaceae    | -                                                                                                              | -             | -         | +            | -           | -              | -          |
| <i>Lidgettonia lidgettonioides</i> † | Lidgettoniaceae    | -                                                                                                              | -             | -         | +            | -           | +              | -          |
| <i>Lidgettonia elegans</i> †         | Lidgettoniaceae    | -                                                                                                              | -             | -         | +            | -           | +              | -          |

\* change/emendation published; † change/emendation still to be published; § change/emendation tentatively proposed (awaiting additional information); + change effected/ recommended; - no change; ? additional information required.

## CHAPTER 2 MATERIALS AND METHODS

### 2.1 GENERAL METHODOLOGY

#### 2.1.1 FOSSIL SPECIMENS

Most of the specimens examined are housed in the palaeobotanical herbarium at the Bernard Price Institute, University of the Witwatersrand, Johannesburg, although collections were loaned from the Vaal Teknorama Museum in Vereeniging, the National Botanical Institute in Pretoria, the Council for Geosciences in Pretoria and the Natal Museum in Pietermaritzburg.

Specimen numbers are given the following prefixes according to the institution of origin:

**BP** – Bernard Price Institute for Palaeontological Research, University of the Witwatersrand (Johannesburg);

**GSP** (= CGS) – Council for Geosciences (previously called the Geological Survey of South Africa), Pretoria;

**NM** – Natal Museum (Pietermaritzburg);

**Pre** – South African National Institute for Biodiversity (Pretoria); (previously called the National Botanical Institute);

**VM** – Vaal Teknorama Museum (Vereeniging).

For a complete list of all specimens examined and described during the course of this study please refer to Appendix I.

#### 2.1.2 SPECIMEN COLLECTION AND PREPARATION

Fresh collections were made at Lawley, Rietspruit and Vereeniging. All three locations were open quarries, and material was collected directly from the rock faces (blocks were removed with chisels, hammers etc.) as well as from the scree slopes below. Crude splitting of large blocks was performed on site, and fossil-rich blocks of a transportable size were wrapped in packing material and taken back to the herbarium. These blocks were then carefully cleaved and broken into smaller slabs according to the fossils present. Each surface was



scanned under a dissecting microscope to ensure that less conspicuous fossils, such as insect wings and small fructifications, were not overlooked. Blocks were then accessioned to the BPI Palaeobotanical collection, each being assigned a catalogue number with the prefix 'BP/2'. Parts, counterparts and blocks originating from the same slab, were assigned the same catalogue number, and designated a letter of the alphabet, e.g. BP/2/1667a, BP/2/1667b, BP/2/1667c. A catalogue of the specimens was compiled, detailing the fossils present on each consecutively numbered block. In cases where fossils were present on both surfaces of a block, one of the surfaces was arbitrarily called the 'reverse' side, and designated the letter 'R' in the specimen number, e.g. BP/2/1667aR.

Most of the material derived from existing collections had already been prepared prior to accession. However, some specimens required further preparation to expose certain features that had been overlooked. Careful dissections were performed under a Zeiss Stemi SV6 microscope with fine chisels and needles and a toffee hammer, as per Leclercq's *dégagement* technique (Fairon-Demaret *et al.*, 1999). Serial photographs were taken to record each step in the process. Destruction of certain parts of the fossil to expose underlying features was unavoidable in some cases, but this was kept to an absolute minimum.

### **2.1.3 PHOTOGRAPHY**

Specimens were photographed under strong unilateral, low-angled light with a Sony Cybershot digital camera or with a Sony Soundvision digital camera attached to a Zeiss Stemi SV6 dissecting microscope. Images were scaled and adjusted with Adobe Photoshop 5LE software.

### **2.1.4 DATA COLLECTION AND ANALYSIS**

Measurements were taken using Zeiss Axiovision 2.5 image-analysis software. Images generated with the Sony Cybershot or Soundvision camera were archived and individually calibrated prior to analysis with the various tools available in the Zeiss Axiovision Measurement Module.

Microsoft Excel was used for data entry, basic statistical analyses, and graphical representations.

A summary of quantitative data for all taxa has been prepared in Appendix II. 'Total length' and 'total width' refer to the overall dimensions of the fructification excluding the pedicel. The pedicel is fairly long in some specimens, and its inclusion in the length measurement would have reduced the utility of this measurement when comparing taxa. It is also a delicate feature, often not preserved in its entirety. The 'approximate number of seed scars' was calculated, where possible, by counting each scar. However, in cases where the fructification was incomplete, or preservation of parts of the receptacle surface was poor, an average seed scar density was calculated, and the total number of scars on the fructification was extrapolated from the area measurement of the receptacle.

### **2.1.5 ILLUSTRATIONS AND FIGURES**

All maps and most line and stipple illustrations of fossil specimens were drawn in Adobe Illustrator 8. A Wacom Graphire stylus and tablet ensured a high degree of accuracy. Illustrations and reconstructions of *Scutum* were drawn in pen and ink on Bristol board, with the aid of a *camera lucida* microscope attachment. Reconstructions were usually based on the type specimen or on a particularly well-preserved specimen of each taxon. Please note: unless otherwise specified, all reconstructions are of the impression fossils themselves, not the original plant structures they represent.

Photographic plates were prepared from digital images, using Adobe Photoshop 5LE software. The scaling of photographs was standardised as much as possible, most fructifications being depicted at twice life-size. Scale bars rather than magnifications were used in each plate.

## 2.2 LOCALITY INFORMATION

### 2.2.1 KEY GEOLOGICAL FORMATIONS OF THE PERMIAN

As discussed earlier, the *Glossopteris* flora of Gondwana is almost entirely restricted to sediments of Permian age. In South Africa, the flora is particularly abundant in the Vryheid and Estcourt Formations of the northern and eastern parts of the Karoo Basin. The Pietermaritzburg Formation, which forms the base of the Ecca Group, has not yielded any noteworthy plant fossil material over the years, presumably because it was deposited in a deep-water setting. The predominantly sub-aqueous Volksrust Formation has similarly not provided us with an abundance of fossil material, although there is some debate as to whether the highly fossiliferous rocks exposed at the Cedara and Lawley localities belong within this formation.

|          |        | GROUP    |   | FORMATION        |
|----------|--------|----------|---|------------------|
| TRIASSIC | Lower  | Beaufort | L |                  |
|          | Upper  |          |   | Adelaide*        |
| PERMIAN  | Middle | Ecca     |   | Volksrust        |
|          | Lower  |          |   | Vryheid          |
|          |        |          |   | Pietermaritzburg |
|          |        | Dwyka    |   |                  |

\* Subgroup: includes Estcourt/Normandien Formations

**Text-figure 2.2.1** Permian lithostratigraphic units of the north-eastern and eastern Karoo Basin of South Africa (adapted from Keyser, 1997).

According to Johnson (1994), upper, middle and lower sub-divisions of the Ecca are not officially recognised, but have been used here in an informal context.

**2.2.1.1 Vryheid Formation** (Ryan, P.J.; proposal to South African Committee for Stratigraphy, 1974 - see SACS 1980, p.554)

*Ecca Group (middle), Karoo Supergroup (see text-figs 2.2.1 & 2.2.2)*

Described as a thick (up to 500 m) sequence of sandstone, shale<sup>1</sup> and subordinate coal seams (Johnson, 1994), the Vryheid Formation conformably overlies the Pietermaritzburg Formation, except in Gauteng and the northern Free State, where it lies unconformably on Dwyka or Precambrian rocks. It is conformably overlain by the Volksrust Formation. Veevers, Cole and Cowan (1994) characterised the deposits as a regressive-transgressive fluvio-deltaic wedge.

Johnson *et al.* (1997) recognised three basic units in the Vryheid Formation of the eastern Karoo Basin, viz. a lower deltaic interval, a fluvial interval, and an upper deltaic interval. The No. 4 and 5 coal seams present at the Rietspruit locality (listed below), lie in the upper deltaic interval, and there is evidence that, in places, the No. 5 seam was formed in back barrier settings.

The age of the Vryheid Formation deposits has been a source of controversy in the past. Kovács-Endrödy (1991) correlated the palaeofloras of the Hammanskraal and Vereeniging localities, in rocks of the Vryheid Formation, with the Upper Permian deposits of India. She based her work on the occurrence of similar *Glossopteris* leaf taxa, and on the presence of *Scutum*, in both regions. However, *Scutum* is not considered here to be a useful index genus, as it is a highly variable taxon with a fairly unspecialised morphology. The Vryheid Formation contains *Ottokaria*, *Arberia*, *Plumsteadella*, *Liknopetalon*, and *Botrychiopsis*, which are all typical components of Lower Permian assemblages elsewhere in Gondwana (Adendorff *et al.*, 2002). Palynological studies by (Millstead, 1994) support an Early Permian (Artinskian) age for the Vryheid Formation.

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<sup>1</sup> Lithological terminology used for shale types as per Potter *et al.* (1980).

**2.2.1.2 Volksrust Formation** (Johnson, M.R.; proposal to SACS 1979 - see SACS 1980, p.554)

*Ecca Group (upper), Karoo Supergroup (see text-figs 2.2.1 & 2.2.2)*

The Volksrust Formation is predominantly an argillaceous succession, consisting of black, silty shales. These are most often finely laminated, but structureless beds are also present, and are thought to be the result of intensive bioturbation (Johnson *et al.*, 1997). According to Johnson *et al.* (1997), the Volksrust Formation is widely considered to be an open freshwater 'shelf' sequence, although Taverner-Smith *et al.* (1988) concluded that parts of it may have been deposited in lacustrine to lagoonal and coastal embayment environments. These lacustrine deposits conformably overlie the Vryheid Formation, and are conformably overlain by the Beaufort Group. The underlying Vryheid Formation pinches out to the South-East, and the Volksrust Formation merges with the Pietermaritzburg Formation to form the undifferentiated Ecca Group in this area. It grades into the Tierberg Formation to the west, north of Bloemfontein (Johnson, 1994; Johnson *et al.*, 1997).

The Volksrust Formation is generally considered to be Middle Permian in age (Anderson & Anderson, 1985). There are no localities yielding glossopterid ovuliferous fructifications that can be assigned with confidence to this formation. Anderson & Anderson (1985) considered the deposits at the Lawley and Cedara localities to belong to the Volksrust Formation, since the palaeofloras had elements that were chronologically intermediate to those found in beds of the Vryheid and Estcourt Formations. Beds at Lawley are tentatively regarded here as a Volksrust Formation equivalents and the Cedara deposits are considered to belong to the Vryheid Formation (see discussion, section 9.3.2.1, p. 358).

### **2.2.1.3 Estcourt Formation** (Linström, 1973; SACS 1980, p. 552)

*Adelaide Subgroup, Beaufort Group (Lower), Karoo Supergroup (see text-figs 2.2.1 & 2.2.2)*

The Estcourt Formation is described as 'about 400 m of carbonaceous shale, subordinate sandstone (often coarse-grained but occasionally pebbly) and a few thin coal seams' in the SACS Lexicon of South African Stratigraphy (Johnson, 1994).

The Estcourt Formation is only recognised in the north-eastern and eastern Karoo Basin, where it forms the lower part of the Beaufort Group (SACS 1980). It conformably overlies the Volksrust Formation, and is conformably overlain by the Tarkastad Subgroup. It is correlated with the Emakwezini Formation in north-eastern Kwa-Zulu Natal, and grades northwards into the Normandien Formation of Groenewald (1984, 1989).

As discussed by Botha and Linström (1978), the Eccu Group was deposited in a large, possibly marine body of water, whereas the Beaufort Group is a fluvatile, continental deposit. The change in depositional environments was not immediate in all parts of the basin, which resulted in a degree of heterogeneity in the lower parts of the Beaufort sequence. According to Johnson *et al.* (1997), typical fluvial characters are uncommon in the Estcourt Formation, and the lithology points rather to deposition under lacustrine and deltaic conditions. The dark, carbonaceous, plant-fossil bearing shales may have accumulated in coastal or deltaic marshes, swamps and interdistributary bays.

Since the Estcourt Formation has features in common with both the Eccu and Beaufort Groups (Botha and Linström, 1978), this has led to a degree of confusion as to where in the stratigraphy these deposits belong. Botha and Linström (1978) were indecisive as to whether the Estcourt Formation should be grouped with the Eccu or the Beaufort Group, or should remain a separate stratigraphic unit. Johnson *et al.* (1997) mentioned that the Estcourt Formation

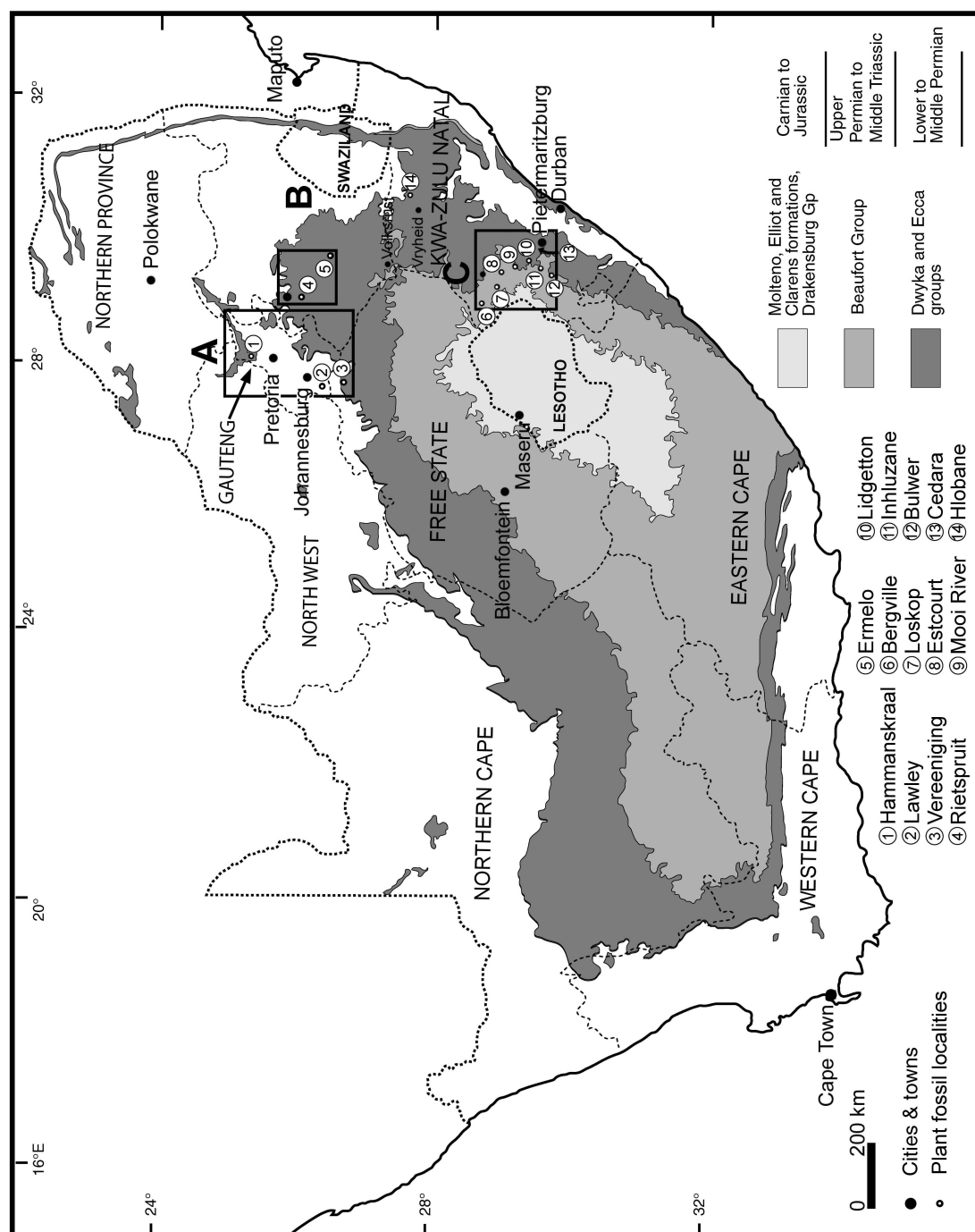
would probably be included in the Normandien Formation in the future. Here it is regarded as a separate formation, within the lower Beaufort Group.

Virtually all we know about Upper Permian plants of South Africa has resulted from studies of material from the Estcourt Formation in the eastern Karoo Basin (KwaZulu-Natal Province). This material was studied in some detail by W.S. Lacey, D.E. van Dijk and K.D. Gordon-Gray (eg. Lacey, 1978; Lacey *et al.* 1974, 1975), A. Benecke (1976) and later by Anderson & Anderson (1985).

The floras of the eastern Karoo Basin probably fall mostly within the *Dicynodon* zone as circumscribed by Rubidge (1995) on the basis of tetrapod fossil distributions, but attempts to make biostratigraphic comparisons and inferences has been hindered by uncertainties regarding the stratigraphic relationships between individual sites (Anderson & Anderson, 1985). The area is heavily intruded by dolerite dikes, modern vegetation is dense, and exposures are not laterally extensive.

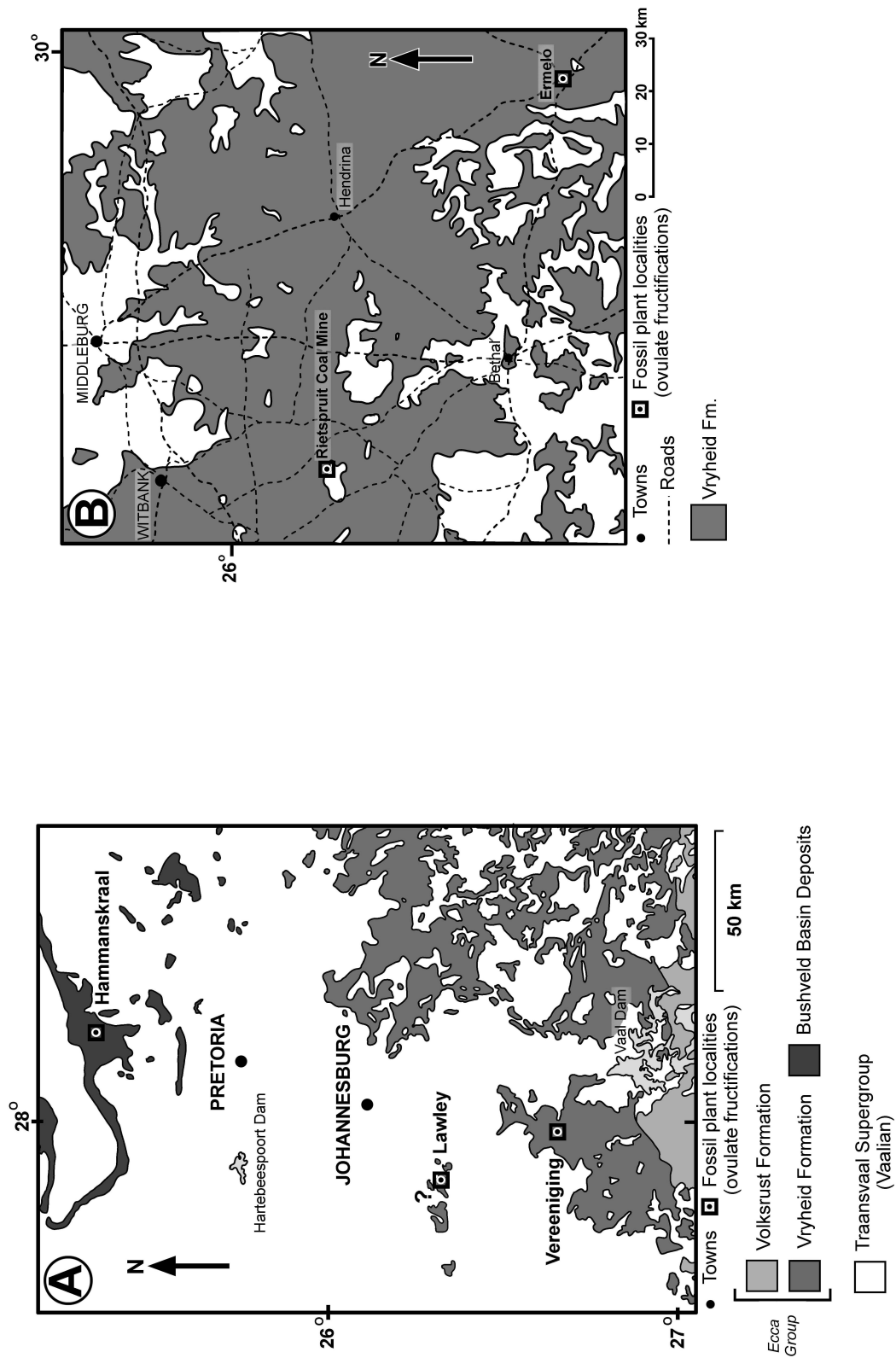
Lacey *et al.* (1975) based their decision that the Mooi River (Estcourt Formation) deposits were Upper Permian, on the basis of *Glossopteris* leaf taxonomy. As discussed above, this was probably not the most reliable means of assigning a date to the sediments. However, the presence of *Dictyopteridium*, *Rigbya*, *Lidgettonia* and *Eretmonia* fructifications and the data supplied by associated insect material (Riek, 1973, 1976), provide more convincing evidence of a Late Permian age for the Estcourt Formation. Anderson & Anderson (1997) supported a Late Permian age for the Estcourt Formation on the basis of the palynoflora (Anderson, 1977), the megaflora (Anderson & Anderson, 1985) and the tetrapods (Rubidge, 1995) that have been found in these deposits.

## 2.2.2 LOCALITIES

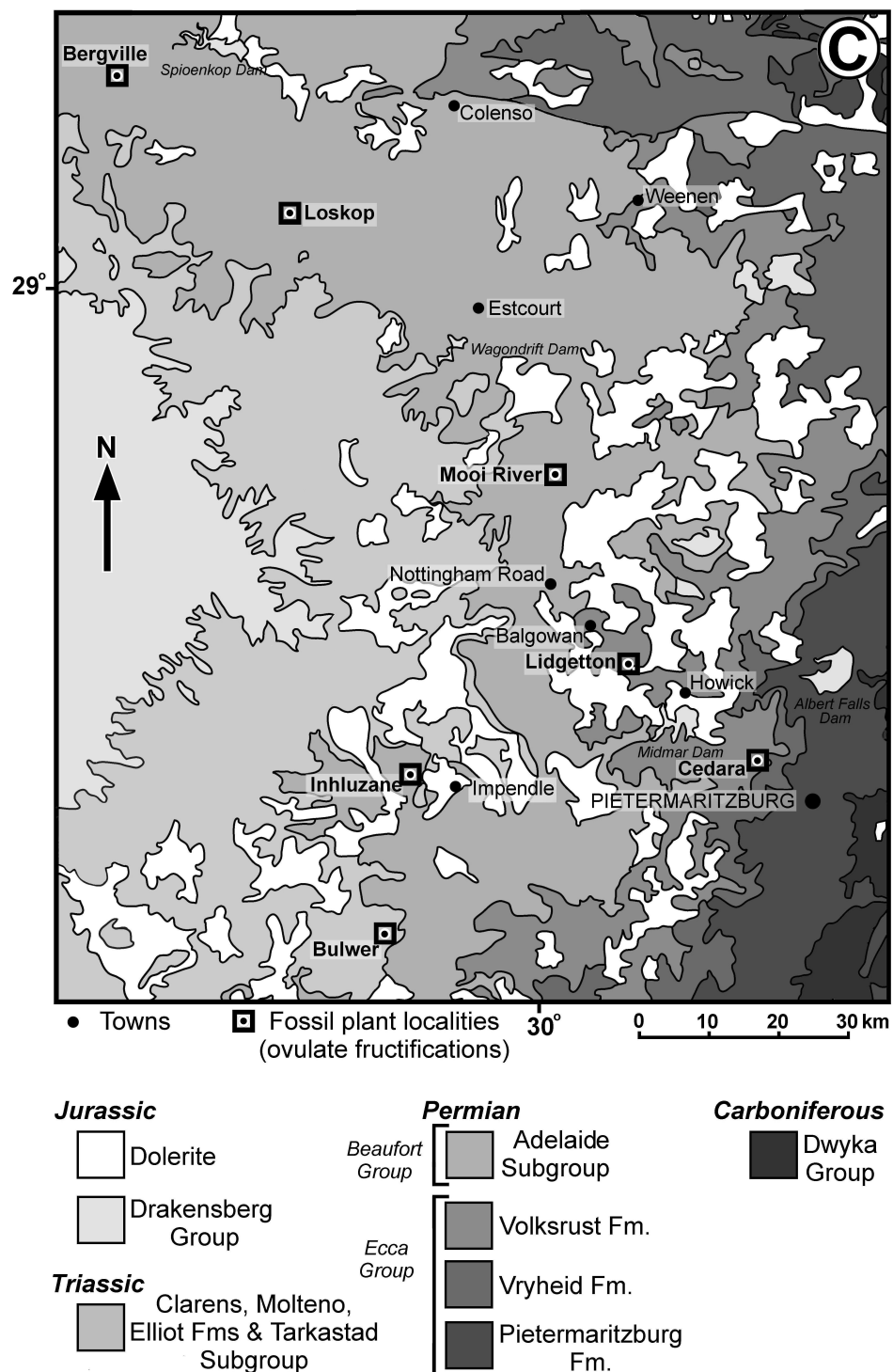


Text-figure 2.2.2. A map of South Africa illustrating the positions of localities where glossopterid fructifications have been recorded (adapted from Keyser, 1997).





Text-figure 2.2.3. Geological maps of (a) the Johannesburg-Pretoria area (inset A in fig.2.2.2), and (b) central Mpumalanga (inset B in fig. 2.2.2), illustrating the positions of key plant fossil localities.



**Text-figure 2.2.4.** Geological map of western Natal, illustrating the positions of important fossil localities in the region (inset C in fig. 2.2.2).

#### 2.2.2.1 Bergville

**Age** Upper Permian

**Lithostratigraphy** Lower Beaufort Group; Estcourt Formation (Anderson & Anderson, 1985; Keyser, 1997).

**Lithology** Olive grey, irregularly laminated mudstone (Anderson & Anderson, 1985).

**Location** Anderson & Anderson (1985) did not give details of the location of the fossil site. Bergville lies in the north-eastern Kwa-Zulu Natal [see text-figs 2.2.2, 2.2.4].

**Fossil material** All impression fossils: two sphenophyte genera (*Raniganjia*, *Phyllothea*), a fern (*Sphenopteris*), several species of *Glossopteris*, *Lidgettonia lidgettonioides* and a conifer (*Pagiophyllum vandijkii*) (Anderson & Anderson, 1985).

#### 2.2.2.2 Bulwer

**Age** Upper Permian

**Lithostratigraphy** Lower Beaufort Group; Estcourt Formation (Anderson & Anderson, 1985; Keyser, 1997).

**Lithology** A quarry exposure representing a generally upward-coarsening sequence of mudrocks and siltstones. A highly fossiliferous layer described by van Dijk (2000) lies at the interface between the predominantly mudrock layers and upper silty layers, roughly eye- to shoulder-level in the quarry. The fossiliferous rocks are greyish-orange to light olive grey, hard, well-laminated mudshales (Anderson & Anderson, 1985). The quarry was mined for its siltstone, which was used in road construction. Quarrying activity ceased in 2001.

**Location** A stone quarry on the outskirts of the town Bulwer, in western Kwa-Zulu Natal. The quarry is to the right (western side) of the main road (R617) into Bulwer, from the N3 National Road [see text-figs 2.2.2, 2.2.4].

**Fossil material** High quality impression fossils, stained with brown oxides. A fairly diverse flora is present, including the sphenophyte taxa *Sphenophyllum*, *Phyllothea* and *Raniganjia*, several species of *Glossopteris* leaf, *Eretmonia*

and two ovuliferous glossopterid fructification genera (*Rigbya*, *Lidgettonia* spp.). This site is also an important Upper Permian fossil insect locality (see van Dijk & Geertsema, 1999; Geertsema *et al.*, 2002).

### **2.2.2.3 Cedara**

**Age** Lower Permian (Artinskian) (?)

**Lithostratigraphy** Ecca Group, Vryheid Formation (?)

Keyser (1997) mapped the rocks in this area as Volksrust Formation, a view supported by Anderson & Anderson (1985). However, according to Linström (1987), there is a gradational change from strata of the Vryheid Formation to those of the overlying Volksrust Formation in the area. The uppermost sandstone units of the Vryheid Formation are intercalated with clayey layers, and it is difficult to define a precise boundary between these units. The boundary is generally placed 'above the last sandstone layer that underlies a very thick shale layer' (Linström, 1987). Since strata in the Cedara area are poorly and discontinuously exposed, the precise stratigraphic position of the Maidstone farm fossiliferous beds is uncertain. Based purely on the palaeofloral similarities with other sites, the strata may well belong to the Vryheid Formation.

**Lithology** Irregularly laminated, pinkish to yellowish grey mudshales; impression fossils commonly coloured red by iron oxides.

**Location** Cedara is situated approximately 10 km north of Pietermaritzburg in the midlands of the KwaZulu-Natal province. The material was collected on the farm "Maidstone", which lies approximately 3 km west of Cedara [see text-figs 2.2.2, 2.2.4].

**Fossil material** In addition to over 20 *Gladiopomum* fructifications, the samples housed at the BPI include several species of glossopterid leaves (including gangamopteroid forms), *Palaeovittaria*, sphenophytes (*Raniganjia kilburnensis* Anderson & Anderson 1985), lycophyte stems, scale leaves and a diversity of winged seeds.

#### 2.2.2.4 Ermelo

**Age** Lower Permian

**Lithostratigraphy** Eccca Group, Vryheid Formation (Anderson & Anderson, 1985).

**Lithology** Hard, buff to medium grey siltstone with orangey, light brown and pale off-white oxide staining; bedding planes fairly irregular, and of variable thickness, poorly fissile.

**Location** Anderson & Anderson (1985) did not provide information about the exact location of this fossil site. The town of Ermelo is situated in the Mpumalanga Province [see text-figs 2.2.2, 2.2.3(b)].

**Fossil material** All fossils are impressions. H.M. Anderson made a single collection from this site in 1974, and reported the occurrence of several species of *Glossopteris* leaf as well as *Noeggerathiopsis*, the glossopterid fructification *Scutum*, the lycopod *Cyclodendron leslii*, and various seeds and scale leaves (Anderson & Anderson, 1985).

#### 2.2.2.5 Estcourt (Rondedraai)

**Age** Upper Permian

**Lithostratigraphy** Lower Beaufort Group; Estcourt Formation

**Lithology** light olive grey, well laminated shale.

**Location** A roadcutting a short distance East of Estcourt, near the entrance to the farm Rondedraai (van Dijk, 2000) [see text-figs 2.2.2, 2.2.4].

**Fossil material** All impression fossils, including *Lidgettonia inhluzanensis*, *Eretmonia*, several species of *Glossopteris* leaf, various seeds (see Anderson & Anderson, 1985).

#### 2.2.2.6 Hammanskraal

**Age** Lower Permian (Artinskian)

**Lithostratigraphy** Eccca Group, Hammanskraal Formation (Vryheid Formation equivalent)

The Hammanskraal refractory clay quarries are situated in the Springbok flats, on the southern edge of the Bushveld Basin, also known as the Springbok Flats Basin (Johnson *et al.*, 1996), which is an outlier of the main Karoo basin.

Keyser (1997) mapped these sediments as undifferentiated Eccca Group, but Bennetts (1965) regarded them as lateral equivalents of the middle part of the Eccca Group (Vryheid Formation) in the Karoo Basin. Johnson *et al.* (1996) referred to the deposits as the Hammanskraal Formation, and also equated them with the Vryheid Formation of the main Karoo Basin.

**Lithology** Continuous sequence of fine-grained mudstone; light brown shales with little carbonaceous material graded through to dark grey shales containing high levels of carbonaceous matter. Non-plastic aluminium silicate clay with some impurities; coarsely bedded, poorly fissile with irregular bedding planes, although may be finely laminated; locally referred to as 'flint-clay', because of its dense texture and conchoidal, flint-like fracture (Bennetts, 1965).

**Location** The quarries lie in the vicinity of Hammanskraal, 33 km north of Pretoria and 6.8 km SSE of Hammanskraal station, on the farm Haakdoornfontein 119 JR (Smithies, 1978) in the Mpumalanga Province of South Africa. According to Smithies (1978), who collected most of the specimens from this locality, the majority of the fossil material came from a quarry previously worked by Cullinan Refractories Ltd., situated at 25°27'54" E; 28°17'47"S [see text-figs 2.2.2, 2.2.3 (a)].

**Fossil material** The fossils are predominantly impressions, although there are some coalified compressions. Cuticle is rarely present. A typical Early Permian Gondwanan assemblage, dominated by glossopterid leaves, roots (*Vertebraria*) and fructifications (*Arberia madagascariensis*, *Hirsutum leslii*, *Ottokaria hammanskraalensis*), ferns (*Sphenopteris*, *Asterotheca*), lycophytes (*Cyclodendron*), sphenophytes (*Annularia*, *Sphenophyllum*), and various platyspermic seeds (Smithies, 1978; Anderson and Anderson, 1985).

#### 2.2.2.7 Hlobane

**Age** Lower Permian (Artinskian)

**Lithostratigraphy** Ecca Group, Vryheid Formation (Anderson & Anderson, 1985; Keyser, 1997)

**Lithology** Soft, poorly laminated, light brown to pinkish buff mudstone and mudshale; some slabs dark grey, and rich in carbonaceous material.

**Location** The Hlobane Colliery is situated near the town of Vryheid, in northern KwaZulu-Natal [see text-fig. 2.2.2]. The material was collected from an opencast mine.

**Fossil material** The palaeoflora at this site is dominated by several species of *Glossopteris* (including gangamopteroid forms). Specimens of *Palaeovittaria*, conifer stems and cones (*Podozamites hlobanensis* of Anderson & Anderson, 1985), several types of winged seed, scale leaves, lycophyte axes and sphenophyte stems are also present. A single *Gladiopomum* specimen was recovered from this locality. The only fructification previously documented from this site was a single specimen of *Arberia hlobanensis*.

#### 2.2.2.8 Inhluzane

**Age** Upper Permian

**Lithostratigraphy** Lower Beaufort Group; Estcourt Formation.

**Lithology** Greyish-orange to light olive-grey, well-laminated mudshale.

**Location** At the foot of Mpendle Mountain, near Impendle in the Kwa-Zulu Natal Midlands [see text-figs 2.2.2, 2.2.4; Anderson & Anderson, 1985, p. 35, fig. 6 for photograph].

**Fossil material** The palaeoflora at Inhluzane includes the sphenophyte genera *Raniganjia*, *Phyllothea* and *Schizoneura*, several species of *Glossopteris* leaves, seeds and scale leaves, *Eretmonia* and the ovuliferous glossopterid fructification *Lidgettonia* (Anderson & Anderson, 1985). Anderson & Anderson (1985) also listed the occurrence of 100 specimens of an 'Ottokariaceae fruit'. Here they have been placed in *Plumsteadia gibbosa*.

#### 2.2.2.9 Lawley

**Age** Middle Permian (?)

**Lithostratigraphy** Ecca Group; Volksrust Formation equivalent (?)

The deposits represent an outlier of the main Karoo Basin and are difficult to place lithostratigraphically. The clay deposits unconformably overlie dolomites and cherts of the Proterozoic Chuniespoort Group (Bredell, 1979). Bredell (1974; 1979) argued that Karoo sediments in the Witwatersrand area are represented by outliers of the Vryheid and Dwyka formations and on the basis of borehole studies proposed that the principal refractory clay deposits are stratigraphically positioned at or near the base of the Vryheid Formation. Regional mapping supports the occurrence of Vryheid Formation exposures near Lawley (Keyser, 1997). However, Anderson and Anderson (1985) and Rayner and Coventry (1985) considered the Lawley deposits to be equivalent to the younger Volksrust or Estcourt Formations in the main Karoo Basin (see text-fig. 2.2.1) based on the presence of various plant taxa (especially *Eretmonia* and *Lidgettonia*) that are characteristic of the Middle to Upper Permian elsewhere in South Africa (Lacey *et al.*, 1975).

**Lithology** Kaolinite-rich clayshales, claystones and siltstones with minor sandstone and conglomerate beds towards the top of the sequence; plants are typically preserved as impressions in pale buff to whitish, soft, finely laminated, fissile claystones.

**Location** Fossils are derived from a refractory clay quarry 30 km southwest of Johannesburg, near the town of Lawley (27° 50' E, 26° 20' S) [see text-figs 2.2.2, 2.2.3(a)].

**Fossil material** The Lawley deposits are host to a typical Permian Gondwanan flora dominated by *Glossopteris* leaves, associated with abundant microsporangiate organs (*Eretmonia*) but few ovuliferous fructifications (*Lidgettonia*). *Noeggerathiopsis* and *Vertebraria* are common, together with sparse examples of sphenophytes, ferns (*Sphenopteris* spp.; *Liknometalon gracilis*), mosses, herbaceous lycophytes, seeds, and possible *Walkomiella* (conifer) fragments. What is not typical about the flora is that there is a mix of what are generally considered to be Upper Permian and Lower Permian elements, which has created confusion as to the age of this outlier deposit.



#### **2.2.2.10 Lidgetton**

**Age** Upper Permian

**Lithostratigraphy** Lower Beaufort Group; Estcourt Formation

**Lithology** Laminated, carbonaceous shales.

**Location** The site is on a farm, Bellavista, near the village of Lidgetton, in the Kwa-Zulu Natal Midlands (approximately half-way between Pietermaritzburg and Mooi River) [see text-figs 2.2.2, 2.2.4]. This fossil site was in a streambed, but has been flooded following the construction of a farm dam (van Dijk, 1981, 2000).

**Fossil material** Fossils are impressions and compressions; included in the palaeoflora, as described by Lacey *et al.* (1975) and Anderson & Anderson (1985), are the moss, *Butholezia mooiensis*, a sphenophyte *Phyllothea*, fragments of *Sphenopteris*, several species of *Glossopteris* leaf, *Eretmonia*, *Vertebraria*, seeds and pyritised wood fragments. In addition, this is the type locality for the ovuliferous glossopterid fructification *Lidgettonia* (Thomas, 1958). Several important insect specimens have been found at this site (see van Dijk & Geertsema, 1999).

#### **2.2.2.11 Loskop**

**Age** Upper Permian

**Lithostratigraphy** Lower Beaufort Group; Estcourt Formation

**Lithology** Light olive grey, laminated mudrock with orangey brown to light brown oxide staining of impressions.

**Location** An exposure along the Little Tugela River, 5 km beyond Loskop railway siding on the south side of the provincial road R35 between Estcourt and Bergville, just above the Courton bridge and the Soolaer monument. According to Beneke (1976), the site was a quarry used for road-building material. The fossiliferous bed was a metre thick and was exposed for 200 m, continuing into the hillside. The fossil-bearing stratum lay immediately beneath a thick sandstone layer. Loskop is a village to the north-west of Estcourt, in the KwaZulu-Natal Midlands [see text-figs 2.2.2, 2.2.4].

**Fossil material** The Loskop locality has yielded the sphenophyte taxa *Sphenophyllum* and *Phyllothea*, the fern *Sphenopteris*, *Plumsteadia gibbosa* (here referred to *Dictyopteridium gibbosa*), a single specimen of *Rigbya arberioides*, *Lidgettonia*, several species of *Glossopteris* leaf, *Noeggerathiopsis*, diverse seeds, wood and *Vertebraria* (Benecke, 1976; Anderson & Anderson, 1985).

#### **2.2.2.12 Mooi River (National Road)**

**Age** Upper Permian

**Lithostratigraphy** Lower Beaufort Group; Estcourt Formation

**Lithology** Well bedded, thinly laminated, fine-grained shale; off-white to buff and light reddish brown to light olive grey (Lacey *et al.*, 1975; Anderson & Anderson, 1985).

**Location** The site was found 80 km north-west of Pietermaritzburg, on the first road cutting a few hundred metres beyond the bridge over Grantleigh Spruit (north of Mooi River) along the road-works for the National Road in 1971 & 1972, (van Dijk, 2000); the site was destroyed during construction of the road (Lacey *et al.* 1975) [see text-figs 2.2.2, 2.2.4].

**Fossil material** Impression fossils are of good quality, with a high level of detail preserved; some carbonaceous compressions, fragments of cuticle (Lacey *et al.* 1975). Diverse plant fossils were recovered from the site, including a bryophyte (*Buthelezia mooiensis*), the sphenophyte genera *Phyllothea*, *Raniganjia* and *Sphenophyllum*, fern material (*Sphenopteris*), *Noeggerathiopsis*, several species of *Glossopteris* leaf, *Eretmonia*, several ovuliferous glossopterid fructifications (*Rigbya arberioides*, *Lidgettonia* spp., *Estcourtia vandijkii*, *Dictyopteridium* spp.), seeds and scale leaves (Lacey *et al.*, 1975; Anderson & Anderson, 1985). A large collection of insect fossils has been made from the site (see Riek, 1973, 1976).

#### **2.2.2.13 Rietspruit**

**Age** Lower Permian (Artinskian)

**Lithostratigraphy** Eccca Group, Vryheid Formation

The Witbank coalfields are a major source of coal in South Africa, consequently the geology of the deposits has been extensively documented. The strata are assigned to the Vryheid Formation, Eccca Group (Cairncross & Cadle, 1987; Falcon, 1986; Plumstead, 1957).

**Lithology** Hard, irregularly laminated, fine-grained, black to dark grey mudstones positioned between the No. 4-Lower and No. 4-Upper coal seams.

**Location** Material was collected from opencast pits at the Rietspruit Colliery, near Witbank (just over 100 km east of Johannesburg) [see text-figs 2.2.2, 2.2.3(b)].

**Fossil material** Glossopterid leaves are dominant at the site but the presently undescribed fossil flora also contains numerous lycophyte stems, sphenophytes, scale leaves and ferns.

#### **2.2.2.14 Vereeniging**

**Age** Lower Permian (Artinskian)

**Lithostratigraphy** Eccca Group, Vryheid Formation

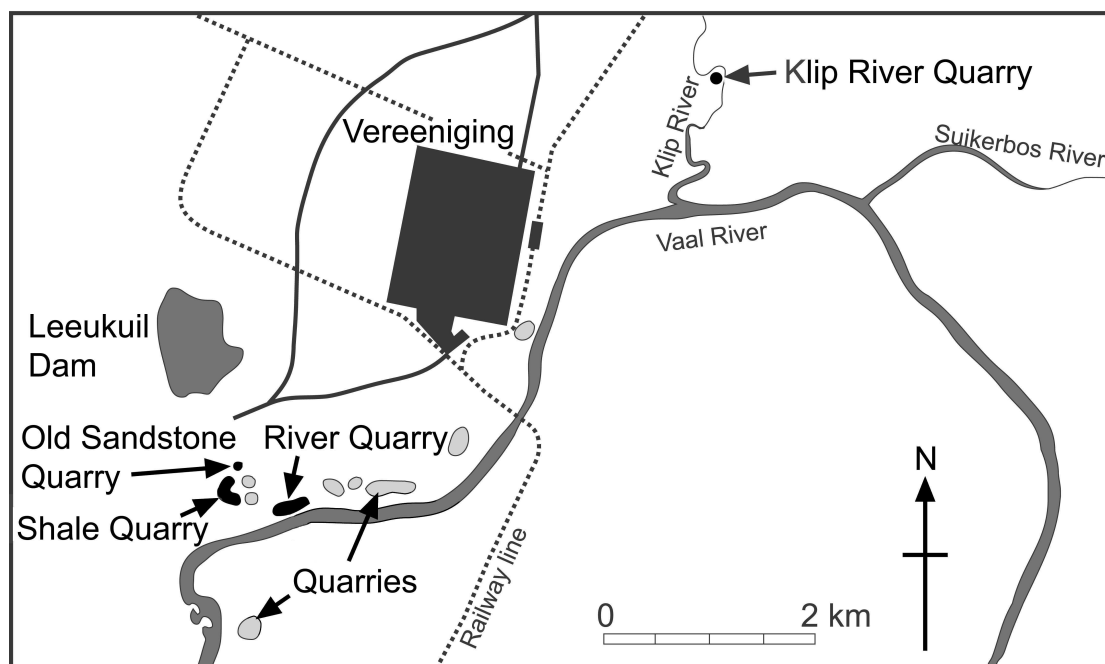
Plumstead (1956a) attempted to use the palaeofloral composition of the Vereeniging deposits to determine their age. However, since her observations were based mainly on the presence of loosely defined glossopterid leaf taxa, these have not contributed towards useful stratigraphic correlations with other basins. Le Roux & Anderson (1977) and Anderson & Anderson (1985) placed the fossiliferous sediments at Vereeniging in the Vryheid Formation, Eccca Group (see Figure 2). They based their conclusion principally on lithological correlation with strata in nearby coalmines. Their correlation was supported by Keyser's (1997) mapped distribution of the Vryheid Formation. Studies of spore-pollen assemblages from Vereeniging have supported an Artinskian age for the Vryheid Formation based on correlations with Australian palynozones (Millstead, 1994).

**Lithology** Hard, compact, fine-grained, carbonaceous mudshales to red ferruginous shales and buff-coloured siltstones; majority of well-preserved fossils found in beige or buff-coloured, thinly laminated mudshale (Le Roux & Anderson, 1977; Anderson & Anderson, 1985).

**Location** The town of Vereeniging lies about 60 km south of Johannesburg, Gauteng Province [see text-figs 2.2.2, 2.2.3(a), 2.2.5]. The fossils were collected from several quarries on the northern bank of the Vaal River, 6 km south of the town. They were opened by Vereeniging Refractories (ex. Vereeniging Brick and Tile Co.), and were situated on a portion of the original farm Leeukuil No. 81 (Le Roux & Anderson, 1977). The property was bought by the Rand Water Board in 1963 (Le Roux & Anderson, 1977), and the quarries are now largely infilled, vegetated or flooded.

Le Roux & Anderson (1977) gave the following co-ordinates for the Leeukuil quarries:

- i) Klip River Quarry                    27° 57' 32" E, 26° 39' 26" S;
- ii) Old Sandstone Quarry            27° 53' 56" E, 26° 42' 08" S;
- iii) Shale Quarry                    27° 52' 56" E, 26° 42' 12" S;
- iv) River Quarry                    29° 54' 20" E, 26° 42' 18" S.



**Text-figure 2.2.5.** Location of the Leeukuil and other quarries relative to the town of Vereeniging (adapted from Adendorff *et al.*, 2002).

**Fossil material**      The palaeoflora preserved at Vereeniging is relatively diverse, and has been well-documented (e.g., Leslie, 1904; Le Roux, 1976; Le Roux & Anderson, 1977; Anderson & Anderson, 1985). The flora is dominated by glossopterid leaves, including gangamopteroid forms. Also present are *Palaeovittaria*, *Noeggerathiopsis*, numerous lycophytes (including *Cyclodendron leslii*), ferns (*Asterotheca leeukuilensis*, *Sphenopteris lobifolia*, *Liknopetalon enigmata*), conifers (*Walkomiella transvaalensis*), ginkgoalean leaves (*Ginkgophyllum* spp.), sphenophyte stems, *Botrychiopsis*, numerous scale leaves and several winged seeds. Vereeniging has yielded the most diverse array of capitate glossopterid ovuliferous fructifications in South Africa, many of them preserved in attachment to subtending glossopterid leaves (Anderson & Anderson, 1985; Plumstead, 1952; 1956a; 1958a). The majority of fossil specimens from Vereeniging were collected by Mr. S.F. Le Roux in collaboration with Dr E.P. Plumstead in the 1940's and 1950's.

## **CHAPTER 3 MORPHOLOGY OF OVULIFEROUS GLOSSOPTERID FRUCTIFICATIONS**

This chapter deals with perhaps the most crucial aspect of the entire revision – the structure and morphological features of the glossopterid fructifications. The morphological characterisation of these polysperms has affected every aspect of this study, not only the basic taxonomy at species and generic level, but also considerations regarding the suprageneric affiliations of the glossopterids. It has also raised some interesting questions regarding homologies between polysperms belonging to the different families recognised here, as well as the phylogenetics of the group.

Section 3.1 outlines the model of impression/compression fossil formation and structure as it is understood here, and how this has facilitated a revision of the morphological interpretation of the various families of glossopterid fertile structures. Previous theories regarding the interpretation of members of these families are discussed, and new ones proposed, along with diagrams explaining the terminology used throughout this document.

Sections 3.2 and 3.3 provide detailed accounts of the taxa that have been most affected by this approach to the interpretation of impression fossils.

### **3.1 *STRUCTURAL INTERPRETATIONS AND TERMINOLOGY***

#### **3.1.1 THE NATURE AND INTERPRETATION OF IMPRESSION AND COMPRESSION FOSSILS**

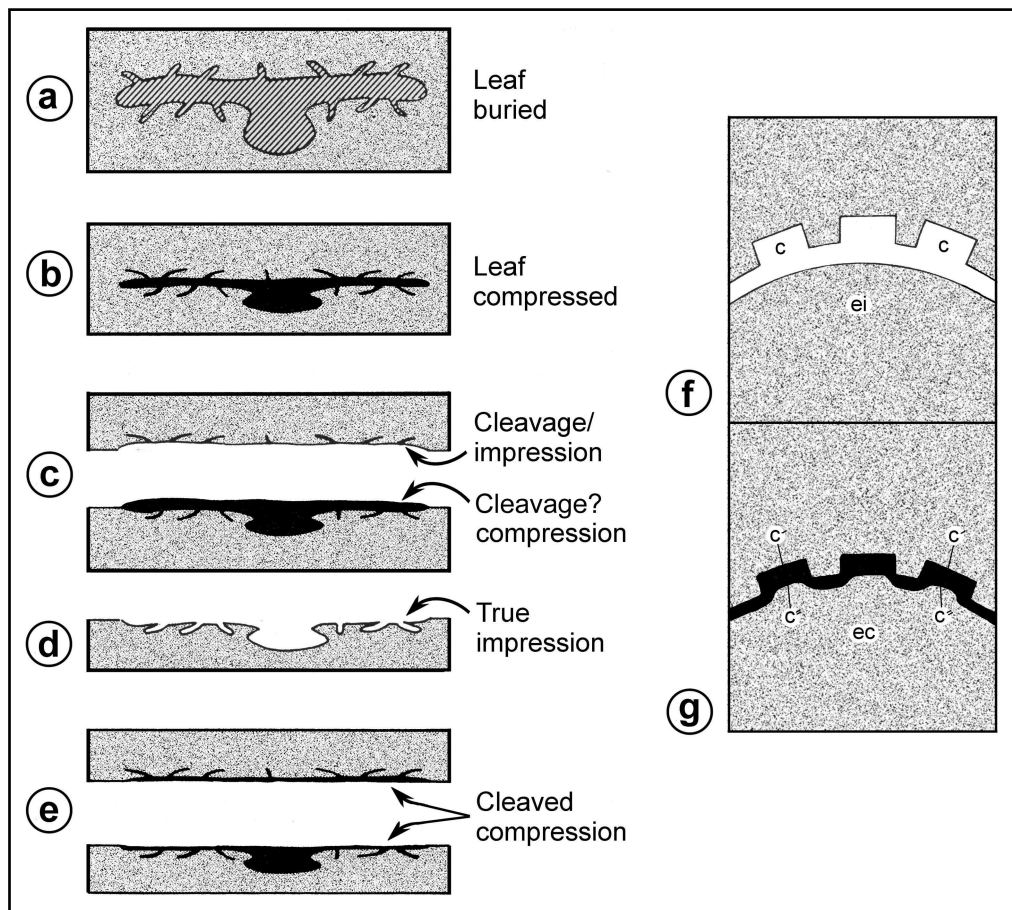
Many of the conflicting viewpoints about the morphology of glossopterid fructifications have arisen from ambiguities regarding fossil preservation. The wide variety of preservation types encountered, in addition to the presence of artefacts such as thick mineralised crusts and distortion, can result in similar plant structures having a very different appearance in the fossil form. The South African ovuliferous glossopterid fructifications are all compression or impression fossils. A clear understanding of the nature of these fossil types has proven to

be critically important during the course of this study, and has helped to resolve some significant taxonomic quandaries.

Although the processes involved in the formation of compressions and impressions are not fully understood, both mechanical and chemical factors appear to be involved. There was probably a complex chemical interaction between sediment and altering organic material, as evidenced by the sometimes very intricate deposition of oxides in association with the fossil, particularly along the more robust parts such as leaf venation.

In Schopf's (1975) definitive paper on 'Modes of fossil preservation', he explained how compressions are formed through the alteration of buried plant material in anoxic environments, under pressure and coincident with diagenesis of the surrounding matrix, resulting in the formation of a coalified compression of the original plant matter. When this coalified material (the 'anthracolemma' or 'phytolemma') is removed by weathering or preparation of the fossil, all that remains is a vertically compressed mould of the original plant - an impression fossil. An impression fossil is therefore not simply an imprint on the surface of the rock, such as would be achieved by briefly pressing a leaf into soft mud, but instead represents a detailed three-dimensional mould of the original plant.

Chaloner (1999) gave an excellent overview of the formation of compression and impression fossils, and how they are variously exposed during cleavage of the matrix (see text-fig. 3.1.1). He also made an important observation that the plant material undergoes a higher degree of compression than the surrounding matrix (text-fig. 3.1.1 f, g). This can lead to the formation of what will be referred to here as 'secondary imprints', where features in strong relief on one surface of the plant organ (e.g. seed scars) form vague impressions on the opposing surface.



**Text-figure 3.1.1.** Formation of impression and impression fossils, beginning with the burial of a leaf with hairs and a midrib on the lower surface (a). The leaf undergoes collapse and compression, and the original plant material becomes coalified (b). Figures (c) & (d) represent scenarios resulting from cleavage along the upper surface of the leaf, resulting in a cleavage impression and a compression on the part and counterpart respectively. The cleavage compression differs from the true impression in (d), in that the face was exposed by a fracture rather than removal of the inorganic material. In (e) the plane of fracture has passed through the coaly matter, resulting in complementary cleavage compressions. Figures (f) and (g) represent a cortical cylinder of a lycopod buried in sediment (f), and then compressed and coalified (g). As the plant material compacts, the originally smooth inner surface of the endocortical cast adopts a similar topography to that of the outer surface of the stem [ei - endocortical infill; ec - endocortical cast; c - leaf base cushion; c' - outer surface of compressed leaf base cushion; c'' - bulge on matrix surface of endocortical cast corresponding to the cushion on the original outer surface] (Adapted from Chaloner, 1999; Ch. 8, p. 37, fig. 8.1).

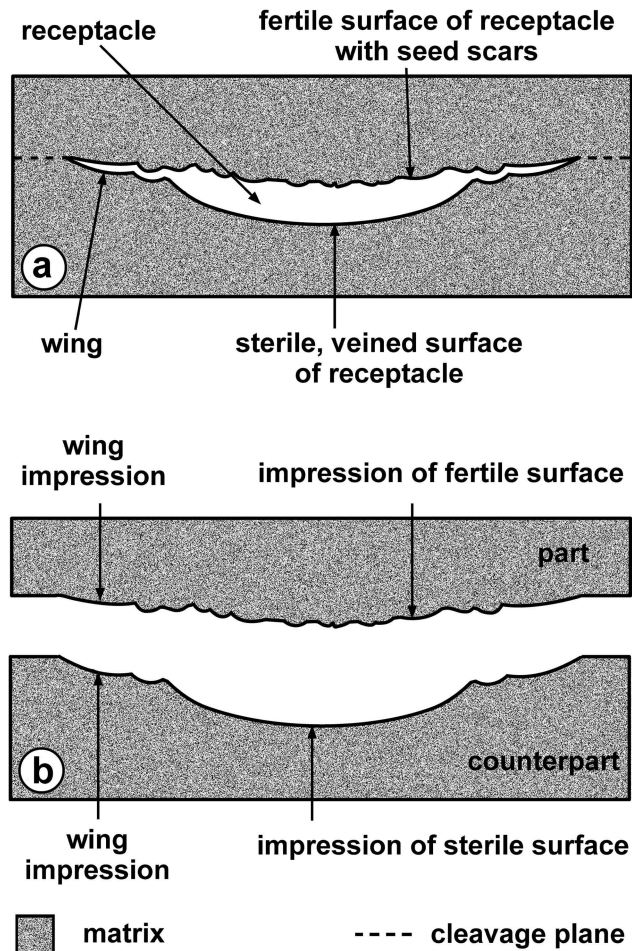
This effect is pronounced in some ovuliferous fructifications and can cause confusion as to which side is the seed-bearing, fertile surface. It has probably also contributed to ideas of radial symmetry in some fructifications, e.g. *Dictyopteridium* and *Plumsteadia*. As illustrated by Rigby (1978; fig. 4 A & B, p. 8), this effect can be particularly apparent when a fructification is closely positioned relative to its subtending leaf. In *Dictyopteridium* and '*Lanceolatus*' (the latter here transferred to *Plumsteadia lerouxii*), the impression of the



subtending leaf has in many cases been observed to form a raised boss beneath the impression of the fertile surface of the fructification. This boss has been interpreted in the past as a sterile bract lying between the fructification and the leaf or as evidence of another fructification lying beneath the leaf (as discussed by Rigby, 1978). The raised boss in leaf impressions of '*Lanceolatus*' fertiligers (here referred to *Plumsteadia lerouxii*) led Plumstead (1952) to surmise that the fructification had been borne within the leaf tissue. It should be noted here, that the secondary impressions are not as clear and well defined as the original or true impressions of the fertile surface, and in most cases details of venation of the sterile surface are still apparent.

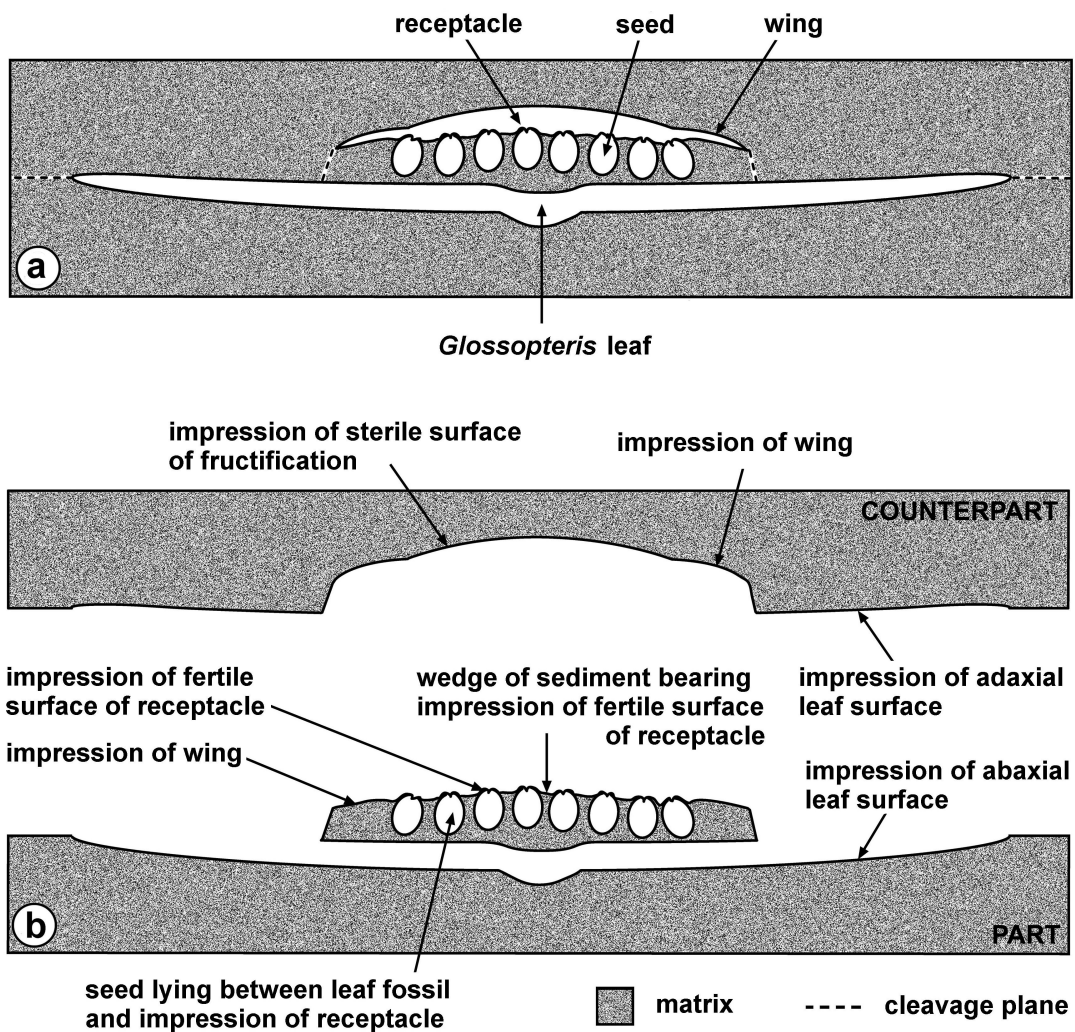
McLoughlin (1990b) was the first to consistently apply a logical model of impression fossil formation to the glossopterid fertiliger. His text-figs 3b,c&d illustrated the path of a cleavage plane through a mould of a *Plumsteadia* fructification, resulting in an impression of the fertile surface of the fructification on the part, and an impression of the sterile surface on the counterpart. This simple concept, that each impression fossil represents a compressed three-dimensional mould of the original plant material, has formed the cornerstone of impression fossil interpretation during the course of this study (text-fig. 3.1.2).

By expanding on McLoughlin's (1990b) model of glossopterid fructification impressions to include the subtending leaf, we can develop a hypothesis as to whether the fertile surface of the fructifications faced the leaf surface or not. In text-fig. 3.1.3, the assumption was made that the fertile surface did face the leaf. Exposure of the fructification and leaf along the same cleavage plane resulted in the impression of the fertile surface of the fructification lying at higher level in the sediment than the impression of the leaf [in the part, text-fig. 3.1.3 (b)]. The impression was borne on the sediment that had infiltrated between the leaf and fructification during burial. The impression of the sterile surface of the fructification [in the counterpart in text-fig. 3.1.3 (b)] lay deeper within the sediment, at a level below the impression of the glossopteris leaf.



**Text-figure 3.1.2.** Diagram of a cross-section through an impression fossil of a generalised glossopterid ovuliferous fructification, before and after exposure through cleavage of the matrix; the fructification originally lay in the matrix with the seed-bearing surface facing up; the thin extensions on either side represent lateral parts of the wing. When the matrix is cleaved along the dashed line in (a), the part and counterpart show impressions of the fertile and sterile surfaces of the fructification respectively; the impressions are continuous, uninterrupted surfaces showing seed scars and the upper surface of the wing in the part, and the sterile surface of the receptacle and the lower surface of the wing in the counterpart.

When actual impression fossils of ovuliferous glossopterid fructifications were examined and compared with the model, they conformed precisely to the predicted pattern of impression fossil exposure. Every single one of the hundreds of fructifications with subtending leaves in the South African collections had the fertile surface of the fructification borne on a wedge of sediment overlying the impression of the *Glossopteris* leaf, and a sterile surface lying below the level of the leaf impression. When seeds were present, they lay within the wedge of sediment bearing the impression of the fertile surface. This pattern was consistent amongst all genera of the Dictyopteridiaceae found in attachment to glossopterid leaves, viz. *Scutum*, *Dictyopteridium*, *Elatra* (previously *Hirsutum leslii*), *Plumsteadia* and *Gonophylloides*.



**Text-figure 3.1.3.** A medio-lateral section through a generalised ovuliferous glossopterid fertiliger. The model is an elaboration of text-fig. 3.1.2, and includes attached seeds and a subtending *Glossopteris* leaf. In (a) the assumption was made that the seed-bearing surface of the fructification faced the attached *Glossopteris* leaf. Exposure of the entire fructification and part of the leaf would result from cleavage along the plane indicated by a dashed line in (a). This would result in the part and counterpart illustrated in (b). In the part, there is a wedge of sediment bearing an impression of the fertile surface of the fructification and the peripheral wing, which *overlies* the impression of the leaf. Fossils of the seeds are present within this overlying wedge of sediment. The counterpart bears an impression of the sterile surface of the receptacle and continuous peripheral wing, and this impression lies at a *deeper level* in the sediment than the impression of the *Glossopteris* leaf.

### 3.1.2 OLD AND REVISED THEORIES ON MORPHOLOGIES OF THE OVULIFEROUS GLOSSOPTERID FRUCTIFICATIONS

The structure of the ovuliferous glossopterid fructifications has been a subject for debate since Feistmantel (1881) described *Dictyopteridium* as a flat, fern leaflet bearing sori. Zeiller (1902) later re-described *Dictyopteridium* as a fleshy rhizome with caudaceous hairs. Even today, although most authors accept that *Dictyopteridium* is a glossopterid reproductive structure, they are divided as to whether it is sporangiate or ovuliferous in nature, whether it exhibits radial or bilateral symmetry, and whether or not it possesses a sterile subtending bract. These features are all crucial factors in a system of classification that relies on form alone. *Dictyopteridium* is just one example of a fructification that has evoked controversy amongst students of *Glossopteris*. Each glossopterid ovuliferous fructification seems to have its own set of contentious issues regarding its structure and affiliations.

Four basic morphological types of glossopterid ovuliferous fructification are recognised here, corresponding to four families: the Rigbyaceae, Dictyopteridiaceae, Lidgettoniaceae and Arberiaceae. A brief historical account of these families and their diagnoses are given in the next chapter (section 4.1, p. 119). A brief overview is presented below of how the morphology of members of the four families has been interpreted in the past and how they are viewed here.

Certain features have been recognised which unify these families to a greater extent than has been formerly appreciated. The relationship between the seed-attachment sites and the associated scale-like features or marginal wing is identical in all four families. Plate 1 illustrates the seed scars and associated wings/scales of members from each of the families. In all cases there is a proximal cushion or platform representing the seed-attachment site which is flanked distally by a flange-like extension of the branch terminus or receptacle edge. This flange or wing is finely striated, the striations extending from the cicatrix of the seed-attachment cushion to the distal margin of the wing. In the

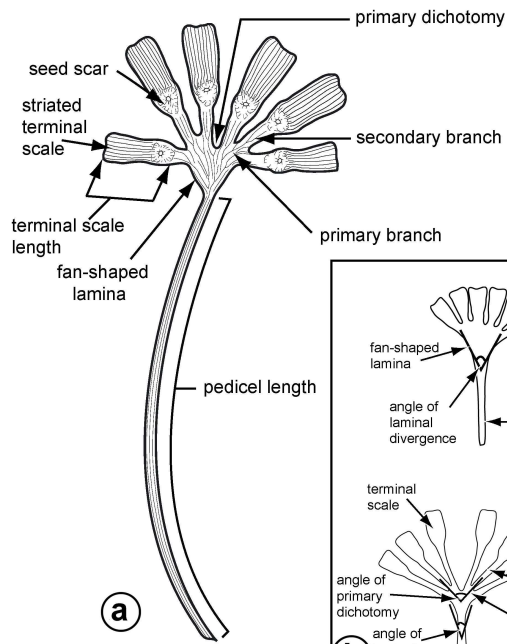
Dictyopteridiaceae and Lidgettoniaceae, this arrangement is only apparent in the marginal row of seed scars on the receptacle.

The pedicel in all the groups of proposed glossopterid fructifications bears prominent longitudinal striations which continue uninterrupted into the primary axis and into all subsequent branches and terminal scales in members of the Rigbyaceae and Arberiaceae, or onto the sterile surface of the receptacle and into the wing in the case of the Dictyopteridiaceae and Lidgettoniaceae.

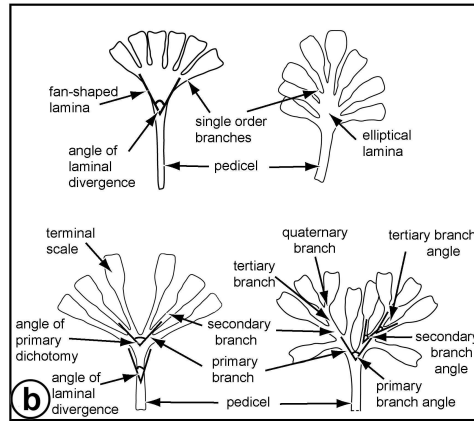
It has already been acknowledged by some workers that fructifications of the Dictyopteridiaceae, Lidgettoniaceae and Rigbyaceae are bifacial structures, with a sterile surface and a fertile, seed-bearing surface. A fresh look at members of the Arberiaceae, has demonstrated that at least some of these branched fructifications are also bifacial. This is discussed in more detail in section 3.3. (p. 105)

The descriptive terminology used in this document mostly follows that of Chandra & Surange (1979) and McLoughlin (1990a,b, 1992, 1993a,b, 1995). See text-figs 3.1.4 & 3.1.5 for illustrations of fructification and leaf structures and terminology.

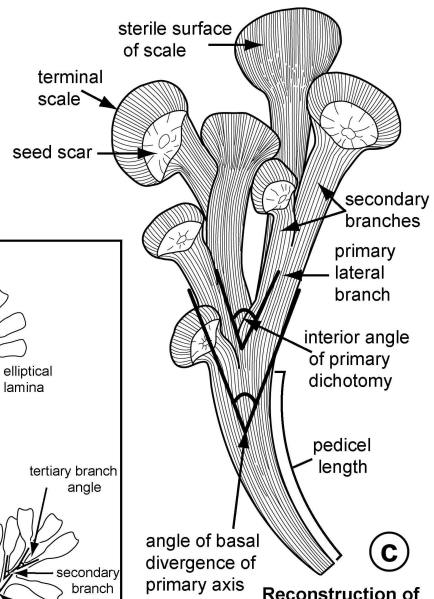
**Text-figure 3.1.4.** (overleaf). Diagrams indicating the basic morphological features observed in members of the four families of ovuliferous glossopterid fructification recognised in this study. Figs (a) & (b): important features in members of the Rigbyaceae, including various branching angles; fig. (b) illustrates the basic morphological forms/branching patterns that have been observed in the group (*Rigbya arberioides*); fig. (c): a reconstruction of an impression fossil of *Arberia hlobanensis* illustrating the various measurements and features considered important in the Arberiaceae; figs (d) & (e): reconstructions of impression fossils of two winged members of the Dictyopteridiaceae, demonstrating the types of measurements and characters used to distinguish between different species; figs (f) & (g): a reconstruction of *Lidgettonia africana*, illustrating important features of the Lidgettoniaceae; fig. (f) is a reconstruction of the fertile surface of a dorsiventrally compressed capitulum; fig. (g) is a reconstruction of a scale leaf with attached capitula.



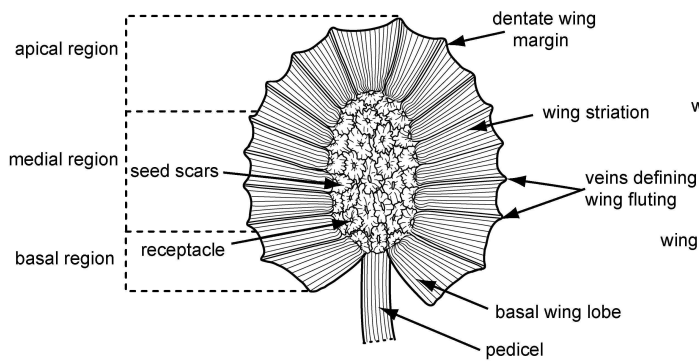
**(a)** Reconstruction of *Rigbya arberioides*  
**RIGBYACEAE**



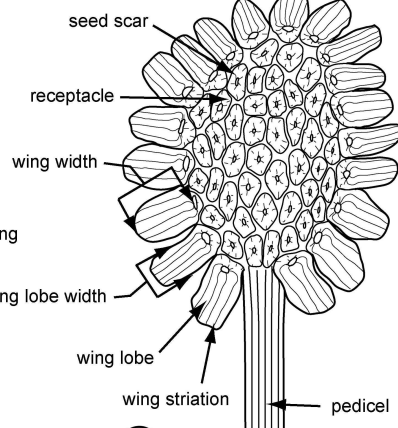
**(b)** Various branching patterns seen in *Rigbya* fructifications



**(c)** Reconstruction of *Arberia hlobanensis*  
**ARBERIACEAE**

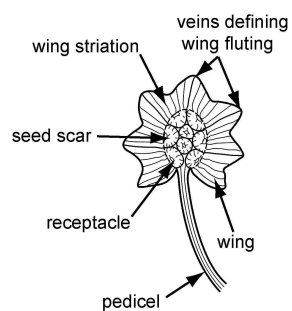


**(d)** Reconstruction of *Scutum leslii*

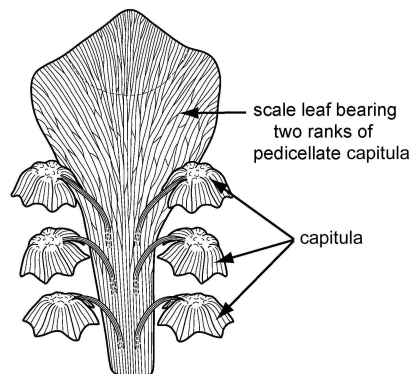


**(e)** Reconstruction of *Ottokaria transvaalensis*

**DICTYOPTERIDIACEAE**

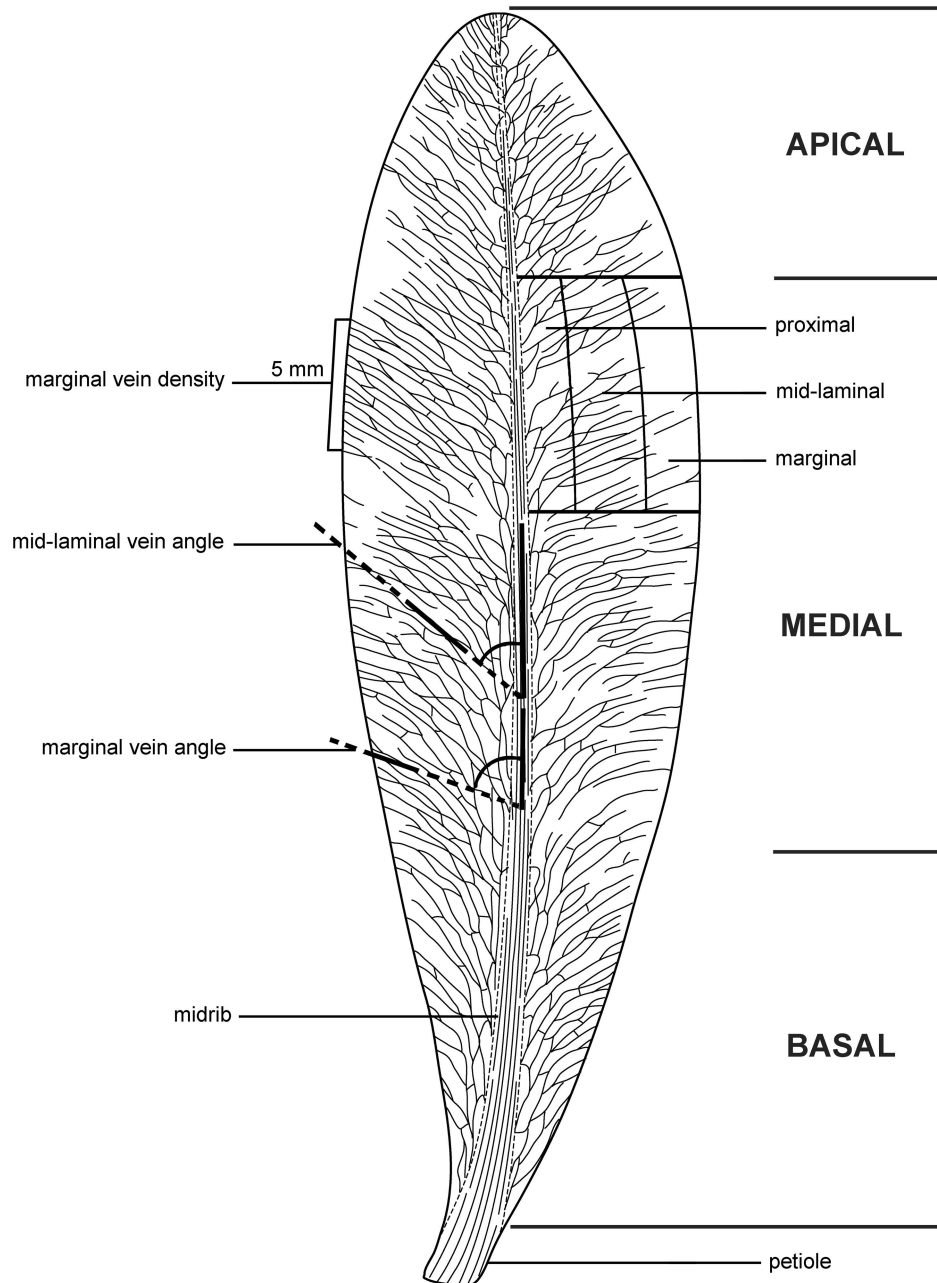


**(f)** Reconstruction of the fertile surface of a *Lidgettonia* capitulum



**(g)** Reconstruction of *Lidgettonia africana*

**LIDGETTONIACEAE**



**Text-figure 3.1.5.** Annotated diagram of a typical *Glossopteris* leaf, indicating the key morphological characters recognised in this study.

### 3.1.2.1. Rigbyaceae

The Rigbyaceae is a group of typically Upper Permian fructifications, with *Rigbya* as the type genus. Lacey *et al.* (1975) created *Rigbya* for specimens they described as ‘an aggregation of seed-bearing scales, or possible cupules, borne in a fan-shaped arrangement on a long slender stalk’.

Melville (1983a) later interpreted *Mudgea*, regarded here to be synonymous with *Rigbya*, as comprising two types of scales borne in tufts on a pedicel. The scales were considered to be either sterile (or possibly pollen-bearing), acute and lanceolate, or oblong to obovate spatulate scales which bore seeds at the base. As discussed by McLoughlin (1995), the figures provided by Melville (1983a) indicate that the sterile, lanceolate scales do not appear to be individual structures, but rather creases in the fan-shaped lamina between fused primary branches of a *Rigbya* fructification.

Anderson & Anderson (1985) described *Rigbya* as a dorsiventrally flattened, bilaterally symmetrical, palmate capitulum, with fused to deeply cleft lobes, each terminating in an elliptical, truncate ovuliferous scale. They used the term ‘receptacle’ for the primary and subsidiary branches of the polysperm, and considered this fructification to be most closely related to *Ottokaria*.

McLoughlin (1990a; 1995) recognised the dorsiventral, bifacial nature of *Rigbya*, and characterised the fructification as having a receptacle with terminal scales/lobes, variously fused, each bearing a single ovule or ovule scar. He also described (1990a) the only other currently recognised member of the family, *Cometia*, which appears to have only two terminal branches which are completely fused into a flabellate, laminar receptacle.

Here, use of the term receptacle has been restricted to the capitate and cupulate forms of glossopterid fructifications, and *Rigbya* is described as being a branched structure, with varying degrees of fusion of these branches [text-figs 3.1.4 (a), (b)]. In cases where the pedicel terminates in a fan-shaped structure, this is referred to as a laminar primary axis. The similarities between



Rigbyaceae and Arberiaceae reinforce the need for consistency in the terminology applied to members of these two families.

Lacey *et al.* (1975) considered the possibility that the terminal scales of *Rigbya* were enclosed, single-seeded cupular structures. This may be why they referred to the scale bases as being 'swollen at right angles to the flattened plane of the fructification' in the diagnosis. Rigby (1978) considered the lobed features in the *Rigbya* fructification 'marginally inserted atropous ovules'. As noted by McLoughlin (1990a, 1995), the scales of *Rigbya* fructifications are thinned, scalloped extensions or wings distal to the naked seed attachment point, and there is no evidence to suggest that the seeds were enclosed in any way. The seeds were only borne on one surface of the fructification, the sterile surface bearing striations which bifurcated and extended uninterrupted from the pedicel and into the lamina/subsidiary branches, through to the distal margins of the terminal scales.

The well-defined seed scars at the termini of the ultimate branches, and the scale-like wing segments that extend beyond the seed scars, are identical in structure to the marginal scars seen in winged members of the Dictyopteridiaceae [e.g. pl. 4, fig. (g); pl. 6, figs (a) & (b)]. The scars are raised cushions (in impressions) with a central tubercle, and bear irregularly placed, discontinuous radial striations; the scale or wing-like extension distal to the scar bears longitudinal striations and is wedge-shaped, in some cases with a concave apical margin. This same concave distal margin is seen in the individual wing segments of *Scutum*, creating the overall effect of a dentate or scalloped wing.

Plate 9 and text-fig. 3.1.4 (b) present an interesting overview of the different morphologies exhibited by South African *Rigbya arberioides* specimens. The reconstructions in pl. 9, figs (a)-(d) represent the four major types of branching patterns observed. In fig. (a), the pedicel expands slightly to form a small, fan-shaped primary axis, which is gently bifurcated, giving rise to six ultimate branches of apparently equal rank. Each of these branches terminates in a truncated terminal wing/scale, with a single seed scar at its base. Fig. (c) is a

variation on this theme, with a reduction in the primary axis, which is more strongly bifurcated, each secondary branch undergoing an additional bifurcation. Only one of the resulting daughter branches on each side bifurcates further, resulting in six seed-bearing ultimate branches. Fig. (b) represents the morphology typical of *Rigbya* fructifications from the Bulwer quarry in South Africa. Specimens from Australia with this branching form were regarded by McLoughlin (1995) as belonging to a separate species (*R. ranunculoides*). The primary axis is a prominent fan-shaped structure, all the secondary branches presumably having been fully fused together. The seed scars and distal scales/wings are borne directly along the distal margin of the fan. In some cases [e.g. fig. (d)] the primary axis is not fan-shaped, but narrowly elliptical. A particularly curious variant of *R. arberioides* is NM/1653, shown on the bottom right of pl. 9 and fig. (j) in pl. 2. This specimen is exceptional in having four orders of branches. This feature is highly reminiscent of *Arberia*. The bifurcation of the primary axis is a consistent feature among specimens of *R. arberioides*, and is also common in certain *Arberia* species.

#### **3.1.2.2. Arberiaceae**

This is a fairly broadly defined group of Lower Permian fructifications that have been found consistently in association with glossopterid foliage. Two genera are recognised here within the family, viz. *Arberia* (section 6.1) and *Vereenia* (section 6.2).

The Arberiaceae is possibly a polyphyletic group of structures. *Arberia minasica* (e.g. White, 1908; Rigby, 1972a) and *A. madagascariensis* (Appert, 1977) have been studied in some depth, but other members are very rare in the fossil record and are not well understood.

*Vereenia* is a group of Lower Permian organs originally described as *Arberia leeukuilensis* by Anderson & Anderson (1985). Although the laminar primary axis and pinnate lateral branches clearly qualify the placement of this taxon within the Arberiaceae, we do not understand the nature of the branch termini. The recurved terminal branch swellings could represent ovules, or sites of seed

attachment, but we cannot know for sure until further, more illuminating specimens are recovered.

*Arberia* has been described in the past as a branched fertile axis, with each ultimate branch bearing a single ovule at the terminus. Some authors have favoured a spiral or irregular arrangement for the branches, acknowledging the three dimensional branching structure of at least some members of the genus (e.g. Schopf, 1976; Anderson & Anderson, 1985; McLoughlin, 1995). Rigby (1972a), however, excluded from the genus those specimens he perceived as having radial symmetry, viz. all those without a dichotomising primary axis, and those bearing branches across the face of the lamina as well as along the margins. This may have stemmed from Rigby's (1972a) theory that these fructifications represent pinnate fronds, which would not accommodate the circumstance of pinnae being borne on the face of the frond. There has been some debate in the literature as to whether *Arberia* is a fertile shoot or a megasporophyll. Most authors agree that if *Arberia* is indeed a glossopterid fructification, it is a basal form, and interpretations of its structure would have a significant influence on models of glossopterid homology and evolution. This is explored further in the Discussion (section 9.2.2, p. 345).

*Arberia* is defined here as a branched fertile axis which may or may not be a planated structure, and which produces simple lateral branches through a series of dichotomies, and/or pinnately along the lateral margins of the primary axis [text-fig. 3.1.4 (c)]. In taxa such as *A. minasica*, *A. surangei* and *A. madagascariensis*, the primary axis is planar, and in many cases exhibits a tendency to bifurcate in the apex. The laminar primary axis may exhibit a bifacial branching form, a theory examined in section 3.3, or the primary axis may be less laminar and produce a more paniculose branching structure through a series of dichotomies, as seen in some of the *Arberia* fructifications described by Rigby (1972a) as *A. minasica*, and in *A. hlobanense* from South Africa (Anderson & Anderson, 1985). All members of this genus have prominent longitudinal striae that bifurcate and pass uninterrupted from the pedicel into the primary axis and into all subsidiary branches. The ultimate branches terminate in a single ovule or seed-attachment site. All past authors, with the exception of

McLoughlin (1995), have insisted on the absence of any scale-like features associated with these seed-attachment points at the branch termini, a stance that is challenged and discussed in detail in section 3.3.1. Here, the ovule/seed-attachment point is considered to be proximal to a wing/scale-like extension of the branch terminus. These features are bifacial, with a seed scar on the fertile surface and a sterile surface with longitudinal striations leading from the ultimate branch directly into the wing/scale. The striations tend to be finer and follow a parallel course in the scale. In several species at least, all the fertile surfaces of the ultimate branches face the same way. The entire fructification could be termed bifacial, with a sterile and fertile surface, and in *A. madagascariensis*, and possibly *A. minasica* and *A. surangei*, the fertile surface of the planated fructification also gives rise to lateral branches across the face of the primary axis (refer to section 3.3). This is a feature which has not been widely recognised, and which could have interesting implications concerning the homologies and phylogenies of the other groups of glossopterid fructifications (see Discussion, section 9.2, p. 340).

### **3.1.2.3. Dictyopteridiaceae**

Feistmantel (1881) and Zeiller (1902) were the first to describe members of this family, but it was only 50 years later that these structures could be indubitably attributed to *Glossopteris*. Edna Plumstead's groundbreaking papers (1952, 1956a&b, 1958a) on the famous Vereeniging specimens, discovered by Stephanus Le Roux, represent one of the great turning points in the study of the glossopterid fertile structures. Her accounts of the Vereeniging material provided the first evidence of fertile structures in organic attachment to *Glossopteris* leaves.

Plumstead (1952, 1956a, 1958a), however, interpreted the Vereeniging fossils as being positive representations of the original plant organs. She also supposed that the part and counterpart of each specimen represented distinct and separate structures that were formed by some mechanism of mineral replacement. Section 3.1.1 explains how impression fossils such as those from

Vereeniging need to be interpreted as three-dimensional moulds, the part and counterpart being impressions of opposite surfaces of the same structure.

As a result of Plumstead's misinterpretations of these fossils, she has been perhaps one of the most controversial figures in the history of glossopterid fructification research. Her interpretations were to have far reaching implications in the study of glossopterid fertile structures, particularly with regard to the Dictyopteridiaceae, and have therefore been given special consideration here. Plumstead's more contentious suggestions can be summarised as follows:

1) the fructifications had a 'bivalved' or bipartite structure, comprising a veined, bract-like, 'empty half' and a seed-bearing 'fertile half'; the two halves fitted together to form a purse-like structure enclosing the seeds (text-fig. 3.1.6) (Plumstead, 1952; 1956a,b; 1958);

2) the fructifications were bisexual structures that bore both seeds and pollen-bearing organs (1956a,b; 1958);

3) the raised cushions or 'sacs' on the surface of the fructifications were fleshy structures each containing an ovule, some bearing a 'stigma-like' mark (Plumstead, 1956a,b);

4) the narrow bract-like features associated with some specimens of *Scutum* represented ephemeral pollen-bearing organs, possibly even analogous to petals, and were possibly 'highly coloured to attract pollinating insects' (Plumstead, 1956a,b; 1958);

5) the apically angled striations in some of the specimens assigned to the genus *Hirsutum*, were thread-like pollen organs (Plumstead, 1956a; 1958);

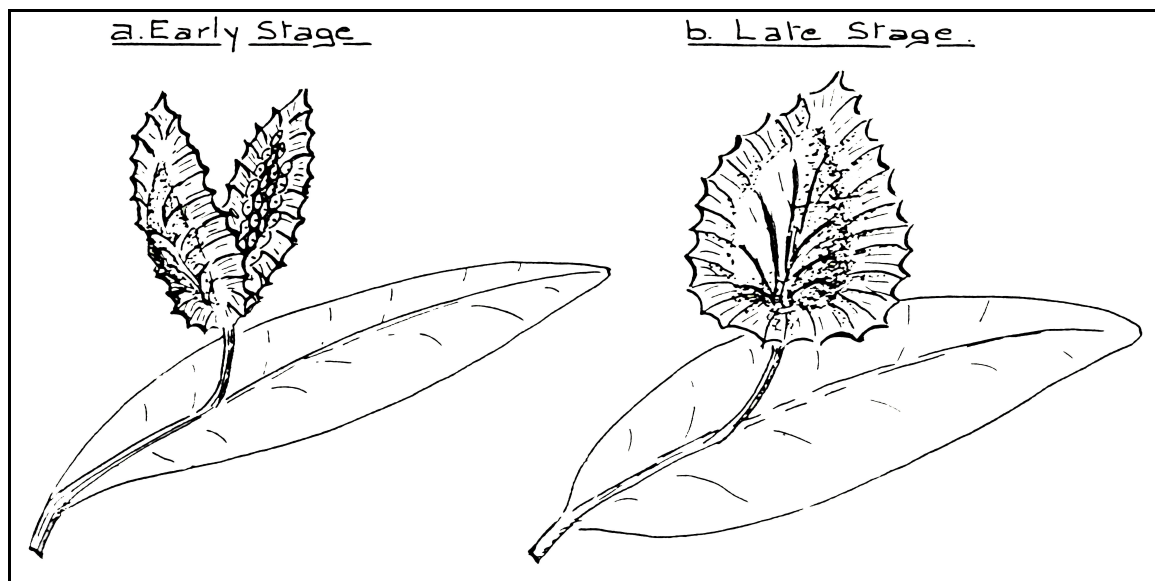
6) the two 'halves' of the fructification were apart in immature specimens to allow for cross-fertilisation of the ovules; this stage of development was referred to as the 'flower stage' (p. 219; Plumstead, 1956);

7) following fertilisation, and once the pollen organs were shed, the two halves of the cupule fused and 'the veined half served as a protection for the developing fruit' (p. 219; Plumstead, 1956b).

These last two concepts are summarised in the following statement made by Plumstead (p. 219; 1956b):

'The two stages constituted therefore the first known bisexual flower of the Palaeozoic era which developed later into something resembling a modern compound fruit'.

Plumstead (1956 a&b; 1958) regularly alluded to the strong possibility that the closed cupulate structure and bisexual nature of the fructifications reflected affinities with the angiosperms, and this theory was reinforced by her use of the words 'flower' and 'fruit', which are most commonly used when referring to angiosperm reproductive structures.



**Text-figure 3.1.6.** Plumstead's vision of the *Scutum* fertiliger according to her 'bivalve' theory (from Plumstead, 1956a; p. 5, Text-fig. 1a&b). Part (a) represents an early stage in the life of the fructification, where the two cupules are parted to allow for fertilisation of the ovules. Part (b) represents a later stage, when the two halves of the fructification were closely appressed to protect the developing seeds.

Most of these theories were questioned by Plumstead's contemporaries from the start. The open discussion sections in her 1952 and 1956(b) papers included comments and suggestions from leading figures in the field of

palaeobotany. Of particular interest were the comments made by Harris (p. 322 in Plumstead 1952) who suggested the 'empty half' may be the sterile back of the 'fertile half', and the 'burst sacs' the scars of fallen seeds. Hughes (p. 224 in Plumstead, 1956b) concurred with Harris' interpretation, and commented that the fossils appeared to be typical compression fossils in which the carbonised organic matter had been destroyed, leaving a small air space between part and counterpart. In the case of Plumstead's Vereeniging fossils, the space would then represent a simple organ with a veined abaxial and a fertile adaxial surface.

Plumstead more or less dismissed all the suggestions made by authors in these papers, and vigorously adhered to her assertion that the glossopterid fertile organs were bisexual and bi-cupulate. Possible reasons for her determination in this course of reasoning are discussed in section 3.2, but certainly a large part of her ideas stemmed from her erroneous interpretation of the physical nature of the Vereeniging fossils.

Schopf (1976) appeared to take a very dim view of impression fossils and their value in general, but particularly when it came to Plumstead's (1952, 1956a&b, 1958) glossopterid fructifications from Vereeniging. He considered 'these relatively poorly preserved plant fossils' to be of limited value, stating it was 'inconceivable ... that we should adopt interpretations based on limonitic molds as a standard for morphologic interpretation of such a widespread and important group of plants'. He even went as far as to state: 'It now seems doubtful that the Vereeniging fossils can provide more than a fertile ground for further morphologic speculation'. Presumably Schopf's (1976) poor opinion of the Vereeniging material was compounded by Plumstead's controversial interpretations of the glossopterid fructifications themselves.

Numerous schools of thought have developed and evolved since Plumstead's descriptions were published. Essentially the only broad consensus that has been reached among researchers of the glossopterids, is that these structures were fertile, the basic fertile 'units' represented by tubercles or raised cushions in impressions of a central, somewhat fleshy receptacle, and that at least some

of these fertile structures were ovuliferous and were borne on the midrib of an otherwise typical *Glossopteris* leaf. Different fructifications have been interpreted in different ways by the same authors, and the models they have developed over the years have incorporated various combinations and permutations of central concepts regarding the basic morphology and organisation of the fructifications. Text-figs 3.1.4 (d), (e) illustrate the features and terminology recognised here for this group.

### ***The receptacle***

The receptacle is the main body of the fructification which supports the fertile units. Authors have been at odds in the past as to whether this structure exhibits radial symmetry or is dorsiventrally flattened. When Feistmantel (1881) tentatively characterised *Dictyopteridium* as a fern-like organ, he described it as a dorsiventrally flattened, leaf-like organ. Plumstead (1952, 1956a, 1958a), as we have already seen, also described these structures as dorsiventral organs, but leading experts of the time were divided on the symmetry of the Vereeniging fructifications. W.N. Edwards (p. 321 in Plumstead, 1952) and J. Walton (p. 322 in Plumstead, 1952) favoured radial symmetry, whereas others, e.g. N. Hughes (in Plumstead, 1952; p. 224 in Plumstead, 1956b) and T.M. Harris (p. 322 in Plumstead, 1952) supported Plumstead's model of a dorsiventral structure, although they differed regarding other aspects of her interpretations.

Rigby (1963, 1972b, 1978) regarded *Isodictyoteridium* (later synonymised with *Dictyopteridium*), *Plumsteadia* and *Scutum* to be dorsiventral structures, but maintained that *Dictyopteridium* and *Ottokaria* were strobiloid. Over a period of 20 years, Pant (1977) and Pant & Nautiyal (1965, 1966, 1984) were remarkably consistent and accurate in their observations of *Ottokaria* specimens from India. Pant (1962, 1977) questioned both the bisexual nature of Plumstead's (1952, 1956a,b; 1958) fructifications and their purported bivalved structure. He found no reason to assume that the 'two counterparts of the same fossil which showed its two different faces were the two valves of a bivalved bisexual structure' (Pant, 1977). Pant & Nautiyal (1965, 1966, 1984) recognized that



these organs were dorsiventral, isobilateral, spoon-like structures with a central receptacle and sterile lobes along the periphery.

White (1963) described several fructifications attributed to *Cistella* species, but which are considered here to belong to *Plumsteadia* and *Dictyopteridium*. The *Plumsteadia* ('*C. ampla*') specimens were characterised as cone-like features, and White (1963) considered the *Dictyopteridium* ('*C. bowenensis*') fructifications to be sporangiate, scale-like cupules. White (1986) later reconstructed all members of the Dictyopteridiaceae (the 'megafructi') as radially symmetrical structures with an accompanying sterile bract.

Rex (1986) interpreted the seed scars on taxa such as *Scutum* as the casts of seeds, and deduced from this that these fructifications were radially symmetrical.

Banerjee (1973) and Smithies (1978) opted for a dorsiventral receptacle in *Dictyopteridium* and *Hirsutum leslii* (= *Elatra leslii*) respectively, but which bore seeds on both surfaces of the receptacle.

The most likely explanation for all the members in this family, bearing in mind the interpretation methods discussed in section 3.1.1, is that the receptacle is a simple, dorsiventrally flattened, often concavo-convex structure, which has a veined, sterile surface and a fertile surface. This is the model that was adopted by Schopf (1968; 1976), Anderson & Anderson (1985), McLoughlin (1990a,b; 1995), Adendorff *et al.* (2002), and it has been supported by evidence from permineralized material (e.g. Gould & Delevoryas, 1977; Taylor & Taylor, 1992). Although Plumstead's (1952, 1956a,b 1958a) reconstruction of the Vereeniging fossils as bipartite structures, with a pollen-bearing half and an ovuliferous half, was not accepted by other workers, this model probably inspired the persistent reports of a sterile scale-like feature subtending, and of similar size to, the receptacle of some of the fructifications.

### ***The fertile units***

Feistmantel (1881) suggested that the raised tubercles on the surface of *Dictyopteridium* were sori. Zeiller (1902) considered them to represent the attachment sites of caudaceous hairs. Later, these and other members of the Dictyopteridiaceae were recognised as seed-bearing organs, but authors have interpreted the raised mound-like features on the surface of the receptacle in different ways.

Plumstead (1952, 1956a, 1958) went into great detail about the ‘sacs’ on the surface of the Vereeniging impressions, recognising different stages of development of these structures. She regarded each one as a sac-like feature enclosing an ovule, and proposed that the tubercle visible in the centre of the sac was, in many cases, a stigma or equivalent feature allowing for pollination of the ovule. According to her theory, the mature sacs burst to release the enclosed seed. Plumstead’s (1952) stages of development can be attributed to preservational differences in the impression fossils which affected the resolution of the details visible in any one specimen.

Benecke (1976) described these structures in great detail, and created several new genera on the basis of their morphology. She considered the tubercles in *Plumsteadia* and *Dictyopteridium* to represent ‘discs’ on a layer of tissue which enclosed the seeds.

Pant (1977), Pant & Nautiyal (1965, 1966, 1984), Rigby (1978), Anderson & Anderson (1985) and White (1986) considered the sac-like features on the receptacles of fructifications such as *Scutum*, *Ottokaria* and *Plumsteadia* to represent ovules or seeds, but Rigby (1978) interpreted the tubercles on the surface of *Isodictyopteridium* (= *Dictyopteridium*) as seed attachment points. Surange & Maheshwari (1970) described them as seeds borne on flattened, scale-like structures, and both they and Anderson & Anderson (1985) interpreted the central tubercle to be a micropyle.

The elliptical to rectangular units present on the fertile surface of all members of this family, are considered here to represent the impressions of seed scars, as described by McLoughlin (1990a,b, 1995) and Adendorff *et al.* (2002). In the original plant they would have been hollow, cup-shaped structures with a central pit (as we see in compression fossils), but in the impressions they are cushions, or mounds with a central tubercle. The seed bases presumably would have nestled within these hollows in the receptacle surface, the pit representing the site of vascular attached to the plant. In most cases, these cushions bear radiating striations which are somewhat irregular and discontinuous, and may result from the creases surrounding the hilum of the seed when it was still attached. These creases appear to be a feature of seed scars in the majority of glossopterid fructifications.

*Dictyopteridium* has been one of the most contentious glossopterid fructifications, with many authors having considered it to be a sporangiate organ (White, 1963; Lacey *et al.*, 1975; Anderson & Anderson, 1985). Rigby (1972b) initially described *Isodictyopteridium* (here regarded to be a junior synonym of *Dictyopteridium*) as a sporangiate structure, but he later (1978) characterised it as a seed-bearing organ. Examination of the South African specimens of this taxon as well as those figured in the literature, have led to the confident conclusion that these organs are ovuliferous structures, similar in almost every respect to other genera such as *Plumsteadia*, apart from the fact that their seed scars are reduced to small tubercles on a smooth receptacle (see section 7.9).

### ***The wing***

The wing is perhaps one of the most mysterious and mistrusted features of members of the Dictyopteridiaceae. This has been most unfortunate, since it is one of the primary features used in the classification of these organs. Some researchers still question the existence of this feature at all, suggesting that it may be some artefact of preservation (e.g. S. Archangelsky, pers. comm., International Organisation of Palaeobotany Congress, Argentina, 2004).

Plumstead (1952) described the wing as a thin, sterile flange along the periphery of the receptacle. This view was challenged by J. Walton (in Plumstead, 1952; p. 322), who suggested that the wing segments were laterally compressed, tubular appendages.

Surange & Chandra (1974a) considered the presence of a wing in *Dictyopteridium* to be 'untenable' because they regarded it to be a radially symmetrical structure. They dismissed the wing-like feature apparent in specimens of this genus as being an artefact of laterally compressed seeds. Rigby (1978) refuted the existence of a wing in *Dictyopteridium* for the same reasons, but described a wing in *Isodictyopteridium*, as an extension of the fructification with fluting related to the position of the marginal tubercles. He also considered *Plumsteadia* to have a wing which represented a flap of sterile tissue with a protective function, but he described the wing of a radially symmetrical *Ottokaria* as comprising a circlet of fused bracts at the base of the fructification.

Lacey *et. al.* (1975) refuted the existence of a wing in their specimens of *Plumsteadia natalensis*. They explained in detail how lateral compression of the very fleshy marginal ovules created the appearance of a wing-like feature. This has been refuted here, in light of the 'ovules' actually representing impressions of depressed seed scars. They were not alone, however, in their argument that *Plumsteadia* lacked a wing. Plumstead (1952; '*Lanceolatus*' = *Plumsteadia*), White (1963) and Surange & Maheshwari (1970) all excluded the presence of a wing in this genus. This was mainly because the wing is in most cases very narrow in these fructifications, and it is easy to overlook this feature or account for it in terms of representing the sides of the fleshy receptacle, particularly since it is often angled slightly away from the plane of the fructification. It is only when we look at other genera that have broader wings, e.g. *Scutum*, that we can confirm the similarities in the relationship between the marginal seed scars and the finely striated wing, and can conclude with confidence that a wing is in fact present.

The idea that the wing is composed of separate but contiguous units has been a recurring one in the literature. For instance, several authors have suggested that the wing of *Scutum* comprises a marginal row of partially overlapping, dorsiventral seeds (Surange & Chandra, 1974a; Rigby, 1978; White, 1986), and Surange & Maheshwari (1970) proposed that the wing of *Scutum* represented ovule-bearing scales that were fused together. Anderson & Anderson (1985) considered the wing to represent fused modified ovules. The pattern of fluting in the wing could not have resulted from impressions created by adjacent ovules, as the pattern is too regular, without any sign of the overlapping seed wings seen in fructifications with seeds still in attachment. Also, we see this same wing structure in taxa known to have rounded seeds with lateral wings (eg. *Dictyopteridium*, *Plumsteadia* and *Lidgettonia*). The fluting in the wing of members of the Dictyopteridiaceae is very clearly delimited by veins which extend from the receptacle and into the wing between adjacent marginal seed scars.

Following publication of the work by Gould & Delevoryas (1977) on permineralized fructifications, most authors have accepted that the wing, in at least some genera, structurally represents a thinned flange of tissue along the periphery of the receptacle (Banerjee, 1968, 1973; Surange & Chandra, 1974a; Benecke, 1976; Rigby, 1978; Pant & Nautiyal, 1984; Anderson & Anderson, 1985; McLoughlin, 1990a,b, 1995; Adendorff *et al.*, 2002), with some workers characterising it a thinned extension of the receptacle (e.g. Benecke, 1976; McLoughlin, 1990a,b, 1995). Theories on wing homologies are discussed later in section 9.2.2.2 (p.346).

### ***Pedicle insertion***

In all the South African members of the Dictyopteridiaceae, the impression of the pedicle lies at a slightly higher level in the sediment than the fertile surface, and is flush with the sterile surface. Plumstead (1956b) noted this feature in her annotated reconstruction of the 'fertile half' of *Ottokaria*, referring to it as the 'broken ledge of junction with common pedicle'. The 'common pedicle' referred

to her theory of a bicupulate fructification, with the fertile and sterile half sharing a common point of attachment to the pedicel.

This discontinuity of the impression of the pedicel is probably a result of the differential thicknesses of the slightly fleshy receptacle and the pedicel. In many cases, more so in specimens of *Ottokaria* and *Elatra*, the impression of the pedicel extends significantly onto the receptacle surface, partially obscuring some of the basal seed scars or wing details. This would suggest that the base of the receptacle extends down in the basal region, forming a lip past the point of pedicel insertion. In other words, the pedicel is not inserted laterally, but at a slight angle, and a few millimetres in from the receptacle edge. Smithies (1978) discussed this phenomenon in *O. hammanskraalensis*, favouring an eccentric or oblique insertion of the pedicel into the base of the receptacle. This trend is apparent in specimens of *Ottokaria* from other parts of the world, including *O. bengalensis* (Seward & Sahni, 1920), *O. ovalis* (White, 1908) and *O. santacatarinae* (Dolianiti, 1971).

### ***The elusive sterile scale***

The existence of a sterile scale attached to members of the Dictyopteridiaceae, has not been adequately demonstrated in the literature. Virtually all reports of such a structure can be attributed to misinterpretations of impression fossil structure. Surange & Chandra (1973a, 1974a, 1975; Chandra & Surange, 1977a-d) have been tenacious in their insistence that such structures exist in taxa such as *Dictyopteridium*, *Scutum* and *Plumsteadia*. Banerjee (1973, 1978, 1984) has also consistently promoted the presence of a sterile, veined bract-like feature covering the fertile surface of members of the Dictyopteridiaceae, and Melville (1960, 1983b) has supported the presence of this feature in line with his 'gonophyll theory'.

Researchers working on cuticles extracted from glossopterid fructifications have been at loggerheads for many years regarding the number of cuticle layers they have extracted from individual compression fossils of glossopterid ovuliferous fructifications. Banerjee (1984) cited the presence of two cuticle layers in

sporophylls of various members of the Dictyopteridiaceae, but still supported the presence of a sterile bract in most members of the family. Chandra & Surange (1977b,c) however, described instances when up to four cuticle layers were extracted from a single polysperm, suggesting that there was more than one structure within a single fructification, i.e. a radially symmetrical, seed-bearing receptacle, and a protective sterile bract.

Rigby (1963) initially described *Plumsteadia* with a sterile bract, but later (1971, 1978) revised his interpretation, characterising the fructifications as dorsiventral structures with a sterile and fertile surface.

Surange & Chandra (1975) reconstructed *Ottokaria* as a strobiloid axis with a funnel-shaped circlet of fused bracts surrounding base of fructification, an interpretation supported by Rigby (1978). Banerjee (1978) developed an unusual model for the *Ottokaria* specimens she examined from India, possibly inspired by Melville's (1960) gonophyll theory. She reconstructed these fructifications as bipartite organs comprising a shield-shaped, dentate bract and a dichotomously branched network of delicate branches, with ultimate branches each terminating in an ovule. Here *Ottokaria* is interpreted as a simple, dorsiventral fructification, with a sterile and fertile surface and a wing which is in most cases divided into lobes (see section 7.4).

It is not inconceivable that there may be glossopterid fructifications with some sort of protective scale, but this would indeed be a drastic divergence from the apparently conservative body plan of the ovuliferous glossopterid fructifications as a group. Chandra & Surange (1977d) appeared to consider the scale leaf of the cupulate fructifications such as *Lidgettonia*, to be analogous to their purported protective bract. Most researchers consider the scale leaf of *Lidgettonia* to be a reduced, homologue of the large subtending *Glossopteris* leaves which bear fructifications of the Dictyopteridiaceae on the midrib or axially. This is a reasonable assumption, since the capitula of *Lidgettonia* clearly represent reduced homologues of the larger capitate fructifications of the Dictyopteridiaceae.

### ***Orientation relative to the subtending leaf***

Use of the terms adaxial and abaxial, when referring to the sterile and fertile surfaces of the capitate fructifications, has led to some confusion in the past. Lam and Wesley (pp.225-227 in Plumstead, 1956b) explained how Plumstead had misused these terms by regarding the subtending leaf as the axis of origin, and therefore referring to the side of the fructification facing the leaf as the adaxial surface. Lam considered the axis bearing the leaf to be the appropriate reference point, which would make the side facing the leaf the abaxial surface of the fructification. To minimise confusion, the terms abaxial and adaxial have been avoided in this study. But this problem does raise some interesting questions, which reflect on the homologies of the glossopterid fructifications. For instance, are all members of the Dictyopteridiaceae axillary structures with pedicels which have become adnate to the glossopterid leaf, or are these structures borne directly on the midrib? In many cases, the midrib of the *Glossopteris* leaf is significantly more robust below the point of polysperm attachment. This has been cited in the past as evidence for a fused or adnate pedicel, the fructification therefore being essentially axillary to the leaf. However, if we consider the amount of vascular tissue required to sustain the development of a polysperm, and if we bear in mind that *Glossopteris* leaves do not possess true midveins, it is hardly surprising that a large number of vascular strands would divert into the pedicel of the attached fructification, whether there is an adnate portion of the pedicel or not. We could also expect a greater amount of supportive tissue below the point of pedicel attachment to the subtending leaf.

The general consensus in the literature is that the fructifications probably were axillary, with the pedicels adnate to the midrib to various degrees. Some glossopterid fructifications are definitely known to be axillary, e.g. Holmes' (1974, 1990) '*Austroglossa*', which is possibly a species of *Scutum*, and the fructifications figured by Pant & Singh (1974) in attachment to a *Glossopteris* leaf bearing axis. As discussed by Rigby (1978), an axillary fertile structure adnate to its subtending leaf is a phenomenon not unheard of in extant plants.



Each ovuliferous structure of *Ginkgo* is borne in the axil of an apparently regular, vegetative leaf, and in rare instances may exhibit varying degrees of fusion to the petiole or lamina of the leaf.

Plumstead (1956a, 1958a) reconstructed the Vereeniging specimens with the 'fertile half' closest to the leaf, but with the seed-bearing surface facing away from the leaf. This is a reflection of her interpretation of the impressions as exact, positive replicas of the original plant. In the case of *Lanceolatus*, Plumstead (1952) described how this fructification was completely fused with the subtending leaf. The probable reasons for this unusual interpretation were discussed in section 3.1.1.

Pant was very consistent in his view that the ovule-bearing surface of the glossopterid fructifications faced away from the subtending leaf (Pant, 1977, 1982; Pant & Nautiyal, 1984). According to Taylor & Taylor (1992), only a handful of fructifications had ever been found attached to an axis, and the adaxial or abaxial attachment of seeds was therefore only a topic for conjecture. The only examples of fructifications attached to axes that were cited by Taylor & Taylor (1992), were two unidentified fructifications figured by Pant & Singh (1974). The specimens in question (p. 51, Text-fig. 3 B) were impression/compression fossils of two laterally compressed fructifications axillary to *Glossopteris* leaves on an axis. While this is a magnificent specimen, both fructifications are laterally compressed, and any inferences regarding the orientation of the seed-bearing surfaces would be highly speculative. Pant & Singh (p. 60, 1974) certainly made no such commitment, explaining that the fructifications had both been distorted during preservation. They were not even sure if the ovules were present or visible - they noted that the receptacles of both fructifications showed 'a number of small obscure marks of rounded or oval bodies over a shallow scale or cupule' and that the nature of the rounded marks could not be ascertained.

The insistence of Taylor & Taylor (e.g. 1992, Taylor, 1996) about the orientation of the fructifications was partly based on evidence provided by the orientation of xylem tissue in vascular bundles of permineralized fructifications they examined

(see section 3.1.2.5 below). Lacey *et al.* (1975) and Rigby (1978) described *Plumsteadia* as being attached with the fertile surface facing away from the subtending leaf, as did Anderson & Anderson (1985) in their reconstruction of *Hirsutum intermittens* (p.118, text-fig. 3, p.120, text-fig. 7).

Many authors, however, have interpreted the glossopterid fructifications to be oriented with their seed-bearing surface oriented towards the subtending leaf (e.g. Schopf, 1976; Gould & Delevoryas, 1977; Retallack & Dilcher, 1981, 1988; Rex, 1986; McLoughlin, 1990a,b), and this is very clearly supported by the South African material, as explained in section 3.1.1.

#### **3.1.2.4. Lidgettoniaceae**

Members of this family are what Schopf (1976) referred to as 'compound' fertiligers. Multiple, reduced fructifications or capitula, are attached to a single, reduced scale leaf [text-figs 3.1.4 (f) & (g)].

Thomas (1958) referred to the little umbrella-shaped fructifications of *Lidgettonia africana* as 'cupules', a tradition continued by Surange & Chandra (1973b), Lacy, van Dijk and co-workers (e.g. Lacey *et al.*, 1975), Meyen (1984) and more recently by Taylor (1996). However, Schopf (1976), Melville (1983b) and Banerjee (1984) considered 'cupule' to be a term applied to the cup-shaped fertile structures of northern hemisphere pteridosperms, and therefore inappropriate for glossopterid fructifications. They all felt this name inferred homologies that did not exist. Schopf (1976) apparently also thought the name implied that the structures were peltate, rather than dorsiventral with a laterally inserted pedicel. Plumstead (1952, 1956a) referred to the male and female 'halves' in her model of a bivalved ovuliferous glossopterid fructification as 'cupules', which has contributed to the stigma surrounding use of the term as applied to glossopterid fructifications.

Schopf (1976) suggested that the seed-bearing structure of *Lidgettonia* be referred to as a 'flattened campanulum' or capitulum; Melville (1983b) proposed the term 'scutella' and Banerjee (1984) referred to them as small sporophylls.

Anderson & Anderson (1985) simply called them 'ovuliferous scales'. Meyen (1984; p. 23) defined cupules as 'orthotropous containers, in which the orientation of the seed axis follows the axis of the container; seed micropyles are directed towards the mouth of the cupule; the wall is either entire or divided into lobes'. He went on to state that 'The use of the term "cupule" does not imply the homology of pertinent organs'.

The dictionary definition of a cupule is a cup-shaped organ, receptacle, etc. The word is derived from the Latin *cupula*, or cupola, which is a rounded dome. The term is broadly used in botanical, mycological and zoological fields, and I have no real objections to its application to the cup-shaped structures found in the Lidgettoniaceae. However, since 'cupule' appears to have particular connotations in some botanical circles, it is perhaps best used sparingly as an adjective, rather than as a noun for an already highly controversial group of plants. Schopf's (1976) term 'capitulum' has been selected here as an alternative. Of course, although the word is a simple derivation of the Latin '*caput* ', meaning 'head', this term has traditionally been applied to inflorescences of the angiosperm group Compositae, and has its own set of associations.

In the past, the similarities in the reticulate venation of the scale leaves to vegetative *Glossopteris* leaves, and their close association with these leaves, made a strong case for their inclusion within the glossopterids. However, as Schopf (1976) observed, when we look closely at the capitula there can be no doubt that the Lidgettoniaceae are affiliated with the other, larger, capitate forms of glossopterid fructifications that have been found in organic attachment to *Glossopteris* leaves.

In essence, the capitula of members of the Lidgettoniaceae represent scaled-down versions of capitate fructifications of the Dictyopteridiaceae: they are dorsiventral, isobilateral; they are bifacial, with a sterile and a fertile surface; they have a central, seed-bearing receptacle with a fluted, striated, peripheral wing, and as in *Scutum*, the scallops on the wing margin correspond to the positions of the marginal seed scars. The wing is continuous along the

periphery of the receptacle, except at pedicel insertion. The pedicel is laterally inserted. Although the seed scars of *Lidgettonia* are small, in some cases these fall within the size ranges for some of the larger capitate fructifications. The capitula are borne on slender pedicels attached in opposite ranks in the medio-longitudinal area of a scale leaf, in most cases in the base, near the top of the petiole. In all the South African species of *Lidgettonia*, the capitulum-bearing pedicels are clearly arranged in two parallel ranks on the petiole of the scale leaf, but in some Indian species they may be arranged in a single row. Surange & Chandra (1973c) transferred this latter type of cupulate fructification to a new genus, *Partha*, but it is regarded here as a junior synonym of *Lidgettonia*.

Surange & Maheshwari (1970) and Surange & Chandra (1973c) considered the capitula they observed in *L. indica* and '*Partha*' to comprised either a cluster of four seeds or four separate cupules attached to the terminus of each pedicel. Surange & Chandra (1975) created an additional genus, *Denkania* which although clearly affiliated to *Lidgettonia*, bore on each scale leaf a number of enclosed cupules with a lobed apex, bearing perhaps only a single seed per cupule. The validity of this interpretation is questioned here (see section 8.1, p. 314), and these fructifications are considered comparable to *L. elegans*, in having spatulate capitula with a reduced number of ovules. From the photographs available, these do not appear to be enclosed structures.

#### **3.1.2.5. Permineralized ovuliferous glossopterid fructifications**

Permineralization is a complex chemical process resulting in the infiltration and embedding of organic material in a fine crystalline matrix. This process occurs at the cellular level and, incredibly, can lead to the preservation of organelles and even chromosomal material. Relatively few people have worked on permineralized glossopterid fructifications in the past (e.g. Schopf, 1976; Gould & Delevoryas, 1977; Taylor & Taylor, 1992, 1993; Pigg & Trivett, 1994; Zhao *et al.*, 1994; Taylor, 1996; Nishida *et al.*, 2003, 2004), and material of this nature has only been found in Antarctica and Australia. Only permineralized wood has been found in South Africa (e.g. Bamford, 1999).

Permineralized material is of course the most highly regarded form of fossil material in the science of palaeobotany, since it provides a wealth of information beyond the details of surface features provided by impression and compression fossils. This material provides information about the anatomy of plant organs and in many cases presents an undistorted, uncompressed view of the material. Sequential or serial sections of individual specimens can allow for the development of accurate three-dimensional reconstructions of the plants under investigation. Knowledge of anatomy can assist with the correlation of dissociated plant organs and may provide more convincing arguments regarding the homologies of organs than can impression fossils. Some authors feel that the key to solving the phylogenetic mysteries of the glossopterids lies in the analysis of permineralized specimens of their fertile structures (e.g. Schopf, 1970; Taylor & Taylor, 1992; Taylor, 1996). Pigg & Trivett (1994) gave a comprehensive review of the anatomical information that had been gleaned from studies of permineralized fructifications.

It can be difficult to reconcile permineralized fossils with taxa described from impression and compression fossils. Unless a detailed series of serial sections is made of an individual specimen, or the specimen is visible within the matrix, assessment of the exact dimensions of the organ may be problematic. Additionally, features of glossopterid fructifications such as wing fluting, seed scar density and shape are difficult to visualise without the aid of three-dimensional collation of serial sections. For this reason, the permineralized fructifications described in the literature have been examined in a separate section, independent from the above families which were based on information provided by impression and compression fossil material.

Gould & Delevoryas (1977) published the first clearly defined siliceous permineralizations of glossopterid fructifications from the Homevale locality, Late Permian Blackwater Group of the Bowen Basin, Australia. Their paper provided concrete evidence of a dorsiventral, laminar structure for at least some of the glossopterid fructifications. It also demonstrated that the wing was continuous with the receptacle.

Gould & Delevoryas (1977) interpreted the simple laminar structures they observed in cross section as infolded megasporophylls, bearing gymnospermous seeds on the inner surface. The fructifications were inrolled, with the lateral margins loosely overlapping. As discussed by Gould & Delevoryas (1977), some of their specimens, which had already shed all or a portion of their seeds, were more open, or even flat, and probably represent more mature examples facilitating the dispersal of their seeds. Gould & Delevoryas (1977) compared their specimens with other members of the Dictyopteridiaceae, and upon noting the broad range in sizes of the permineralized fructifications (3-11 mm wide, 10-42 mm long), suggested they may belong to several genera. If they represent different developmental stages, this could also account for some of the variation in size. Gould & Delevoryas (1977) also considered the possibility that some of their more spheroidal specimens (in some cases clustered in groups of 2-4) may represent members of the Lidgettoniaceae. According to Gould & Delevoryas (1977), when a *Glossopteris* leaf was found associated with a fructification, it was oriented with the fertile surface of the fructification facing the leaf. There was, however, no evidence of organic attachment in any of these specimens.

Schopf (1976) published the very first example of a permineralized glossopterid fructification, from Mount Augusta, in the Queen Alexandra Range in Antarctica. He described the specimen (fig. 4, pl. 5, p. 58) as an 'oriented group of four "cuneate-shaped" seeds', and explained on pp. 57 & 59 that they were the 'right size, shape and arrangement to suggest attachment to the head of a fertiliger' of the type he referred to as 'Antarcticoid', i.e. a *Rigbya* fructification. Schopf (1976) indicated that he had made many sections of this fructification and was unable to interpret its structure, at least partly due to the poor preservation of the tissues. He noted further that the seeds attached to his permineralized fructification had 'parenchymatous (integumental) cushions' on either side of the micropyle.

A reversed version of precisely the same photograph of Schopf's (1976) fructification (fig. 4, pl. 5, p. 58) was later published as a new discovery by Taylor & Taylor (1992). They renamed Schopf's (1976) permineralized peat

locality as the Skaar Ridge locality, in the Beardmore Glacier region of the central Transantarctic Mountains (Upper Buckley Formation, Late Permian age). Taylor & Taylor (1992) and Taylor (1996) characterised Schopf's (1976) specimen as a leaf-like megasporophyll, 6 mm wide, with partially inrolled margins and three winged ovules attached to its adaxial surface. The seed-bearing surface was described as being uneven, with the seeds slightly recessed into the surface. Taylor & Taylor (1992) had more success than Schopf (1976) in interpreting the poorly preserved tissues of his specimen, describing the anatomy of the 'megasporophyll' as being leaf-like, with an epidermis, hypodermis with large lacunae, and vascular bundles with primary xylem with scalariform thickenings. They considered the xylem orientation to be closest to the surface bearing the ovules. This was confirmed by Pigg & Trivett (1994) and Taylor (1996) on the basis of a re-examination of the Homevale specimens described by Gould & Delevoryas (1977). Taylor & Taylor (1992) cited this orientation of the xylem as evidence that the ovules were borne on the adaxial surface of these structures, and that the fertile surface of the fructification therefore faced away from the subtending leaf. However, without a clear understanding of the homologues of the glossopterid fructifications, the relative positions of the vascular elements alone do not provide adequate evidence for the orientation of the seed-bearing surface relative to the subtending leaf. For example, if the fructification was borne on a highly reduced short shoot axillary to the subtending leaf, the seed-bearing surface could be adaxial, and still be oriented with fertile surface facing the subtending leaf.

Nishida *et al.* (2000), from serial sections of permineralized ovuliferous fructifications from the Upper Permian of the Bowen Basin, Australia, also concluded that each megasporophyll bore ovules on its adaxial surface, and considered this fertile surface of the fructification to face the adaxial surface of the subtending leaf.

A puzzling aspect of the permineralized fructifications described by Gould & Delevoryas (1977), was the filamentous network they observed, continuous with the outer integuments of the semi-enclosed, *in situ* ovules. Various theories have been proposed as to the nature of this mesh-like feature, most suggesting

their involvement in some form of pollination mechanism. Rigby (1978) noted that the meshwork may have been a secondary infection by an alga or fungus which preferentially invaded the ovules through the micropyle. Other authors such as Retallack & Dilcher (1988) and Pigg & Trivett (1994) supported Gould & Delevoryas' (1977) interpretation of these features as filamentous integumentary processes on the seeds.

Zhao *et al.* (1995) figured a longitudinal section through a permineralized fructification very different to the 'megasporophylls' of Gould & Delevoryas (1977). They characterised the fructification as comprising aggregations of cupules in groups of four, arranged in a C-shaped configuration. The cupules were 3.0-3.5 mm long, and up to 1.2 mm wide, and were described by Zhao *et al.* (1995) as extending beyond the apex of the seed to form an elongated tube. Attached seeds were 2 mm long with a prominent wing in the flattened plane of the seed. Zhao *et al.* (1994) considered their fructifications to represent examples of a cupulate type of glossopterid fructification. Taylor (1996) compared this fructification to the Indian species of *Partha* and *Denkania*, although neither of these fructifications has their fertile structures arranged in an arc, and neither taxon has 'cupules' with such a narrow, elongated form. The fructifications described by Zhao *et al.* (1994) may well represent the branch termini of a *Rigbya* fructification (see Discussion, p. 334).

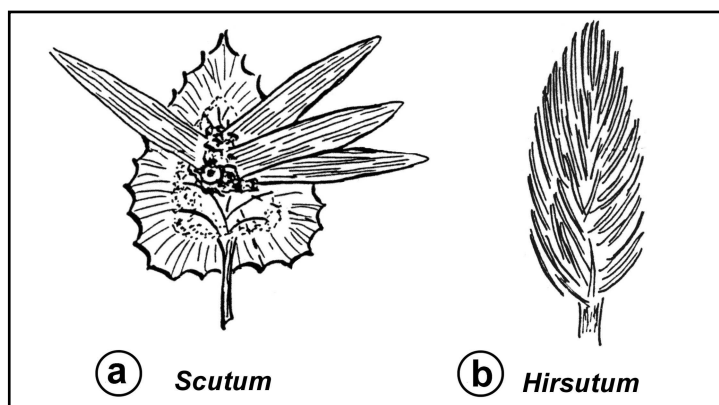
Nishida and co-workers (2003, 2004) recently published astounding results from their work on permineralized ovulate fructifications from the Homevale locality in Australia. Careful examination of sections through unusually well-preserved glossopterid ovules, revealed the presence of several pollen tubes at various stages of releasing sperm cells. These sperm cells were flagellated and had a helical structure. Zooidogamy is only known in *Ginkgo*, cycads, some pteridophytes, and possibly in some seed ferns. Conifers, gnetophytes and angiosperms all have a siphonogamous pollen tube. The discovery of motile sperm in the glossopterids will no doubt have a significant impact on future phylogenetic analyses of the group.



### 3.2 HIRSUTUM: A CASE STUDY IN FOSSIL INTERPRETATION

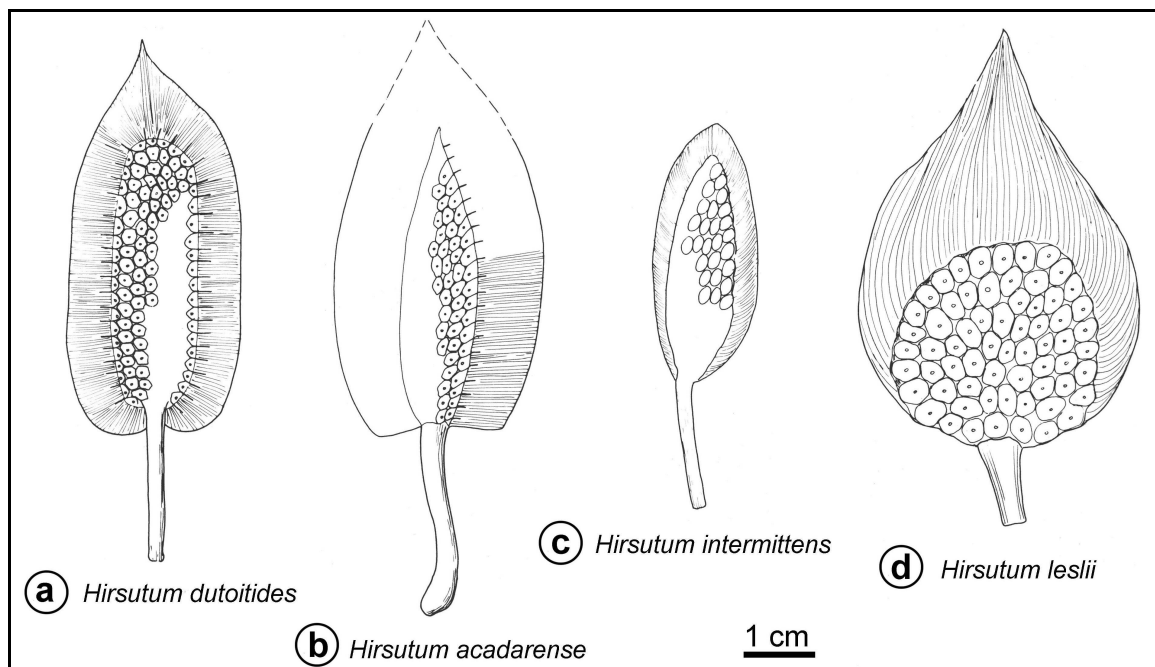
*Hirsutum* has proven to be the most astonishing of the currently recognised genera of ovuliferous glossopterid fructifications that have been found in South Africa. With the possible exception of *Dictyopteridium*, it has been the most hotly debated and misunderstood group of fertile structures found attached to *Glossopteris* leaves. Much of the controversy surrounding the morphological interpretation of *Hirsutum* arose from the bold conclusions drawn by Plumstead in the 1950's, when she originally described the genus (Plumstead, 1952, 1956a, 1958).

Plumstead (1956a) created *Hirsutum* to accommodate *Scutum*-like fructifications from Vereeniging that bore transient hair-like pollen-bearing organs, as opposed to the flat, bract-like pollen-bearing structures she considered to be characteristic of *Scutum*. *Hirsutum* was therefore created on the basis of differences in what Plumstead perceived to be staminate structures (see text-fig. 3.2.1). Most researchers, even proponents of her bivalve theory, found this to be inadequate grounds for a generic diagnosis, particularly as there was insufficient evidence that they were pollen-bearing reproductive structures in the first place (e.g. Mukherjee and Banerjee, 1966; Rigby, 1971; Schopf, 1976; Banerjee, 1984). Current thinking is that none of the described glossopterid fructifications is bisexual. The flat, bract-like structures seen in *Scutum* have since been interpreted as attached seeds with long wings, and the hair-like organs as apically inclined wing striations (Anderson & Anderson, 1985; McLoughlin, 1990a), views which are supported here.



**Text-figure 3.2.1.** Reconstructions of (a) *Scutum* and (b) *Hirsutum* as per Plumstead (1958a), illustrating the transient 'bract-like' and 'hair-like' features she interpreted as pollen-bearing organs.

*Hirsutum* has been an unpopular choice of name, as it does not strictly conform to the International Code of Botanical Nomenclature (Article 20.2; Greuter *et al.* 1994), which states that a descriptive term should not be used as a generic title<sup>2</sup>. Despite the nomenclatural debacle regarding the use of *Hirsutum*, Anderson & Anderson (1985) retained the name. They emended the diagnosis to accommodate their model of a dorsiventrally flattened, bifacial, ovuliferous fructification with a peripheral wing, and they distinguished *Hirsutum* and *Scutum* on the basis of differences in wing morphology. Although this emendation did serve to circumvent the speculative, interpretative aspects of Plumstead's diagnosis regarding pollen-bearing structures, their diagnosis was not unequivocal, as will be demonstrated in this chapter.



**Text-figure 3.2.2.** Reconstructions of (a) *Hirsutum dutoitides*, (b) *H. acadarensense*, (c) *H. intermittens* and (d) *H. leslii* modified from Anderson & Anderson (1985; text-figs 5, 6, 7 and 8, p. 118).

Anderson & Anderson (1985) recognised four species of *Hirsutum* (text-figs 3.2.2 a-d): *H. dutoitides* (Plumstead 1952) Plumstead 1958, *H. acadarensense* Anderson & Anderson 1985, *H. intermittens* Plumstead 1958 and *H. leslii* (Thomas 1921) Smithies 1985. A detailed examination of each of these South

<sup>2</sup> Please refer to Appendix IV for a full discourse on the taxonomic issues surrounding the genus *Hirsutum*.

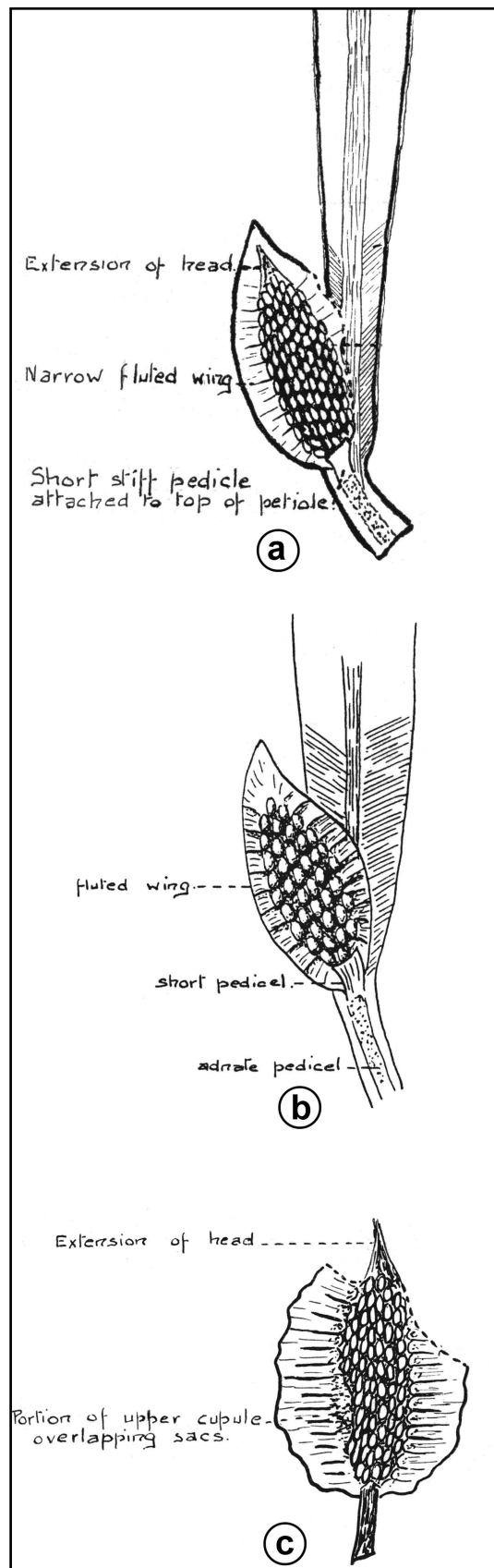
African species has revealed that this genus represents a diverse collection of fructifications bound together by vague and superficial similarities. It can be divided into at least three taxonomic groups that are sufficiently different from one another to warrant their elevation to generic status, in accordance with the currently accepted concept of the form genus as it is applied to glossopterid fructifications.

### **3.2.1 *HIRSUTUM DUTOITIDES* (PLUMSTEAD 1952) PLUMSTEAD 1958 AND *HIRSUTUM ACADARENSE* ANDERSON & ANDERSON 1985**

Plumstead (1952) initially named this taxon *Scutum dutoitides*, and based her diagnosis on a collection of specimens that she later (Plumstead, 1958) transferred to *H. intermittens* and *H. dutoitides*. *Scutum dutoitides* was at that stage distinguished from other members of the genus in being 'nearly twice as long as broad', and in being attached to the top of the petiole of its subtending *Glossopteris* leaf. According to Plumstead, the wing morphology also differed from other species in being relatively narrower and smoother, with poorly defined fluting and an entire margin. She noted that the wing usually tapered away at the base, and that it was 'finely striated in outward and upward curves looking like hairs' (Plumstead, 1952, p. 293). An interesting addition to her description was an annotation on her drawing of the type specimen, where she noted an 'extension of head' (text-fig. 3.2.3 a). This was drawn as a pointed extension of the apex of the receptacle, devoid of seed scars, and with longitudinal striations. In her descriptive catalogue (1952; p. 311), she characterised this feature as a 'strengthened part of the cupule' that extended '8 mm beyond the area covered by sacs (seed scars), to form a sharp point'.

In her 1956 account of the Vereeniging fructifications, Plumstead's reconstruction of *S. dutoitides* had changed (text-fig. 3.2.3 b). The longitudinally striated 'extension of head' had disappeared, and instead the apex was drawn with a few non-committal striations.

Plumstead's ideas on a bisexual fructification with hair-like staminate organs finally culminated in the creation of the genus *Hirsutum* in 1958 (a). She



identified two species, *H. dutoitides* and *H. intermittens*, insisting that both these taxa had a 'male half' which bore transitory pollen organs that left upward-curving impressions on the wing, and a 'female half' that had a narrow wing with fluting, such as that seen in members of the genus *Scutum*. She differentiated the two species on the basis of receptacle shape (which was more oval in *H. dutoitides*), the fact that the wing tapered more abruptly at the base in *H. intermittens*, and that *H. intermittens* tended to be larger than *H. dutoitides*. She also cited differences in associated *Glossopteris* leaves. In creating *H. intermittens*, Plumstead (1958a) transferred all the specimens bearing evidence of 'transient pollen organs' out of the type species of *Hirsutum*. None of the specimens remaining in *H. dutoitides* had upwardly curving striations on the 'male' or 'female' halves.

**Text-figure 3.2.3.** Drawings of the type specimens of: (a) '*Scutum dutoitides*' in 1952 (Plumstead, 1952; text-fig.2, p. 291), (b) '*S. dutoitides*' in 1956 (Plumstead, 1956a; text-fig.2, p. 8) and (c) '*S. stowanum*' (Plumstead, 1952; text-fig.5, p. 299).

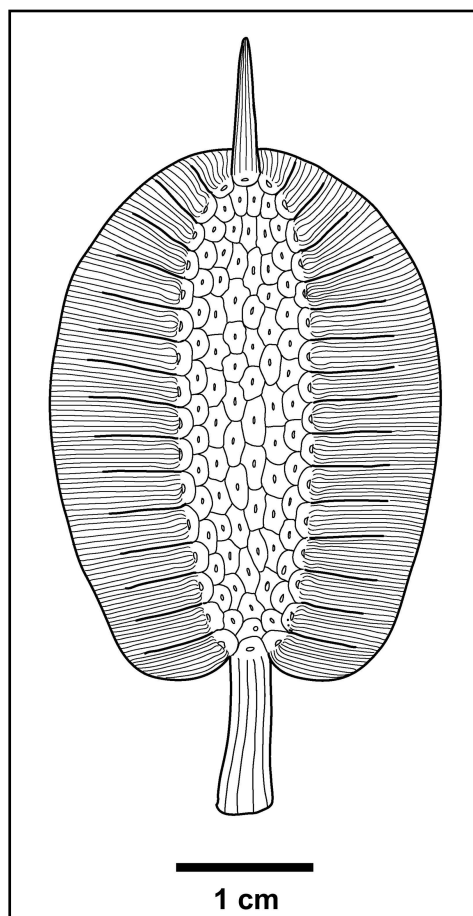
Plumstead described two species, *Scutum stowanum* (1952) and *S. thomasii* (1958a), which were very similar to *H. dutoitides*. *Scutum stowanum* was distinguished on the basis of its high length to width ratio, oval shape and broad wing with transverse as opposed to radiating fluting. However, the only feature Plumstead cited to differentiate it from *S. dutoitides* was its large size. In her drawing of the type specimen, Plumstead once again annotated a pointed, longitudinally striated extension of the receptacle apex as 'extension of head' (text-fig. 3.2.3 c). *Scutum stowanum* was synonymised with *H. dutoitides* by Anderson & Anderson (1985), and *S. thomasii* later proved to be a laterally compressed taphomorph of *H. dutoitides* (Adendorff *et al.*, 2002).

When Anderson & Anderson (1985) revised Plumstead's taxonomy of the South African glossopterid fructifications, they emended her (1958a) diagnosis of *Hirsutum*, describing an isobilateral, dorsiventral fructification that was exclusively ovuliferous, and interpreted her staminate features as wing striae. They considered a contracted, tapering wing base to be a diagnostic feature of the genus, 'except in one sp.' (p.119). In fact, only two of the four species they included within the genus exhibited a tapering wing base. The type species *H. dutoitides* as well as *H. acadarensis* (text-figs 3.2.2 a, b) possessed well-developed basal wing lobes, such as those seen in members of the genus *Scutum*. Ultimately, the only diagnostic character cited by Anderson & Anderson (1985) to distinguish this group of fructifications from *Scutum*, was that the wing was 'striate appearing hirsute'.

A close examination by the author of all the specimens attributed to *H. dutoitides* and *H. acadarensis* revealed that the wings of these species were very similar to those seen in *Scutum*. They all bore the same fine, radially oriented striations and fluting, although in the two *Hirsutum* species, the wing fluting was only pronounced near the receptacle edge, becoming less distinct towards the margin. However, the apices of the *Hirsutum* fructifications presented an interesting feature that immediately distinguished these fructifications from any other that had been described.

The wing was not extended into a pointed apex as described and reconstructed by Plumstead (1952, 1956a, 1958a) and Anderson & Anderson (1985). The wing itself was found to be discontinuous at the apex of the receptacle, and the receptacle was extended into a longitudinally striated spine. This spine was continuous with the sterile surface of the fructification. Referring back to Plumstead's drawings in text-figure 3.2.3, her annotations for 'extension of head' make a lot more sense. Plumstead had noticed the apical spines, but had not recognised them as a significant, diagnostic feature.

The presence of an apical spine, relatively broad wing with weakly defined fluting, together with the high length to width ratio and narrowly lanceolate shape, formed the basis of the diagnosis for a new genus *Gladiopomum*, to accommodate *Hirsutum dutoitides*, *H. acadarensis* and new specimens from the Rietspruit locality (Adendorff *et al.*, 2002; text-fig. 3.2.4).



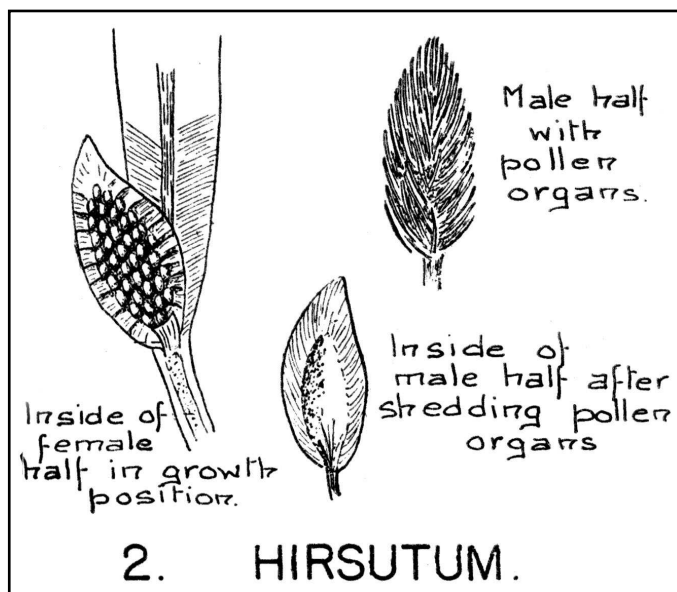
See Appendix III for a copy of Adendorff, McLoughlin & Bamford (2002).

**Text-figure 3.2.4.** Reconstruction of an impression fossil of the fertile surface of *Gladiopomum dutoitides* from Adendorff *et al.* (2002; p. 15, fig. 29).

### 3.2.2 *HIRSUTUM INTERMITTENS* PLUMSTEAD 1958

When Plumstead (1958a) created the species *Hirusutum intermittens*, she described a fructification with a 'male half' bearing transient, thread-like staminate features, and a 'female half' bearing sac-like ovules (text-fig. 3.2.5). The two halves were purportedly fused together early in the development of the polysperm, opening briefly to allow for pollination of the ovules in the 'female half', and dispersal of pollen from the 'male half'. Most authors found these ideas too imaginative, and considered them to be based on a misinterpretation of the impression fossils (eg. Schopf, 1976; McLoughlin, 1990a).

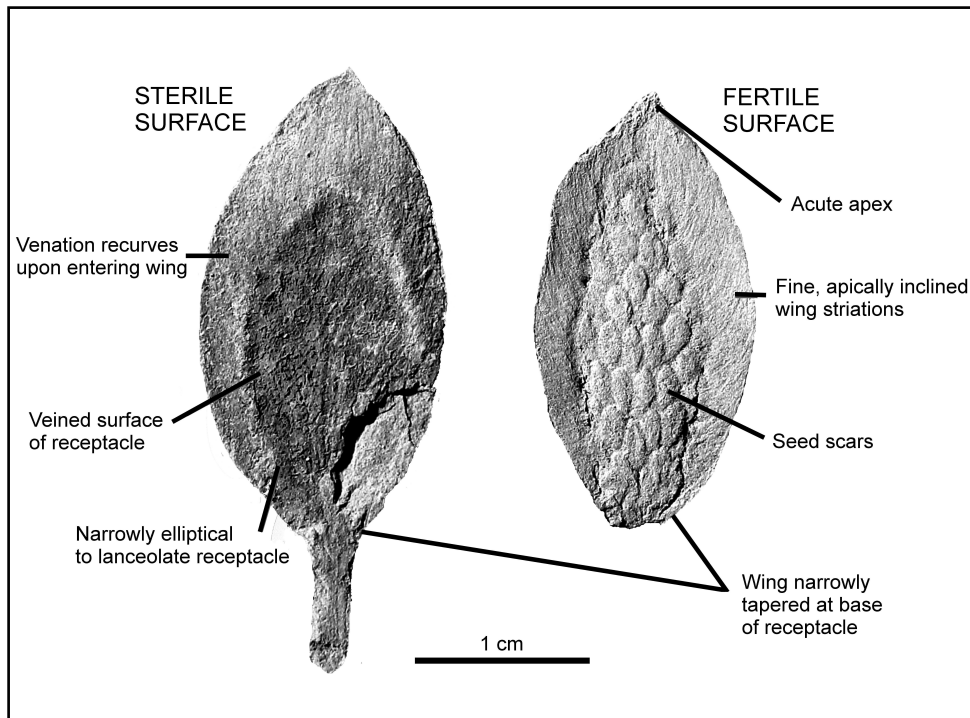
When Anderson & Anderson (1985) revised *H. intermittens* according to the currently favoured model of a simple, dorsiventral structure for the ovuliferous fructifications, they streamlined the diagnosis, describing a polysperm with a



narrowly ovate receptacle with rounded acute apex and a narrow, peripheral wing which tapered away at base and bore striae that curved upwards.

**Text-figure 3.2.5.** Plumstead's (1958a) reconstruction of *Hirusutum*, illustrating the 'female half' and the 'male half' of the fructification (p. 54, fig. 2).

Superficially, this seemed to the author to be a far more reasonable account of the species than Plumstead's theories about fertile and sterile halves and pollen-bearing structures, and there were plenty of specimens that accorded perfectly with Anderson & Anderson's (1985) descriptions (e.g. text-fig. 3.2.6).

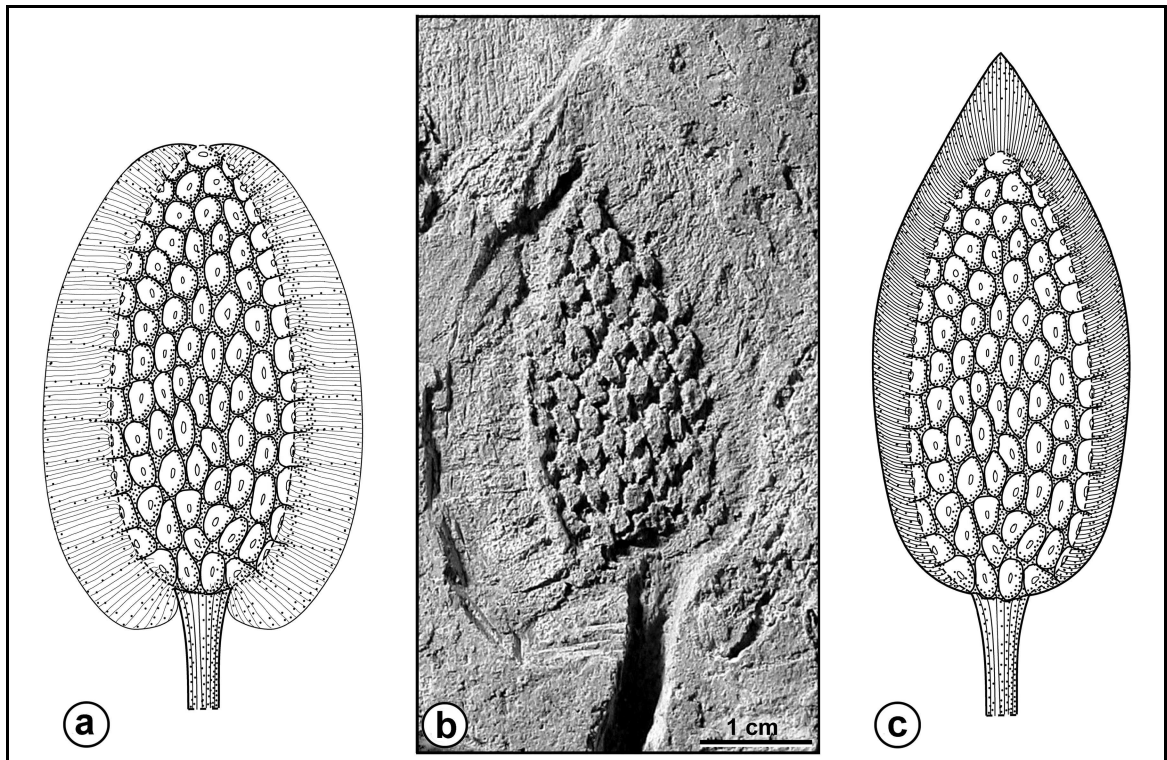


**Text-figure 3.2.6.** 'Typical' examples of impression fossils showing the sterile surface (BP/2/13979) and fertile surface (BP/2/13964) of *H. intermittens*, illustrating the diagnostic features of the species as described by Anderson & Anderson (1985).

However, the type specimen [BP/2/14003; pl. 12, fig. (a)] was problematic. It did not conform to Anderson & Anderson's (1985) clear-cut diagnosis. The right-hand side of the fructification was a perfect representation of the taxon as described by Anderson & Anderson (1985): the pointed apex, tapered base and fine, apically inclined striae were all present. The left-hand side of the impression presented a different picture. The wing was of even width to the base of the fructification, where it formed a truncated lobe at pedicel insertion, and it bore radially oriented striations and fluting. Text-fig. 3.2.7 illustrates the two wing morphologies as they could be reconstructed for each half of the fructification.

The most immediately apparent solution to this dilemma was that there had been some distortion of the plant material during preservation, but it was difficult to envision how this might have happened, as the morphologies were very consistent and apparently well-preserved in each half of the fructification.





**Text-figure 3.2.7.** (b) Holotype of *Hirsutum intermittens* (BP/2/14003), with reconstructions based on (a) the 'scutoid' wing form on the left side of the fructification, characterised by radial striations and fluting and a consistent width to the base of the receptacle and (c) the 'hirsutoid' wing visible on the right side of the fructification with fine, upward-curving striations, a pointed apex and a tapered base.

Close inspection of the fossil revealed that the portion of wing bearing apically inclined striations lay at a shallower level in the sediment, and even appeared to overlie the fluted wing.

Fortunately, *H. intermittens* is one of the more common fructifications to have emerged from the Leeukuil quarries at Vereeniging, and over 40 specimens were available at the BPI and the Vaal Teknorama Museum for examination (see Table A.I.5, Appendix I). Careful observation and dissection of these specimens revealed the following unexpected facts about this group of polysperms:

1) many specimens, including the holotype (BP/2/14003), possessed two marginal wings;

- 2) in impressions of the fertile surface of the fructification, the impression of the hirsutoid wing was consistently at a shallower level in the sediment than the scutoid wing;
- 3) in impressions of the fertile surface, the boundary between the hirsutoid wing and the receptacle edge was slightly irregular and was marked by a crack/groove in the impression;
- 4) the hirsutoid wing was continuous with the sterile surface of the receptacle and the fine striations/veins on the receptacle continued uninterrupted onto the wing, recurving at the receptacle edge and arching upwards towards the apex;
- 5) the scutoid wing, in impressions of the fertile surface of the fructification, continued to the cicatrices of the marginal seed scars of the receptacle, and fluting corresponded to the positions of the marginal scars (as in other taxa such as *Scutum*);
- 6) the scutoid wing always lay at a shallower level in the sediment than the hirsutoid wing in impressions of the sterile surface of the fructification.

Perhaps one of the first explanations that comes to mind to account for an apparent duality in wing structure, is that the wing may have been folded over, as seen in sections of permineralized fructifications (Gould & Delvoryas, 1977). But how could this explain the two, inherently different wing morphologies that occur within the same specimen, and which are both clearly in organic attachment with different surfaces of the same receptacle? The scutoid wing bears radially oriented striations and fluting which exactly match the positioning of the marginal seed scars (as seen in all other members of the Dictyopteridiaceae), and the fine, apically inclined striations on the hirsutoid wing can clearly be followed onto the sterile surface of the fructification without interruption. These features are seen in the part and counterpart of the same specimen. There is no feasible way in which the wing could fold in such a manner as to have the 'free' edge (margin) lining up precisely with features on the receptacle, and moreover, forming a smooth, uninterrupted union with the receptacle on both the sterile and fertile surface.

Dissections of specimens VM/03/3205/60 and VM/03/3205/63 (pls 16, 17) clearly demonstrated that the scutoid and hirsutoid wing impressions were

created by two distinct wing structures that were superposed along the periphery of the receptacle, *each of which was in clear and continuous organic attachment with its respective surface of the receptacle, within the same specimen.*

If we return to the schematic cross-section of an impression fossil discussed earlier in Section 3.1.2 (text-fig. 3.1.2) and extrapolate the model of a simple, dorsiventral ovuliferous fructification to accommodate a double wing structure, the individual observations listed above fall into place.

Text-figure 3.2.8 (a) represents an impression fossil of a glossopterid ovuliferous fructification. All the organic material has weathered out, leaving a space in the matrix that is essentially a detailed, three-dimensional (although compressed) mould of the original plant structure. The fossil is oriented with the seed-bearing surface above and the sterile surface below. The primary wing is continuous with the sterile surface of the fructification, and in *H. intermittens* represents the hirsutoid wing bearing the apically inclined striae. The secondary wing lies in the same plane as (and is contiguous with) the fertile surface, and in *H. intermittens* it represents the scutoid, or radially striated and fluted wing. The dotted lines represent potential cleavage planes in the matrix that would result in exposure of the impression fossil.

Figure (b) is the situation that would result from a cleavage plane which passed through the primary or hirsutoid wing. The part bears an impression of the seed scars of the fertile surface, and the secondary wing is obscured by the wedge of sediment which intruded between the wings prior to fossilisation. This wedge of sediment bears an impression of the upper surface of the primary wing. Note how the wedge encroaches slightly on the marginal seed scars, and how there is a lack of continuity between the impression of the primary wing and the impression of the fertile surface. This discontinuity is what Plumstead described as the 'crack' around the receptacle. If the wedge bearing the impression of the primary wing was removed, the underlying impression of the secondary wing would be exposed. The counterpart in this scenario is an uncomplicated, completely exposed impression of the sterile surface of the fructification, with a

slightly concave veined receptacle flanked by a convex impression of the primary wing.

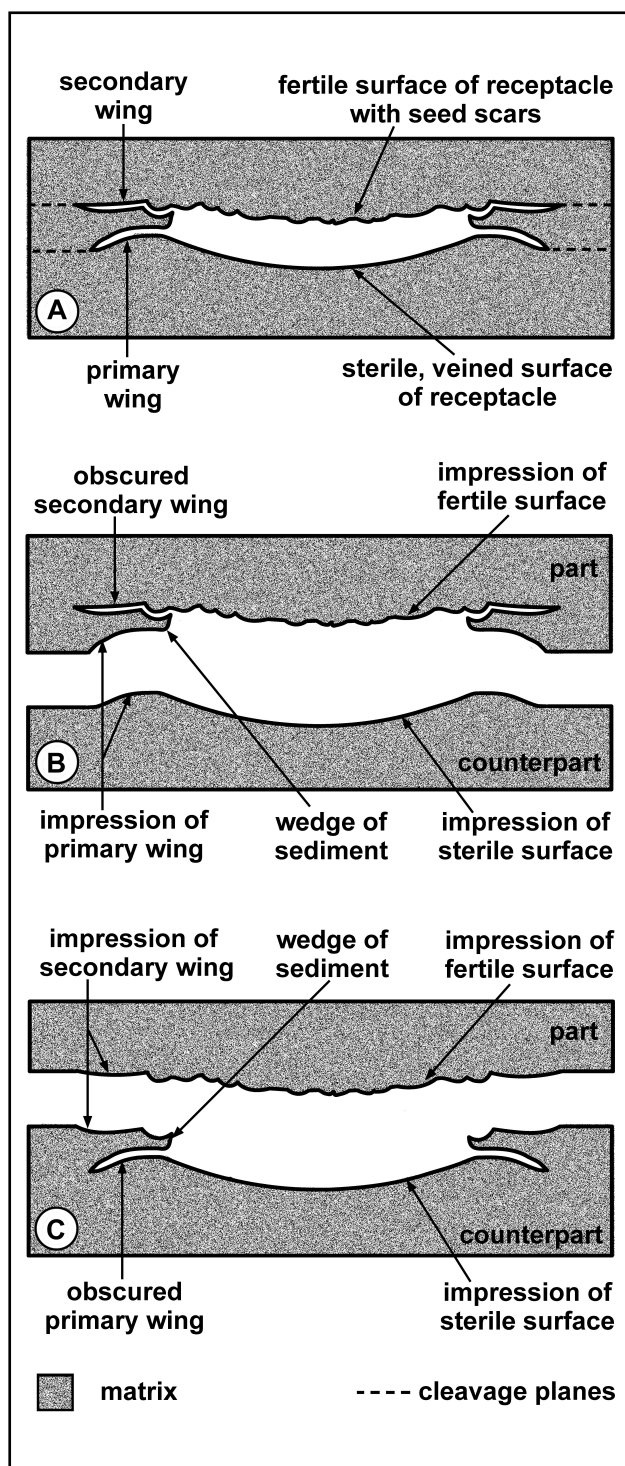
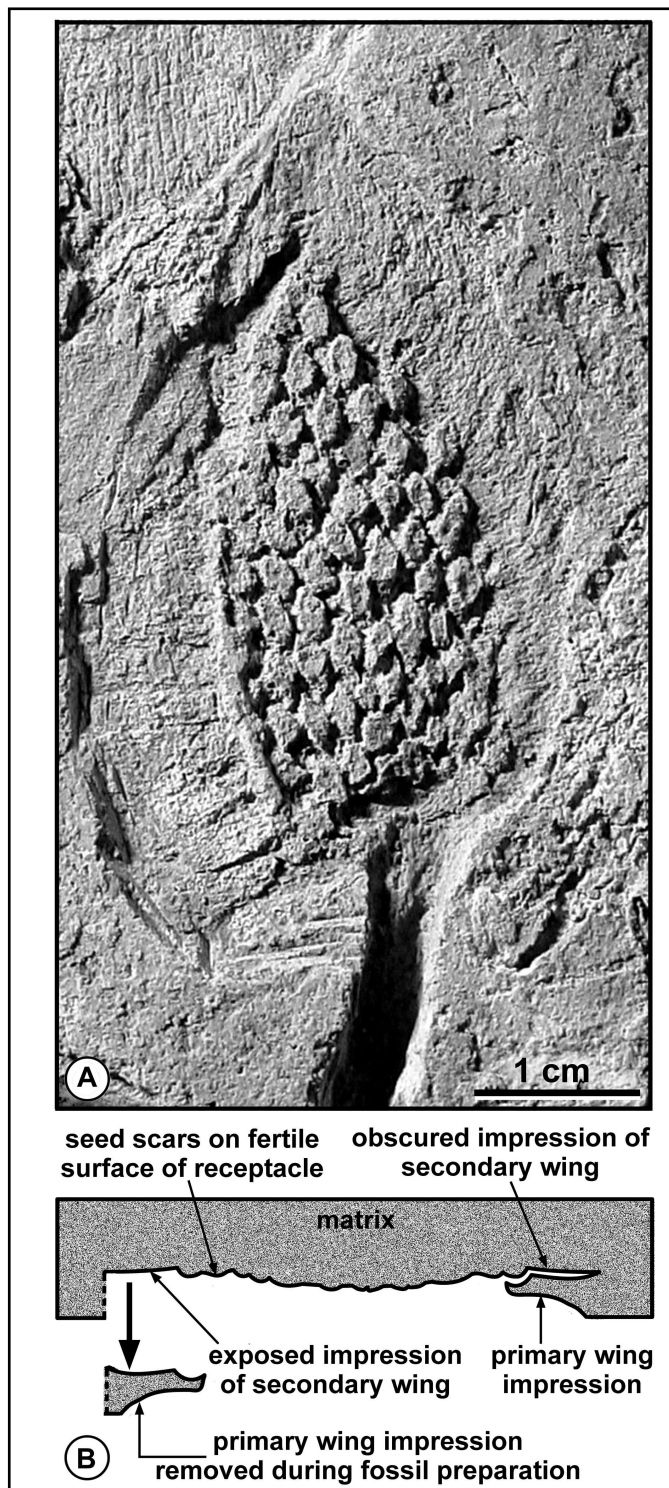


Figure (c) depicts the scenario that would arise if the cleavage plane passed through the secondary wing.

The part bears an impression of the fertile surface of the receptacle and the upper surface of the secondary wing, which is

continuous with the fully exposed marginal seed scars. In the counterpart, the sterile surface of the receptacle is exposed, but the primary wing impression is obscured by a wedge of mud bearing an impression of the lower surface of the secondary wing. If this mud wedge was removed, it would reveal the primary

wing beneath. Note the resulting vertical discontinuity between the impression of the secondary wing, and that of the sterile surface of the receptacle. If we test this model on the confusing holotype, it becomes immediately apparent how the



left side of the fructification can display an impression of a fluted, radially striated scutoid wing, and the right side a hirsutoid wing morphology with apically inclined striae.

In text-fig. 3.2.9 (b), the intact hirsutoid wing lies at a level closer to the cleaved surface of the matrix, than does the impression of the secondary wing. The wedge of mud bearing the impression of the primary wing has been removed on the left side of the fructification, resulting in exposure of the scutoid wing along the left periphery of the receptacle.

**Text-figure 3.2.9.** (a) Impression fossil of the holotype of *Hirsutum intermittens* (BP/2/14003); (b) model of a cross-section through the impression fossil, illustrating how the two wing morphologies were exposed during preparation.

So how do these observations compare with Plumstead's (1952, 1956a, 1958a) descriptions and interpretations? It seems that although Plumstead was a little over-enthusiastic and inflexible with some of her ideas, her basic descriptions

and observations were detailed and accurate. She made a number of vitally important, illuminating revelations that were swept aside amid the controversy surrounding her 'bivalve' theory and her insistence that these fructifications were bisexual. It is only now, in retrospect, that her observations can be fully appreciated and understood.

Plumstead clearly and unequivocally described the presence of two individual wings, but interpreted these wings as belonging to two separate 'cupules', in accordance with her 'bivalve' theory.

In her very first paper on the subject (1952, p. 293), Plumstead described in detail how she chipped away the wedge of mud bearing the impression of the 'male half' to reveal the *Scutum*-like wing beneath:

'In a number of specimens ... the space between the two cupule wings, equivalent to the depth of the swollen sacs, is filled with mud which takes the fine hair-like striations of the upper cupule. In several specimens this mud was lifted and revealed the lower wing beneath ... In these cases the boundary of the head is a crack, giving the impression that the head is a separate spike and not attached to the lower cupule... Attempts to lift the head from the underlying cupule only succeeded at the edge. The main portion was attached.'

She explained how the upwardly curving striae:

'...are the impression on a mud film of the wing markings of the opposite half of the cupule. This film can be chipped away to show the true fluted wing of the adaxial half underneath' (caption to fig. 2 of Plate 7, p23; 1952).

In 1956 (a, p. 9) Plumstead cited this film or wedge of mud as the cause of 'the contradiction of a hair marked wing around the sac-covered head'. She goes on to say that:

'In these cases, the sacs at the edge of the head appear to be broken but the mud, which bears the impression of the upper cupule on its surface can be chipped away to reveal the true fluted wing and normal head margin of the fertile cupule beneath'.

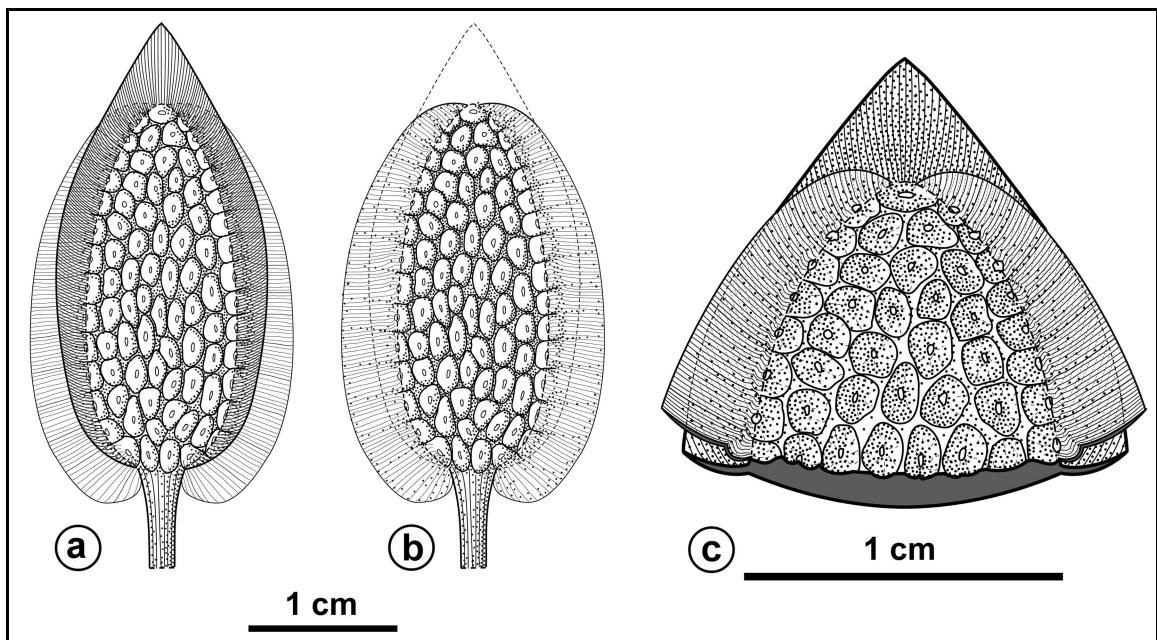
She elaborated on the differences in the morphology of the two wings in her 1958 (a) publication, describing the wing of the 'male half' as having a pointed

apex, a tapered base and fine, upward-curving striae that she interpreted to be impressions of filamentous pollen organs. She referred to the wing of the 'female half' as the 'true wing', and described it as similar to the wing of *Scutum* with well-defined fluting and radiating striations.

Plumstead (1958a) described the type specimen of *H. intermittens* (BP/2/14003) as follows:

'The true wing of this half can be seen on the left-hand side. It is broad, even at the base, and well-fluted, with radiating grooves. On the right-hand side, and at the sharp apex, the hairy impression of the wing of the male half has been left on the intervening wedge of sediment. It may be noticed that this wing tapers sharply to the base and that the hair markings all run upward. *Originally the specimen split so that the hairy wing was visible all round. It had to be chipped away on the left-hand side.* '

In this final passage Plumstead explained how she dissected away the hirsutoid (primary) wing on the left side of the fructification, to reveal the scutoid wing beneath, just as predicted in text-fig. 3.2.9.



**Text-figure 3.2.10.** Fossil reconstructions of (a) *Bifariaia* with the primary or hirsutoid wing exposed and (b) with the secondary or scutoid wing exposed, and (c) a reconstruction of the apical portion of the fructification indicating the positions of the two, superposed wings relative to the receptacle.

In light of the genus *Hirsutum* recently having been disbanded (Adendorff *et al.*, 2002; see also Appendix IV), and because of the unique morphological aspects of this fructification, it has been recommended herein (section 7.1) that the specimens currently residing in *Hirsutum intermittens* be transferred to a new genus. The name *Bifaria*, meaning ‘two wings’ (Latin) has been proposed. A reconstruction of the fossil and the apical portion of the fructification have been prepared in text-fig. 3.2.10.

### **3.2.3 *HIRSUTUM LESLII* (THOMAS 1921) SMITHIES 1985**

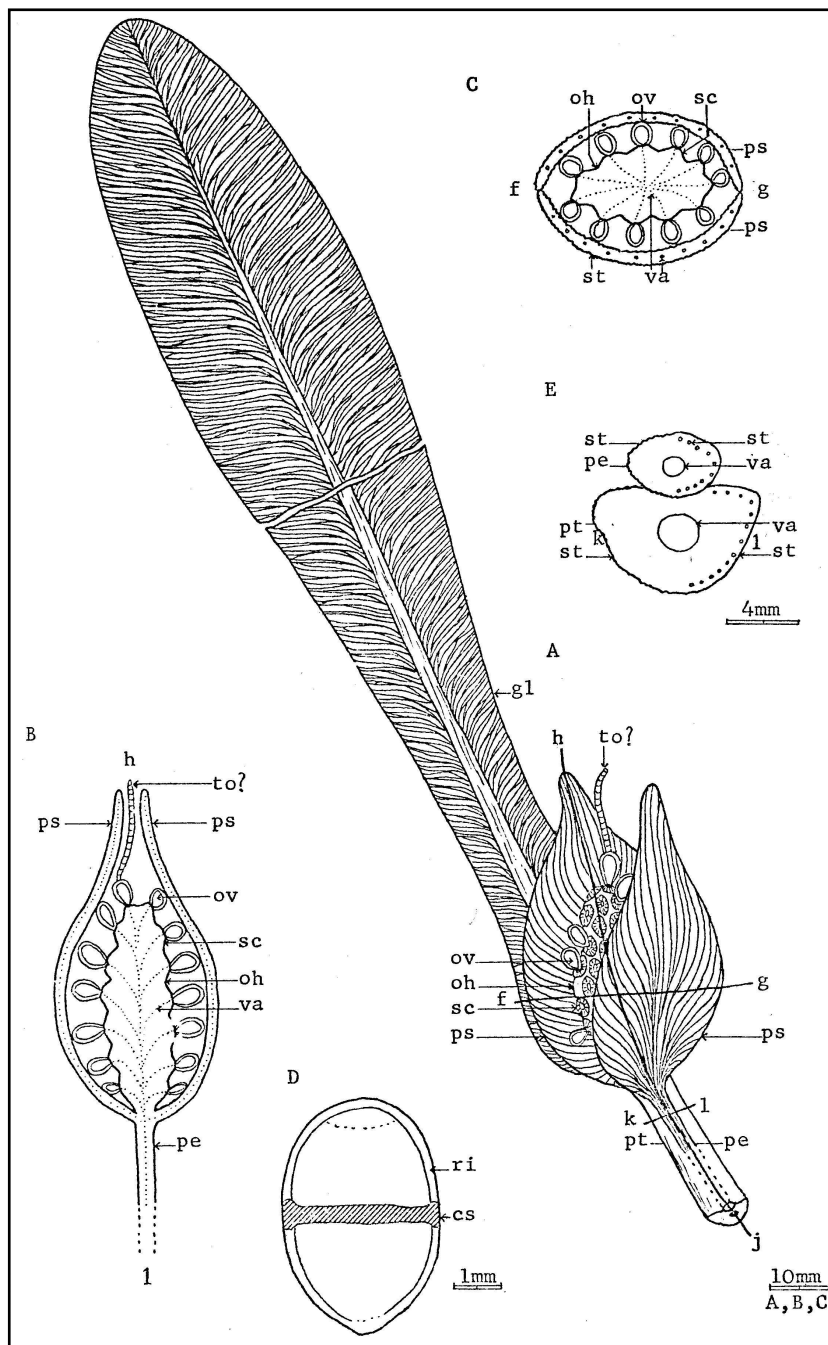
In 1921, H. H. Thomas of Cambridge University wrote a paper describing a peculiar fertile structure from the fossiliferous beds of Vereeniging, which had been collected by an amateur South African palaeobotanist, T.N. Leslie, nearly ten years earlier. Thomas (1921) recognised that the fossilised fructification was closely allied to, but not necessarily referable to, the genus *Ottokaria*. Not wishing to erect a new genus on the basis of a single, poorly preserved specimen, he tentatively named the taxon *Ottokaria leslii*.

Despite intensive collecting at the Vereeniging locality by S.F. Le Roux and E.P. Plumstead over a period of thirty years, further examples of this fructification were never found. Then in 1969 (pl. 13, figs 6-7), Plumstead briefly mentioned two large, unnamed fructifications from the Hammanskraal locality which bore a strong resemblance to the specimen described by Thomas (1921), and which she characterised as ‘new and significant fructifications of Glossopteridae which enclosed the seeds’.

Smithies (1978), in her MSc dissertation, recognised the similarities between the Hammanskraal material and Thomas’ (1921) single example of *Ottokaria leslii*, and realised that these specimens had little in common with other members of the genus *Ottokaria*. The wing was entire with an extended and pointed apex, and tapered towards the base of the receptacle. It also bore fine striations that were apically inclined, converging on the apex or intersecting the wing margin at a steep angle. These were all features reminiscent of Plumstead’s (1956a, 1958a) genus *Hirsutum*, and Smithies (1978) suggested



the new combination *Hirsutum leslii* for the fructifications. The name was officially published by Anderson & Anderson (1985, p. 121).



**Text-figure 3.2.11.** Proposed reconstruction of a fertiliger of *Hirsutum leslii*, extracted from Smithies (1978; fig. 133, p. 310). She depicted the fructification as tripartite, with a separate, central, dorsiventral receptacle that bore seeds on both surfaces, and which was flanked on each side by a sterile scale, all of which shared a common point of attachment on the pedicel.

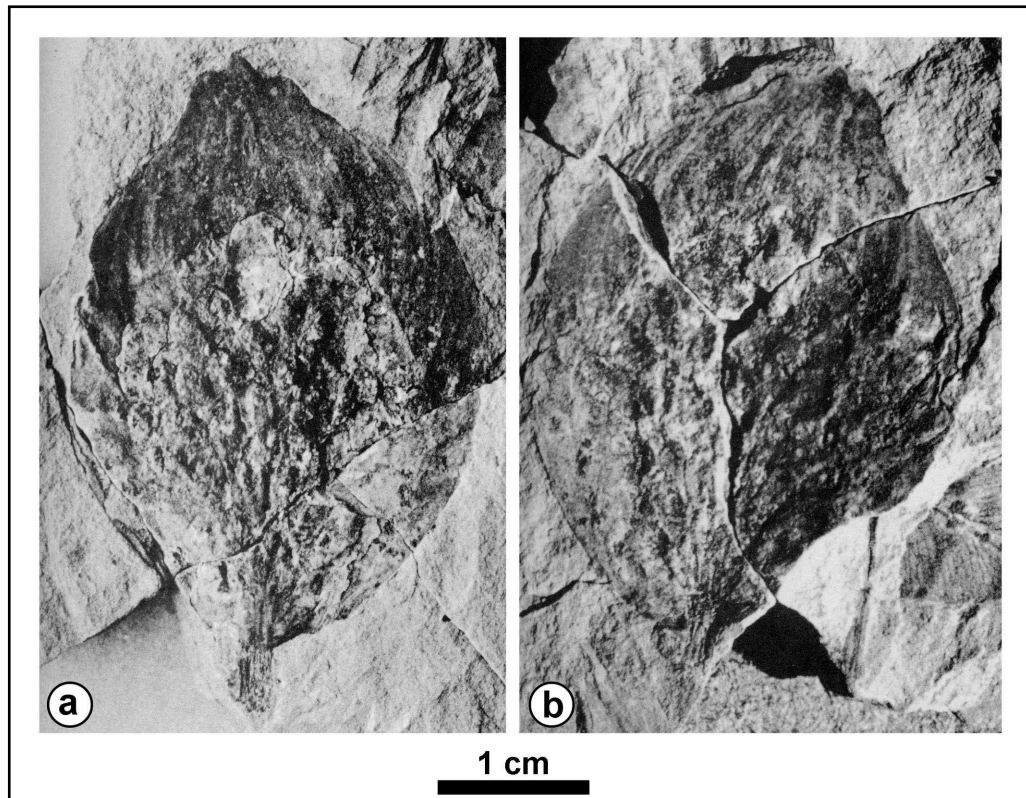
In Smithies' (1978) original description of *Hirsutum leslii*, she made some remarkable observations. She noted that there were multiple layers of phytolium and matrix within individual compression-impression fossils (Smithies, 1978; pp. 253-259). She also noted that the impression of the seed-bearing surface of the receptacle could be dissected away to reveal the wing continuing beneath. Smithies (1978) concluded that the fructifications were tripartite, bilaterally

symmetrical, compound structures comprising a central, biconvex, seed bearing head (seeds borne on both surfaces), flanked dorsally and ventrally by a sterile scale-like structure, all sharing a point of origin on a stout pedicel (see text-fig. 3.2.11).

In the published description of *H. leslii* (in Anderson & Anderson, 1985; p. 121), all of Smithies' original interpretations and observations about a multilayered fructification were omitted. The resulting diagnosis is a streamlined version in line with the model of a simple, dorsiventral fructification with a single, peripheral wing that applies to most of the other members of the Dictyopteridiaceae (the Ottokariaceae in Anderson & Anderson, 1985).

A year prior to Smithies' (1978) account of this taxon, Appert (1977) described an almost identical fructification from the Sakoa Basin in south-western Madagascar, which he called *Elatra bella*. He noted the close similarities between the Madagascan specimen and *Ottokaria leslii* described by Thomas (1921) from Vereeniging, suggesting that the South African specimen probably belonged in his new genus *Elatra*. He also noted that the specimens from Hammanskraal which Plumstead (1969) had figured were very similar to his Madagascan material. *Elatra bella* seemed to differ from the Hammanskraal material in having a shorter wing with a lobed apex, as opposed to the entire-margined, elongated to acuminate wing seen in the South African examples (plates 23 - 42).

Appert (1977), like Smithies (1978), described how the impression of the seed-bearing surface of the receptacle was borne on a mass of sediment which could be removed to reveal the wing continuing beneath. He interpreted this to mean that the receptacle was a hollow structure which allowed for the entry of sediment. He also observed that the receptacle was not joined to the 'wing' for most of its length, only in the basal parts, or at the pedicel. A further interesting observation made by Appert (1977), was that the base of the receptacle was rather smooth, and was evidently covered by a second, smaller wing (see text-fig. 3.2.12 for part and counterpart of *Elatra bella* specimen).



**Text-figure 3.2.12.** Photograph of *Elatra bella* from Madagascar (a) fertile surface, (b) sterile surface (Appert, 1977; pl. 32, figs 2 & 3).

The Hammanskraal specimens share so many similarities with Appert's *Elatra bella* (1977), that the new combination *Elatra leslii* is proposed herein (section 7.3, p. 200) for specimens currently attributed to *Hirsutum leslii*.

Smithies (1978) reported the existence of over three hundred compression/impression fossils of *E. leslii* from Hammanskraal. Unfortunately not all of these could be located, and many that were found proved too fragmentary to be of great benefit. The observations here and the diagnosis in section 7.3 (p. 204), were based on just over 50 fossil specimens (see Table A.I.8, Appendix I for details).

Smithies (1978) based her reconstructions on the assumption that there had been a degree of replacement of the fossil phytolite (organic material) with clay in the Hammanskraal specimens. These fossils certainly are complex, but following close examination of the material, the author found them to be decipherable in terms of straightforward compressions and impressions. There

was no evidence in any of the specimens of replacement of organic material by clay or minerals.

An intensive investigation of the Hammanskraal specimens led to some interesting conclusions that did not accord with Appert's (1977) or Smithies' (1978, 1985) accounts of the fructifications. The following generalisations could be made:

*A. Impression of fertile surface*

- 1) the impression of the seed-bearing surface of the receptacle lies at a shallower level in the sediment than the impression of the primary wing;
- 2) the impression of the receptacle shows no continuity with the primary wing in the apical and medial regions, and either has a jagged, broken outline, or is smooth and slightly curved under, towards the primary wing;
- 3) the basal marginal seed scars are contiguous with a scutoid secondary wing, which extends as two rounded, basal lobes that are angled slightly into the sediment, away from the plane of the receptacle and beneath the impression of the pedicel;
- 4) the secondary wing bears radially oriented fluting and striations typical of members of the Dictyopteridiaceae (grooves corresponding to junctions between adjacent seed scars);
- 5) a few mm beyond the edge of the receptacle, there is a gentle step in the primary wing, the region underlying the impression of the receptacle being slightly depressed relative to the distal part of the wing;
- 6) the primary wing is extended into a pointed to acuminate apex, but tapers towards the base of the receptacle;
- 7) the primary wing is a perfect counterpart of the wing in the impression of the sterile surface, with matching fluting and striations that converge on the apex;
- 8) the impression of the fertile surface of the receptacle can be completely dissected away to reveal the impression of a lateral and distal extension of the primary wing beneath;
- 9) fluting and striations of the primary wing continue uninterrupted into this extension;

- 10) the basal third of the extension is split into a tent-like opening that spans the proximal part of the receptacle;
- 11) the proximal edges of the narrowed basal wedges of the extension are at a shallower level in the sediment than the proximal portions of the secondary wing lobes; the distal edges along the aperture, lie deeper in the sediment, passing beneath the proximal margin of the secondary wing;
- 12) in many specimens, there are impression or compression fossils of multiple seeds within the mass of sediment bearing the impression of the seed scars.

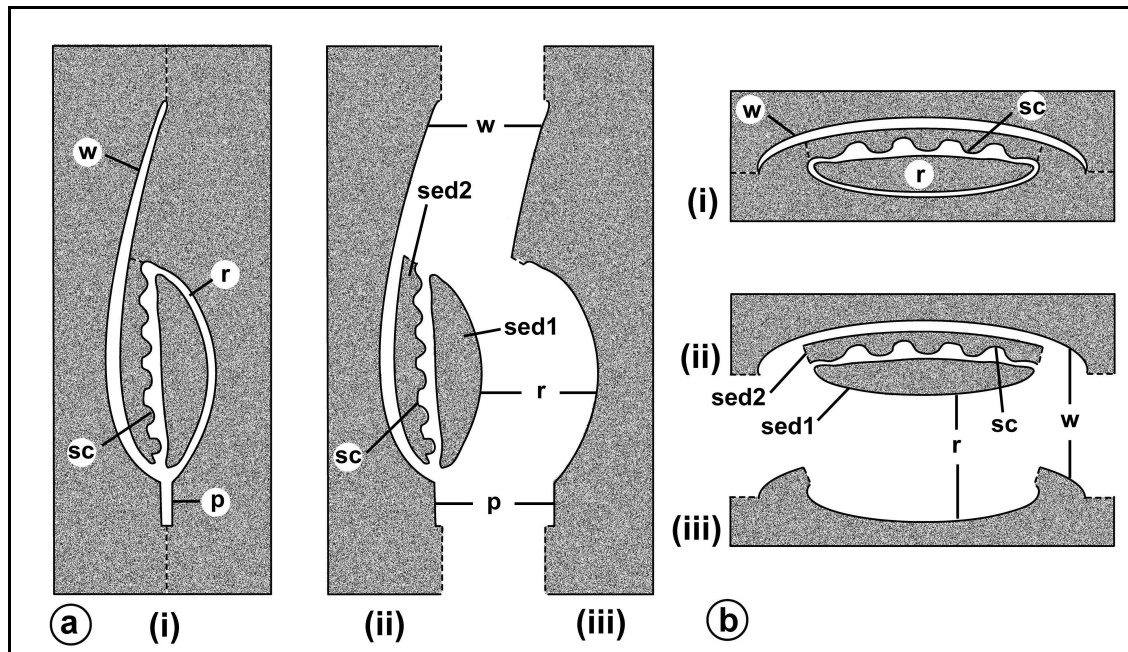
#### *B. Impression of sterile surface*

- 1) venation on the sterile surface of the receptacle continues uninterrupted into the primary wing, recurving at the edge of the receptacle and following a steeply inclined path, converging towards the apex;
- 2) although the impression is a continuous surface, there is a shallow ledge differentiating the edge of the receptacle from the primary wing, the impression of the receptacle being slightly depressed relative to the wing;
- 3) the base of the sterile surface is rounded to truncate, and may have a small, rounded lobe on either side of the pedicel.

Translation of this body of evidence into an understanding of the three-dimensional structure of the fructification was a challenge. The most puzzling aspects were firstly, the isolated mass of sediment bearing the impression of the fertile surface of the receptacle, and secondly, the wing that was an identical match to the primary wing on the counterpart, but which extended beneath the impression of the seed scars.

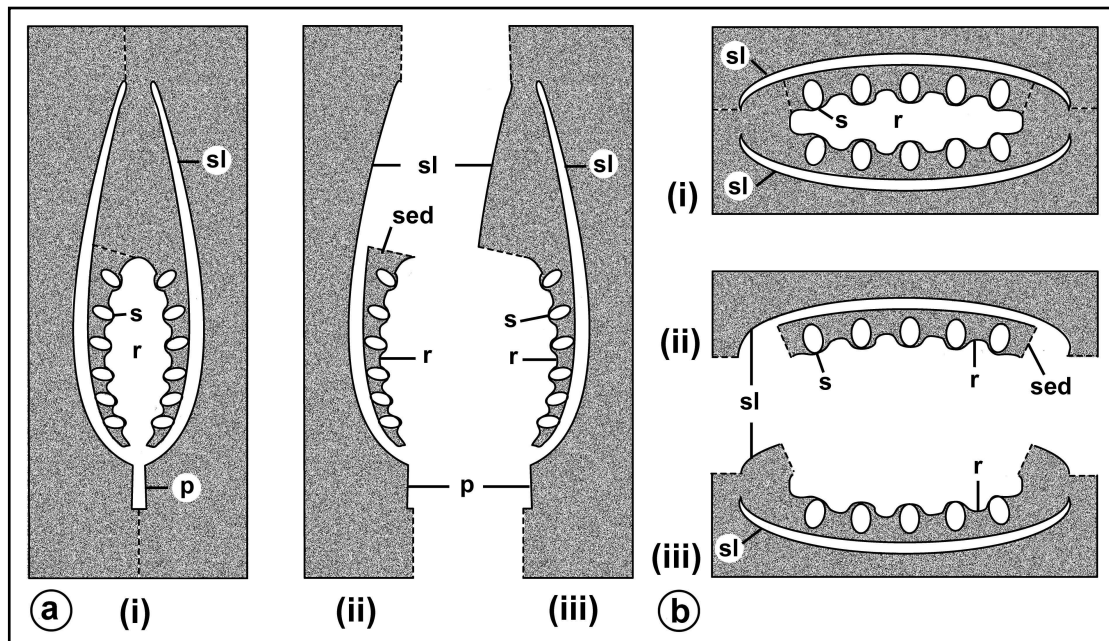
Appert (1977) and Smithies (1978) both described models to explain the occurrence of a free-standing impression of the seed-scar bearing surface of the fructification overlying a continuous wing or scale structure, but neither of their models was able to simultaneously account for the counterpart impression of a simple, uninterrupted sterile surface where the receptacle and primary wing were continuous. These models also failed to accommodate the presence of a basal secondary wing.

Appert (1977) suggested the receptacle had been a hollow structure that had allowed for infiltration of the sediment during fossilisation. If this had been the case, the mass of sediment overlying the wing may have borne secondary imprints of the seed scars, and removal of this matrix would theoretically have exposed the fertile surface of the receptacle on a second mass of sediment, not an underlying wing. Removal of this second wedge of matrix would have exposed the wing continuing beneath. Whether or not the receptacle was hollow, the sterile surface would have been at a different level in the matrix to the primary wing, and could not have been continuous with the wing (text-fig. 3.2.13).



**Text-figure 3.2.13.** Sections through an imaginary impression fossil in accordance with Appert's (1977) model of *Elatra bella*, with a hollow receptacle and partially free wing, attached only at the base of the receptacle. **(a)**(i) Medio-longitudinal section through the fossil showing the position of the receptacle (r), seed-scars (sc), wing (w) and pedicel (p); (ii) & (iii) are the result of one possible cleavage plane through the fossil: (ii) this scenario results in a part with two bodies of sediment overlying the impression of the wing, the uppermost wedge (sed1) bearing an impression of the inner surface of the cavity within the hollow receptacle, and the lower wedge (sed2) bearing an impression of the fertile surface of the receptacle; (iii) in the counterpart, the impression of the scale leaf is at a slightly shallower level in the sediment than the impression of the receptacle - no fossil specimens from Hammanskraal have been found to fit this model. **(b)**(i) Medio-lateral cross-section through the fossil; (ii) & (iii) are the result of the same cleavage plane illustrated in (a) [dashed lines = cleavage planes in the matrix].

Smithies' (1978) model of a tripartite fructification would have resulted in a part and counterpart fossil with an impression of a fertile surface overlying a scale, and an impression of the opposite fertile surface with a discontinuous fragment of the apex of the same scale lying at a shallower level in the sediment (text-fig. 3.2.14).

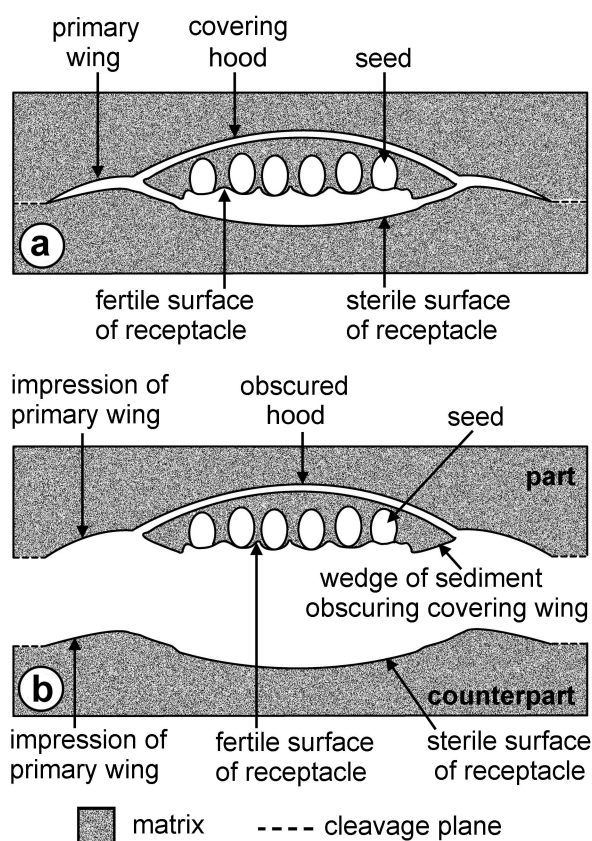


**Text-figure 3.2.14.** Sections through an imaginary impression fossil in accordance with Smithies' (1978) model of a tripartite *H. leslii* fructification, with a central, biconvex receptacle with two seed-bearing surfaces, flanked by a pair of sterile scale leaves. **(a)**(i) Mediolongitudinal section through the fossil showing the position of the receptacle (r), *in situ* seeds (s), scale leaves (sl) and pedicel (p); (ii) & (iii) are the result of one possible cleavage plane through the fossil: (ii) the part partially matches the observed fossils, with a wedge of sediment (sed) bearing an impression of the fertile surface of the receptacle, containing impressions of *in situ* seeds, and overlying an impression of the scale leaf; (iii) in the counterpart, the impression of the scale leaf is at a much shallower level in the sediment than the impression of the receptacle - no real fossil specimens have been found to fit this model. **(b)**(i) Mediolateral cross-section through the fossil; (ii) & (iii) are the result of the same cleavage plane illustrated in (a) [dashed lines = cleavage planes in the matrix].

The only model that adequately accounts for both the part and counterpart of the observed fossil impressions of *E. leslii* is illustrated in text-figs 3.2.13 to 3.2.17. The fructification has the same basic, dorsiventral structure as other members of the Dictyopteridiaceae, with a central receptacle and a peripheral wing, but it is partially enclosed by a covering hood and has a secondary wing developed in the base. The hood is an extension of the primary wing in the apex and along the lateral margins of the fructification, and arches over the seed-bearing surface of the receptacle. The basal third of the hood is split in two,

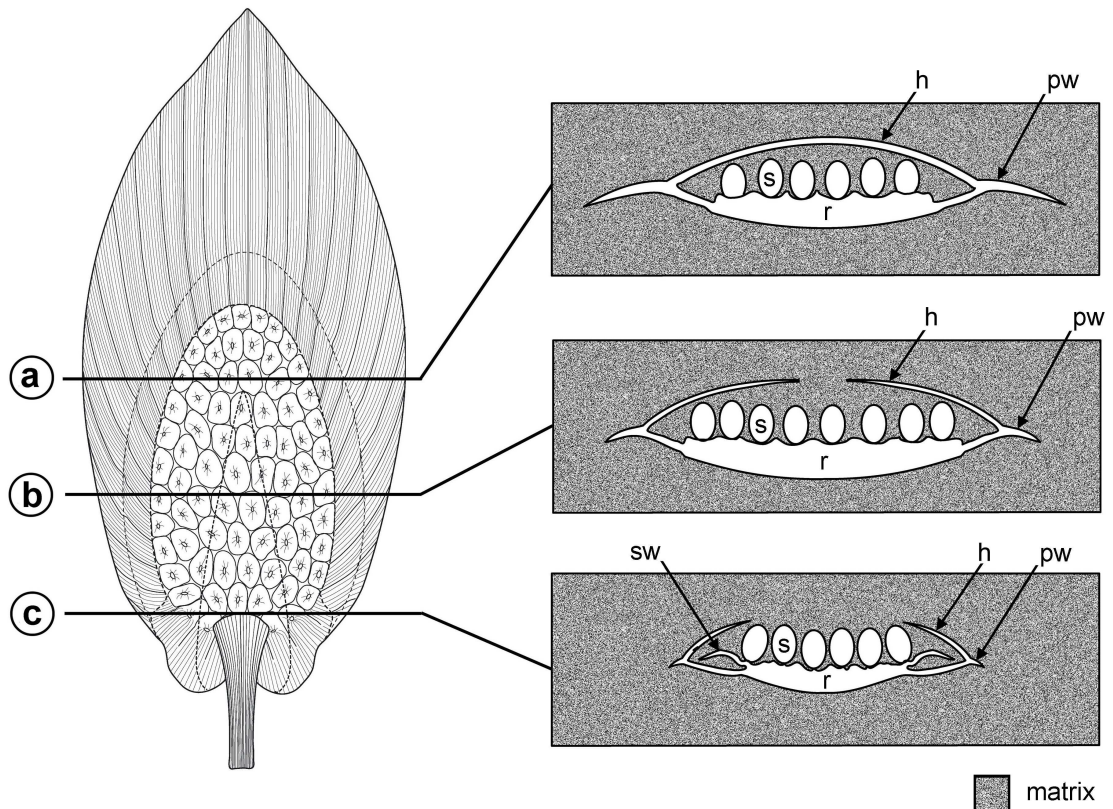
creating a tent-shaped opening that exposes the proximal portion of the receptacle.

It is not entirely clear how the base of the hood relates to the primary wing, but the outer edge of each basal wedge may be continuous with the small basal lobe evident in some specimens on either side of the pedicel in impressions of the sterile surface of the fructification. The secondary wing is only present in the base of the fructification and is associated with the marginal seed scars near pedicel insertion. This scutoid wing is radially striated and weakly fluted, with an entire margin, and well developed lobes that meet at the midline of the fertile surface, overlapping the pedicel. The reconstructions illustrated in text-figs 3.2.13 to 3.2.17 were based on specimen BP/2/7396 [pl. 24, figs (c) & (d); pl. 41, figs (b) & (c)]. In other specimens [e.g. pl. 25, figs (a),(b); pl. 30, fig (e); pl. 32; pl. 41, figs (d), (e), (f)] the primary wing tapers to a greater degree in the medial and basal parts of the fructification. In these specimens the opening in the hood may be broader, with the basal edges of the wing meeting the primary wing at a less acute angle.



**Text-figure 3.2.15.** Proposed structural model of *Elatra leslii*. Section through medial portion of impression fossil: **(a)** impression fossil within matrix, illustrating positions of seed-bearing surface of the receptacle and the primary wing and covering hood; **(b)** exposed impression fossil after cleavage of the matrix; counterpart is a continuous, single layer bearing an impression of the sterile surface of the fructification, with a concave impression of the receptacle, and primary wing; the part bears an impression of the fertile surface of the receptacle (with multiple seed scars) on a wedge of sediment overlying the hood; primary wing is exposed to either side of receptacle and is an exact match of the primary wing on the counterpart; impression of primary wing is continuous with the hood; impressions of seeds are contained within the wedge of matrix obscuring the hood.

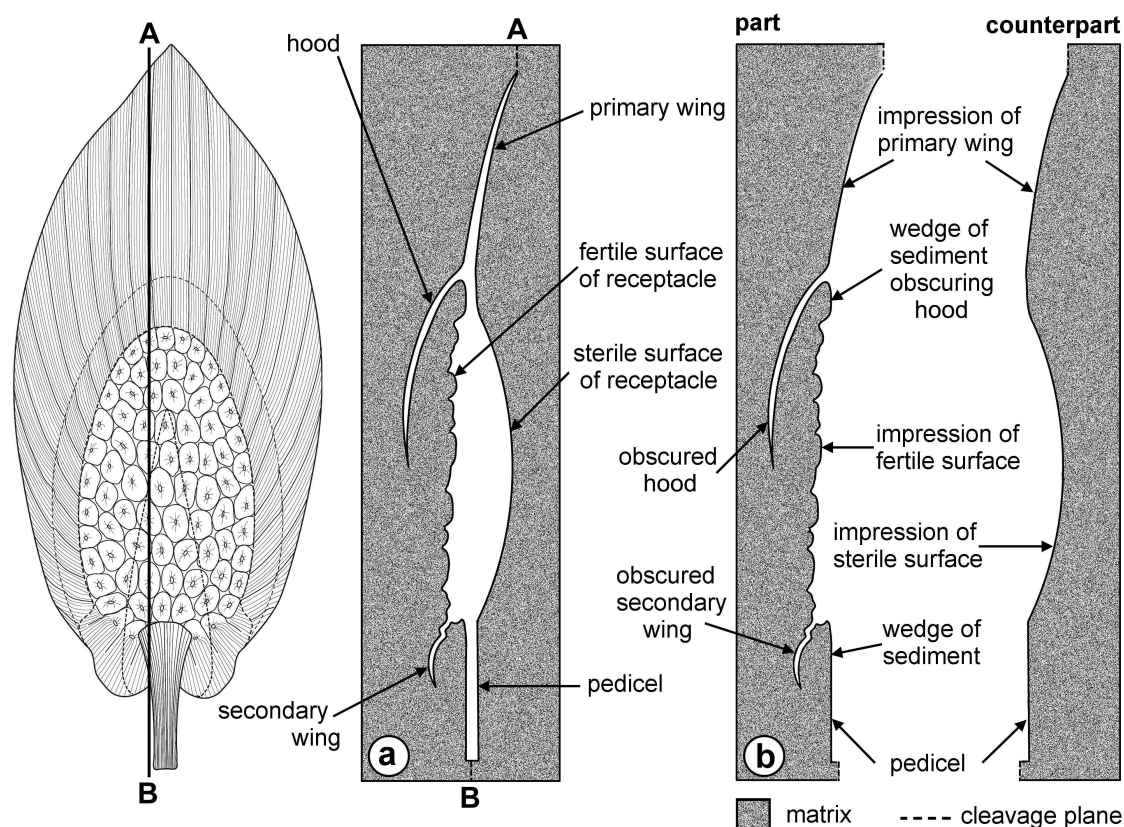




**Text-figure 3.2.16.** Reconstruction of *Elatra leslii* with (a), (b) & (c) representing cross sections through the apical, medial and basal parts of the impression respectively; **(a)** hood completely encloses the seed-bearing surface of the receptacle, the primary wing is broad; **(b)** the tent-like opening in the hood is visible, primary wing is narrower than in (a); **(c)** the opening in the hood reaches maximum development, primary wing is very narrow; secondary wing is visible between the covering and primary wings [h = hood; pw = primary wing; sw = secondary wing; s = seed; r = receptacle].

Apart from the Madagascan specimens described by Appert (1977), there are no fructifications from other parts of Gondwana that can be clearly allied to *Elatra leslii*. However, there is a single specimen figured by White (1986) from the Belmont Insect Beds, in New South Wales, Australia (Late Permian), which may have a similar basic structure to that of *Elatra*. White (1978, p. 499, figs 63, 64; 1986, p. 114, figs 146, 147) referred to the specimen as 'a new glossopterid fruit' and described the structure of the fructification as follows:

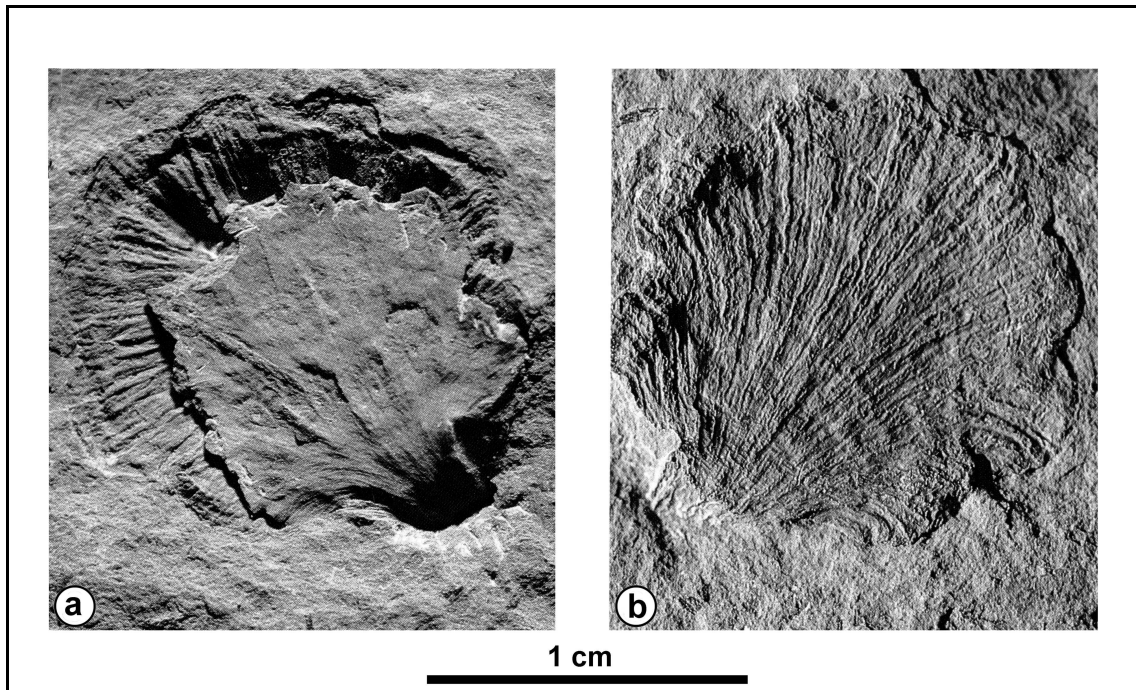
'The receptacle with its attached seeds is held between two cover-leaves. In one half of the specimen the fruit is seen with a cover leaf behind it; and in the counterpart a separate cover-leaf with a lobed margin is preserved'.



**Text-figure 3.2.17.** Reconstruction of an impression fossil of *Elatra leslii*, with a schematic longitudinal transect (AB) through the fossil represented in (a) & (b). **(a)** The unexposed impression fossil, indicating the positions of the hood, primary and secondary wings relative to the receptacle; **(b)** the fossil following cleavage of the matrix: in the counterpart, the impression of the primary wing is continuous with the sterile surface of the receptacle, creating a single, smooth impression fossil; in the part, the primary wing is exposed in the apical region, and the hood is obscured by a wedge of sediment bearing an impression of the fertile surface of the receptacle (note how the hood is continuous with the primary wing); the fertile surface of the receptacle is continuous with the secondary wing in the base of the fructification, and this secondary wing is obscured by the wedge of sediment bearing an impression of the pedicel.

The Australian fructification superficially resembles *Ottokaria* with a gently lobed wing margin and flabellate venation, as opposed to the distinctive campylodromous venation of *Elatra* and *Bifaria*. However, in the part (text-fig. 3.2.18 a) the same wedge of sediment bearing an impression of seed scars is present, apparently overlying the wing, and the counterpart bears an impression of a sterile surface with receptacle and wing forming a continuous surface (text-fig. 3.2.18 b). The impressions of the wing in the part and counterpart are a perfect match, indicating that they do not belong to separate structures as suggested by White (1986). *Elatra bella* has a lobed apical wing margin, and a partially lobed margin has been seen in *Elatra leslii* [pl. 25, fig. (a); pl. 41, fig. (d)], so this feature would not be an entirely unexpected feature for a geographically distant variant. White's (1986) specimen from Australia probably

belongs within the genus *Elatra*, but until further specimens are found and dissected, this cannot be confirmed. Note how the proposed hood, continuing beneath the impression of the receptacle, is creased and concertinaed in the same way as the hood in many *E. leslii* specimens [e.g. pl. 24, fig. (d), pl. 33, fig. (c)]. The equivalent of the primary wing appears to be reduced to a very narrow flange of lobes in this Australian example.



**Text-figure 3.2.18.** The part and counterpart of a glossopterid fructification from the Upper Permian of Australia (White, 1986; p. 114, figs 146, 147): **(a)** the fertile surface of the fructification, with faint impressions of seed scars borne on a central mass of sediment overlying a wing, which appears to continue beneath; **(b)** the sterile surface of the fructification with radiating, fan-shaped veins/striations; the gentle lobes along the wing margin exactly match those in the counterpart [the photographs were labelled as having the same magnification, but were slightly different sizes; the magnification of the photograph of the sterile surface was taken to be the given X4.7, and the photograph of the fertile surface was re-scaled to match its counterpart].

Not only is *Elatra leslii* one of the largest ovuliferous glossopterid fructifications ever described (greatest gross length), it is also morphologically the most elaborate. Such a dramatic divergence from what has long been considered a fairly conservative group of plant organs is a startling and fairly intimidating discovery! The difficulty in presenting this information through photographs and dissections of what is superficially a two-dimensional structure is no doubt going to leave some readers unconvinced. What is perhaps even more difficult to envision, is why this complex wing arrangement evolved, and why it was

apparently limited to a single genus in the Early Permian. I will attempt to address some of these questions later on in the Discussion (section 9.1.3, p. 336).

### 3.3 ARBERIA: A STRUCTURAL RE-EVALUATION

Members of the Arberiaceae and Rigbyaceae have never been found attached to glossopterid foliage, and superficially do not resemble fertile structures of the Dictyopteridiaceae and Lidgettoniaceae. Most authors have been very cautious about affiliating them with *Glossopteris* on the basis of association alone.

Both the Arberiaceae and Rigbyaceae differ from other ovuliferous glossopterid fructifications in that they are branched structures, lacking any form of seed-bearing capitulum. But are they really that different? This section will hopefully convince the reader of several important features apparent in *Arberia* specimens that have been figured in the literature, and that have been overlooked or interpreted differently in the past. Recognition of these features may help these fertile structures to finally gain acceptance within the glossopterids, and may also provide evidence supporting the theory that *Arberia* represents the most basal of the glossopterid fertile structures.

#### 3.3.1 THE BRANCH TERMINI

In section 3.1.2, the ultimate branch termini of *Arberia* were described as having, in many cases, a scale-like extension beyond the point of seed attachment. Almost all authors in the past have considered the branch termini in *Arberia* to be simple, unspecialised, truncated structures, and this feature has been cited as a diagnostic character of the genus (e.g. White, 1908, Rigby, 1972a, Anderson & Anderson, 1985). White (1908) considered the seeds of *Arberia minasica* to be borne directly at the ends of the lateral lobes, and described the truncated lobe ends as having ‘minute laceration fragments at the corners’ indicating the sites of seed detachment. He also compared the width and texture of lobe end with associated seed bases, and arrived at the same conclusions. Anderson & Anderson (1985), in their diagnosis for the genus, described the ovules as being terminal on the ultimate branchlets ‘without protective scale’. However, McLoughlin (1995) acknowledged the presence of ‘expanded branch endings’ in *A. madagascariensis* and ‘expanded cushions’ at the points of seed attachment in the South American *A. minasica*.

Close inspection of figures in the literature and examination of the South African material, has revealed that most of the specimens on record appear to have some differentiation of the branch termini, distal to the point of seed attachment. Of course, it is possible that this is not the case in all species currently attributed to *Arberia* – examining a photograph is never a substitute for seeing the fossil itself.

Appert's (1977) figures of *A. madagascariensis* from Madagascar were particularly informative. His specimens of *A. madagascariensis*, which are very similar to those of *A. minasica*, included one of the rare examples of a seed in indisputable organic attachment to an *Arberia* specimen. Appert's (1977) photographs are magnificently clear, and together with enlargements and line drawings of key specimens, they present a very clear view of the morphology of the taxon. Text-figs. 3.3.2-3.3.5 are reproductions of Appert's (1977) figures.

Appert (1977) described the occurrence of certain branch termini in *A. madagascariensis* specimens which were extended to form an expanded, cup-shaped structure. He noted that in impressions of branches bearing seeds, the part and counterpart showed the same features, but in impressions of these anomalous, expanded branch termini, the part and counterpart showed very different features. On the part, the striations on the ultimate branch extended uninterrupted into the expanded feature, which was convex, but on the counterpart, the striations ended at the terminus of the branch, and the expanded portion was concave and represented the interior surface of a cup-shaped feature. He observed that the striations on the expanded portion were finer than those on the subtending branch, and followed a parallel course to the distal margin. Appert (1977) was puzzled by these features, particularly since they were not apparent in branches which still had seeds in attachment. He suggested the peculiar extensions may represent so-called aborted ovules, such as those seen in some Cordaitalean plants, but could not reconcile their cup-shaped form.

The specimen in text-figs 3.3.1 (b) & (c), 3.3.2 (a) & (b) and 3.3.3 (a) & (b) most clearly shows the nature of the branch termini in *A. madagascariensis*. Their



bifacial nature is revealed by the presence of a seed scar at the base of each wing/scale on the fertile surface of the fructification, in text-figs. 3.3.2 (a) and 3.3.3 (a), as opposed to the very smoothly striated, continuous feature on the counterpart in text-figs. 3.3.2 b and 3.3.3 b. Note the very close similarity in text-fig. 3.3.1 of the fertile surfaces of the *A. madagascariensis* termini, to the fertile surface of a branch terminus belonging to a *Rigbya arberioides* fructification.

But how do we explain Appert's (1977) quite valid observation that whenever we see a seed in organic attachment to a branch terminus, there is no clear evidence for the presence of a scale? This is certainly the case for the specimen illustrated in text-figs 3.3.2 (c) & (d). If we consider the model of impression fossil interpretation discussed at length earlier in the chapter (section 3.1.1, p. 42) this apparent paradox is easily resolved.

Imagine the bifacial branch terminus preserved face-down as a mould in the sediment, with a seed still attached to the fertile surface. Exposure of both, complete surfaces of the terminus would require cleavage of the matrix directly through the mould of the branch, resulting in a part showing the seed-attachment point and scale, and a counterpart displaying the smooth, veined surface of the terminus and scale. The seed is not visible – it is lying beneath a thin wedge of sediment that infiltrated between it and the wing/scale of the branch terminus prior to preservation. For the seed to be fully exposed on the surface of the slab, the cleavage plane must pass through the ultimate branch, through the point of seed attachment (cicatrix) and through the seed. This means that the impression of the terminal scale is completely bypassed, and is not visible at all. The part and counterpart would only show the impression of the seed, attached to a simple, undifferentiated branch terminus. The impression of the scale would be lying beneath the seed impression in the part (the upper slab prior to cleavage). Additionally, the impression of the seed would lie at a higher level in the matrix than the axis, in the block where the seed impression overlies and conceals the scale impression.

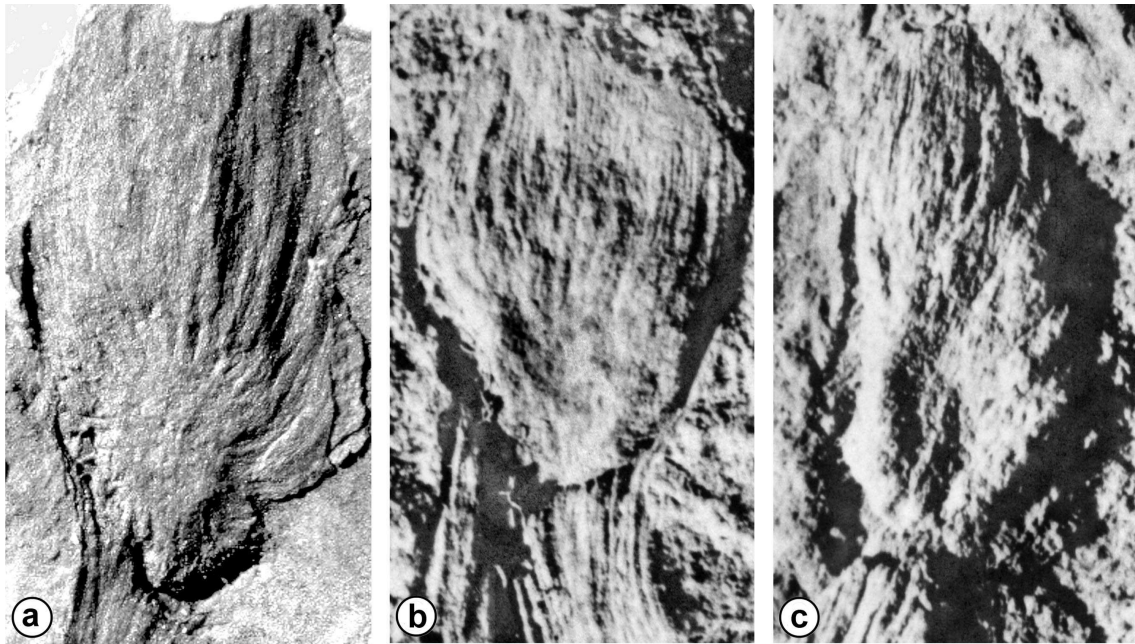
Rigby's (1972) drawings of *A. minasica* clearly demonstrated the presence of expanded scale-like features at the termini of the ultimate branches. His text-fig.

1 (Rigby, 1972a, p. 112) illustrated (in lateral view) a seed attached to the partially overlapping scale. Rigby (1972a) described this seed as being borne 'on the face of some sort of disc'. He acknowledged further on in his paper that ovules are 'not necessarily terminal but may be placed on the side of (the) branchlet just before its end'. Rigby (1972) described the presence of a groove or rim between the branch terminus and the 'rounded head' and commented that the fine striations 'cross unbroken from the branchlet to the ovule'. He also mentioned that these structures did not exhibit any of the features used for even generic identification of isolated seeds. My view is that the 'rounded heads' and expanded termini of the ultimate lateral branches seen in the plates provided by Rigby (1972a), are in most cases equivalent to scale-like features distal to seed attachment points rather than ovules or seeds. Schopf (1976) expressed a similar sentiment, challenging the existence of developing ovuliferous or non-ovuliferous ('aborted') pinnae as proposed by Rigby (1972a), suggesting instead that these may be lateral branches which had shed their seeds.

Chandra & Srivastava (1981) described the presence of a finely striated, unwinged ovule at the end of each branchlet in *A. surangei*. Note how, in their text-fig. 1 (p. 42; reproduced here in text-fig. 3.3.7), the striations in the 'ovule' are continuous with the striations in the branchlet. It is proposed here that these are not in fact ovules, but the same expanded, scale-like features that are seen in *A. madagascariensis*.

Based on the similarities in their seed-bearing sites, and their branched structure (as discussed in the next section), *Arberia* and *Rigbya* are probably closely related taxa, and there would be a good case for someone wishing to synonymise their current host families. Aside from revealing similarities between *Arberia* and *Rigbya*, recognition of the seed-scar/ scale arrangement has also provided a more convincing link between these two families and other glossopterid fertile structures as explained in the previous section.

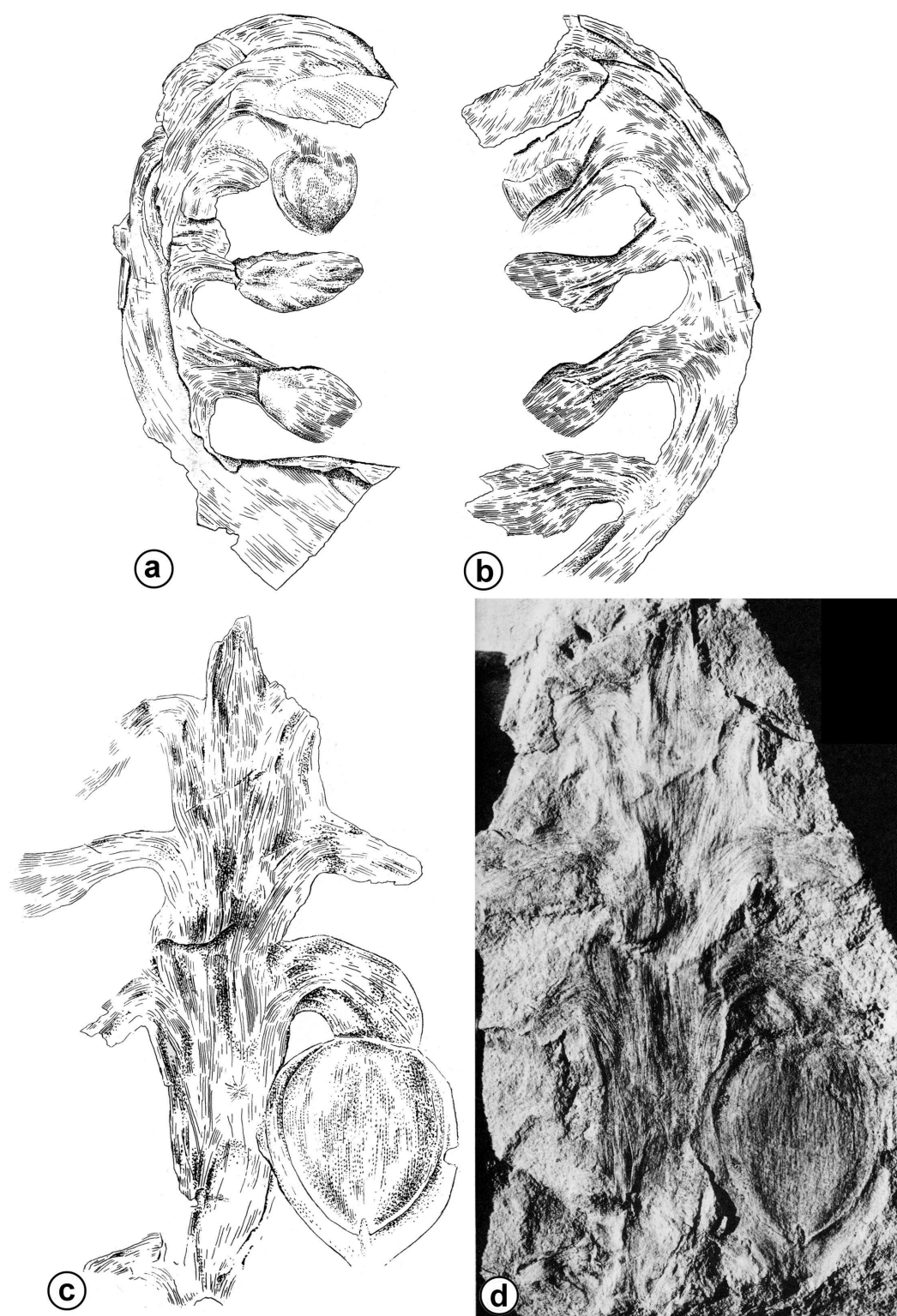




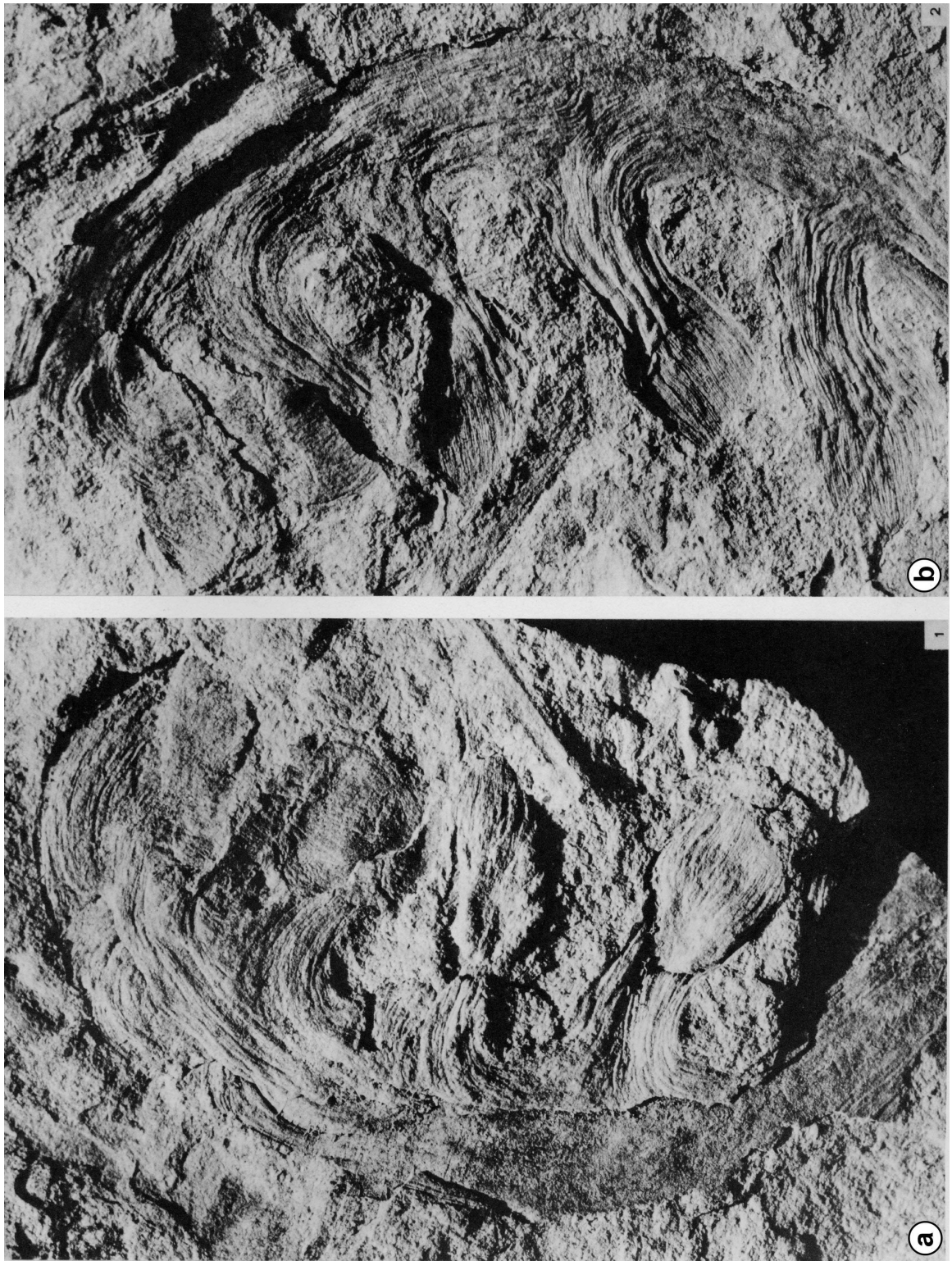
**Text-figure 3.3.1.** Spot the difference. Fig. (a) an impression of the fertile surface of a branch terminus belonging to a South African specimen of *Rigbya* (fig. (a), pl. 1 this document); figs (b) & (c): impressions of the fertile surfaces of two branch termini belonging to a specimen of *Arberia madagascariensis* (enlargements of Appert's 1977 specimen SA 7/1, fig. 1, pl. 40).

### 3.3.2 BRANCHING PATTERNS

As outlined in section 3.1.2 members of *Arberia* have a branched form, the primary axis giving rise to pinnate lateral branches which may dichotomise further, and/or the primary axis itself may bifurcate and give rise to branches via a series of dichotomies. Members of some taxa are characteristically dorsiventral, with fairly laminar primary axes, e.g. *A. minasica* (White, 1908; Rigbya, 1972a) from Brazil, *A. madagascariensis* from Madagascar (Appert, 1977) and South Africa (Anderson & Anderson, 1985), and *A. surangei* from India (Chandra & Srivastava, 1981). These taxa are particularly interesting, because at least some specimens appear to be bifacial, bearing lateral branches across one face of the primary axis.



**Text-figure 3.3.2.** Line drawings and photographs of *Dolianitia madagascariensis* (= *Arberia madagascariensis*) from Madagascar, reproduced from Appert (1977). Figs (a) & (b): part and counterpart of paratype SA 7/3 with attached seed [text-figs 6 & 7, pp. 34 & 35]; figs (c) & (d): holotype with attached seed, SA 7/2 [text-fig. 5, p. 33; pl.36, fig. 2].



**Text-figure 3.3.3.** Figs (a) & (b): part and counterpart of SA 7/1, illustrating the fertile and sterile surfaces respectively of a row of lateral branches of a *Dolianitia madagascariensis* (= *Arberia madagascariensis*) fructification from Madagascar. [Photographs from Appert (1977); pl. 40, figs 1 & 2].

Once again, Appert's (1977) photographs and drawings of the Madagascan *Arberia madagascariensis* fructifications, most clearly illustrated this feature. Appert (1977) described how the primary axis of *A. madagascariensis* was leaf-like, and bore branches along both margins, as well as across the surface of the lamina. He very carefully noted that this was only the case on one surface of the primary axis, the opposing face being smooth and continuous without any evidence of branching. His photographs and line drawings reproduced here in text-figs 3.3.4 & 3.3.5 provide convincing evidence of this morphology. The lateral branches on the face of the axis appear in the impression as deep indentations. Groups of parallel striations on the lamina, which probably represent vascular strands, appear to enter each of these indentations, supporting the theory that they represent branches extending into the sediment and away from the horizontal plane of the fructification. Text figs 3.3.4 (a) and 3.3.5 (a) show the impression of the fertile surface of the primary axis with indentations, and text-figs 3.3.4 (b) and 3.3.5 (b) portray the smooth sterile surface of the axis. The specimen in text-figs 3.3.2 (a) and 3.3.3 (a) has been laterally compressed, but note how the lateral branch with an attached seed appears to correspond to a prominent indentation in the apical part of the primary axis.

One additional feature worthy of mention, is that the fertile surfaces of the branch termini, as elucidated above in section 3.3.2, correspond to the fertile surface of the primary axis. The laterally compressed specimen in text-fig. 3.3.2 (a) & (b) and 3.3.3 (a) & (b) shows this feature most clearly. In text-figs 3.3.4 (a) and 3.3.5 (a), one of the marginal lateral branches in the middle right of the fructification terminates in a seed scar, although the scale-like feature itself is not preserved.

If we bear in mind that these fossils are all three-dimensional moulds portraying negative images of the original plant surfaces, then the deep indentations in the surface of the primary axis are the evidence we would expect to see of branches arising at right angles to the flattened plane of a laminar axis. Exposure of the impression along the plane of the laminar primary axis would result in a part with a smooth, even, striated impression of sterile surface of the

axis with its marginal branches. The counterpart would bear an impression of the fertile surface of the fructification. The lamina would completely obscure the lateral branches arising from the face of the primary axis, which would extend away from the plane of the fructification. However, there would be holes in the smooth surface of the lamina representing the sites of branch divergence from the lamina, i.e. there would be moulds of these branches extending into the matrix. These holes in the lamina would probably be compressed, and could be expected to appear as indentations or pockets on the surface of the impression.

The specimens of *A. madagascariensis* from South Africa only bear lateral branches in the same plane as the primary axis, however these fossils may be impressions of the smooth, unbranched surface of the fructification, and without examining the counterpart of the fossil, we cannot exclude the possibility that there were secondary branches arising from the opposing face of the primary axis.

When describing specimens of *A. minasica* from South America, Rigby (1972a) explained how branches were in some cases borne across the face of the 'rachis' or primary axis, but made a point of excluding these specimens from the genus. Unfortunately Rigby (1972a) did not figure the counterparts of the specimens of *A. minasica* he described, and we cannot therefore confirm whether or not the branches were borne on only one surface of the fructifications.

Chandra & Srivastava (1981; pl. 1, figs 1&2) figured a specimen of *A. surangei* which apparently has the same abrupt hollows/indentations across the face of the primary axis that were observed in *A. madagascariensis*, with striations diverging into the indentations (see text-figs 3.3.6 & 3.3.7). They did not however acknowledge this feature.

Appert (1977) favoured basipetal development of the *Arberia* specimens from Madagascar, with the apical branches being the most mature, and having shed their seeds first. Rigby (1972a, 1978) however, characterised the development of the *A. minasica* axes he described as acropetal, with the largest ovules

present in the basal parts of the fructification. Rigby's (1972a) theory stemmed from his premise that the expanded branch termini in the apex of the fructification represented developing or aborted ovules. If we re-interpret these as branch termini which had already shed their seeds, the reverse is implied, and Appert's (1977) theory of basipetal development in these organs may be more accurate. However, although Rigby (1972a) and Appert (1977) both figured *Arberia* specimens with attached seeds in their basal parts, this does not really provide adequate evidence for the formulation of theories regarding the acropetal or basipetal nature of these fertile structures. We cannot be sure that all the seeds present are exposed in the fossils available for examination. There may well be others obscured by sediment. Also, Appert (1977) figured a specimen bearing a seed in the apex of the fructification, with more basal lateral branches having apparently shed their seeds prior to preservation.

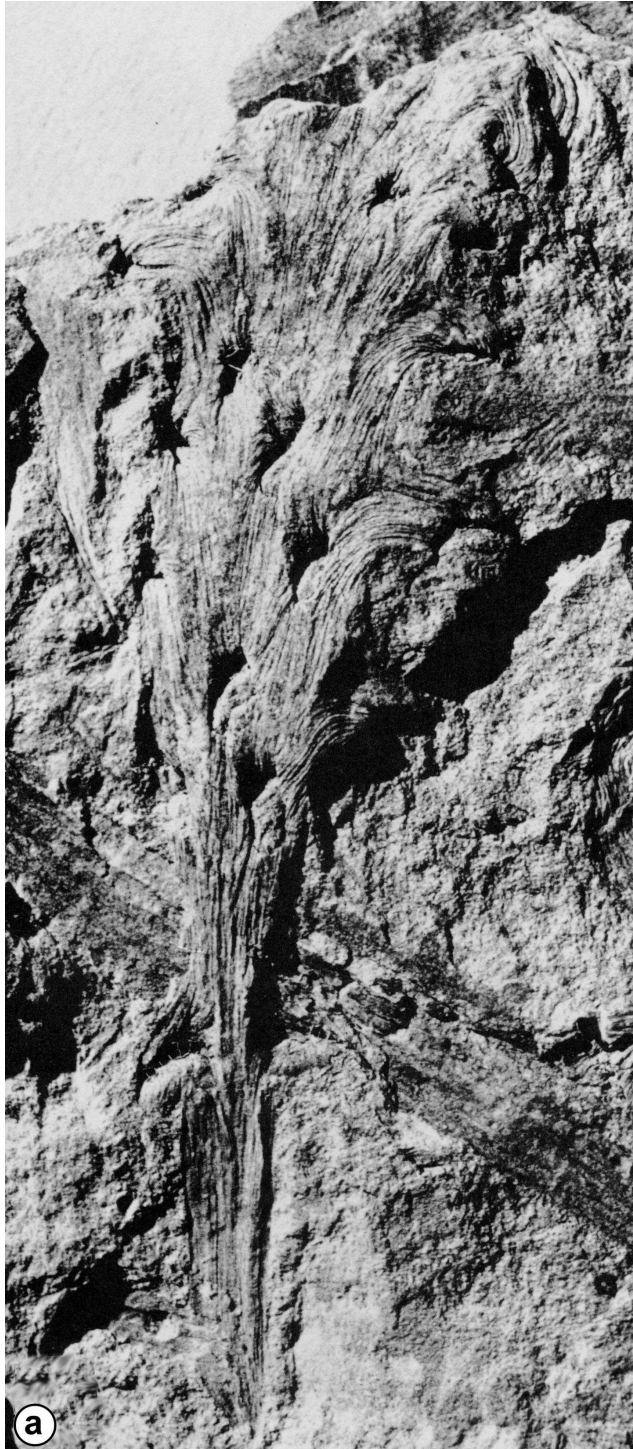
*Arberia hlobanensis* has been cited by Anderson & Anderson (1985) and McLoughlin (1995) as an example of open, irregular, paniculose, three-dimensional branching in *Arberia*. This certainly does seem to be the case upon first inspection of the single part and counterpart available for scrutiny [pl. 10, figs (a), (b); pl. 11, figs (g)-(i)], and this is how the species has been described in section 6.1.4.2 (p. 174). However, it is worth noting at this point how all the branches in this specimen are on the left side of the fructification. It is quite conceivable that this specimen was slightly laterally compressed prior to preservation, and that the primary axis, although not particularly laminar, was a dorsiventral structure which bifurcated and then produced branches to one side of the fructification only.

Whilst the similarities in seed scar and wing/scale structure seen in all four families of fertile structures recognised here, help to unify them within the glossopterids, the acknowledgement of a bifacial branching structure in *Arberia*, may provide some clues as to how they evolved. This fascinating perspective is examined in detail in the homologies and phylogenies section of the Discussion (section 9.2.2, p. 345).



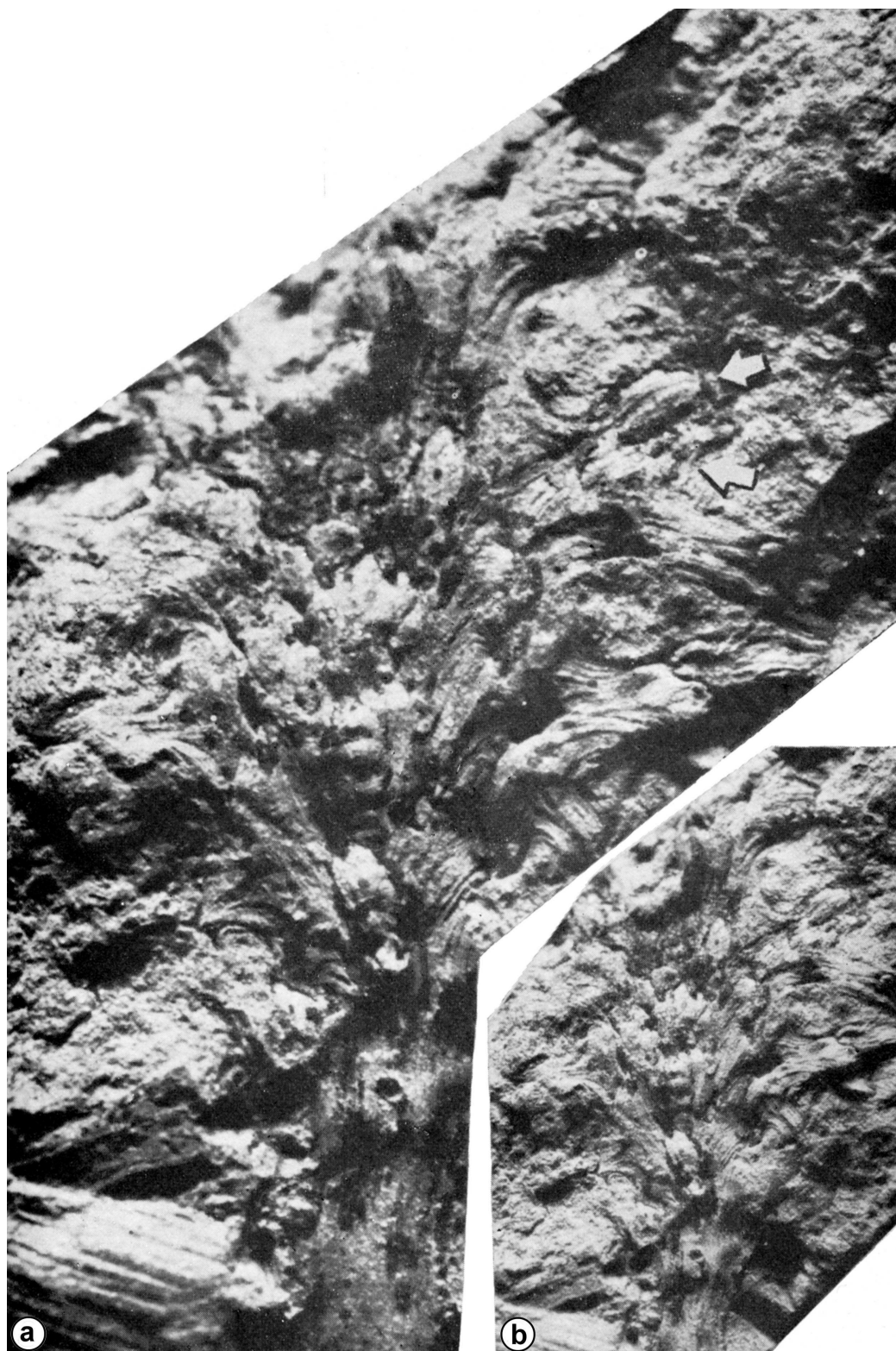
**Text-figure 3.3.4.** Figs (a) & (b): Line drawings of the fertile and sterile surface of a *Dolianitia madagascariensis* (= *Arberia madagascariensis*) fructification, SA 7/3, from Madagascar; [extracted from Appert (1977); text-fig. 6, p. 34; text-fig. 7, p. 35].



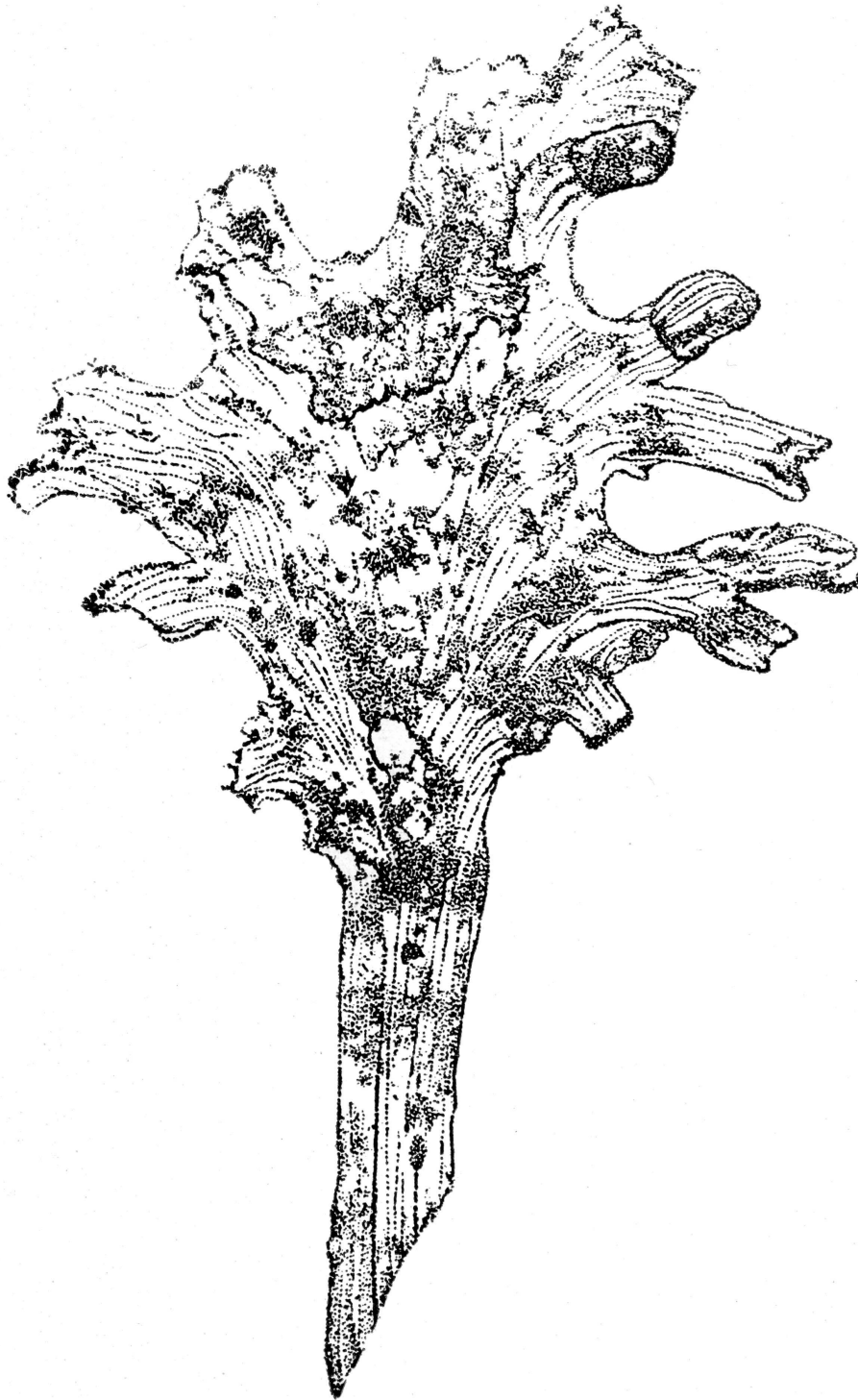


**Text-figure 3.3.5.** Figs (a) & (b): photographs of the fertile and sterile surface of a *Dolianitia madagascariensis* (= *Arberia madagascariensis*) fructification, SA 7/3, from Madagascar; [extracted from Appert (1977); pl. 38, figs. 2 & 4].





**Text-figure 3.3.6.** Photographs of a compression/impression fossil of *Arberia surangei* extracted from Chandra & Srivastava, 1981 (p. 45, pl. 1, figs 1&2).



**Text-figure 3.3.7.** Line drawing of a compression/impression fossil of *Arberia surangei* extracted from Chandra & Srivastava, 1981 (text-fig. 1, p. 42).

## CHAPTER 4 KEY TO THE OVULIFEROUS GLOSSOPTERID FRUCTIFICATIONS OF SOUTH AFRICA

### 4.1 SUPRAGENERIC CLASSIFICATION

Not surprisingly, the suprageneric classification of the glossopterid fructifications has been a source of debate in the literature. So little agreement has been reached on the basic morphology and generic status of these organs, that deciding on familial, ordinal or class distinctions has been largely left to the subjective opinions of each worker and his/her particular set of interpretations.

The reasons for this dissent have mostly stemmed from differences in opinion regarding the structural interpretation of different fossilisation types, as discussed at length in Chapter 3. Other factors such as the typical dissociation of plant organs in the fossil record have exacerbated the situation. The apparent temporal isolation and uniqueness of the glossopterids has also left workers without access to useful analogues, either fossil or extant. The glossopterids suddenly appear in the Upper Carboniferous/ Lower Permian and equally suddenly disappear in the Late Permian/ Early Triassic, without leaving behind any easily identifiable descendants. The phylogenetic aspects of *Glossopteris*, and how perceptions of the morphology and anatomy of the fertile structures have affected the suprageneric classification of this plant, are addressed in section 9.2 (p. 340) of the Discussion. The following is a brief review of past suprageneric classification systems that have been used for the glossopterids, and an outline of the taxonomic hierarchy that has been applied in this study.

#### 4.1.1 PREVIOUS TAXONOMIC SYSTEMS

Virtually all workers on glossopterid fertile structures have acknowledged two main types of ovuliferous glossopterid fructification, differentiated at least to the family level. The first type comprises the capitate forms such as *Scutum*, *Plumsteadia*, *Ottokaria* etc., which have a central receptacle bearing numerous seeds, and which are attached to a typical, full-size glossopterid leaf. The second type comprises a reduced scale leaf, bearing multiple, small, cupulate

fructifications on slender pedicels attached in a uniseriate or distichous arrangement on the petiole or lamina of the scale, e.g. *Lidgettonia*.

Two additional forms, the branched rigbyoid and arberoid types are commonly recognised as being potential fertile structures of *Glossopteris*, although some authors have been reluctant to include these within a formal glossopterid classification system on the basis of association alone. The morphology of each of these types has been dealt with at length in the previous chapter.

Below is a tabulation (Table 4.1.1) of some of the suprageneric classification systems that have been adopted in the past to accommodate and reflect the diversity apparent in the ovuliferous glossopterid fructifications of Gondwana. Although the list is not exhaustive, it gives a good indication of the number of divergent hierarchies that have been developed, even by authors who have reached agreement on the basic morphological features apparent in these fructifications.

As we can see in Table 4.1.1, opinions have differed over where in the taxonomic hierarchy the glossopterids should be given independence, and many authors appear to have been hesitant to commit to a classification scheme beyond the ordinal level because of uncertainties regarding the morphology and anatomy of the glossopterid reproductive structures.

There is general consensus among workers that the glossopterids are gymnosperms, although Plumstead (1956a,b) considered them to be closer to angiosperms than to gymnosperms on the basis of her unusual interpretations of the Vereeniging fructifications as enclosed, bisexual structures. According to the structural interpretations acknowledged by most authors, the gymnospermous seeds which are borne exposed on branched or leaf-like structures, are features which logically place the glossopterids in the division Pinophyta (Meyen, 1984).

Many authors have affiliated the glossopterids with the pteridosperms, particularly in light of the work by Gould & Delevoryas (1977), proving that the seed-bearing structure (at least in some cases) is a thin laminate structure

reminiscent of a leaf. Unfortunately the pteridosperms as a group are poorly defined, with some workers recognising them as a separate division, and others as an order. Schopf (1976) noted that this group is probably an artificial aggregation of polyphyletic taxa sharing superficial morphological similarities. As discussed later (Discussion, section 9.2, p. 340), Schopf (1976) favoured an affiliation between glossopterids and the cordaitaleans rather than the pteridosperms, interpreting the fructifications as planated and fused branching structures. The difficulties in relating the peculiar structure of the glossopterid fructifications to those of other plant groups, and the resulting lack of certainty regarding the affiliations of these plants, have led many authors to place the glossopterids in their own class, most commonly the Glossopteridopsida (Plumstead, 1956b; Smithies, 1978; Banerjee, 1984; McLoughlin 1990a,b; Anderson & Anderson, 1997). Meyen (1984) placed the glossopterids in the class Ginkgoopsida. Anderson & Anderson (1985) initially concurred with Meyen (1984) but later placed the glossopterids within their own distinct class, the Ottokariopsida (Anderson & Anderson, 2003).

In a recent publication by Doweld (2003) a completely different classification system for the glossopterids was proposed. Doweld's (2003) book attempted to revise the suprageneric designations of all plants from Precambrian to extant. Doweld (2003) created two new classes to accommodate the glossopterid fructifications, the Arberiopsida (order Arberiales) and the Dictyopteridiopsida (orders Dictyopteridiales, Rigbyales, Lidgettoniales). Perhaps Doweld (2003), who has had the benefit of sweeping across the entire diversity of plant life as we know it, is in a better situation to judge how best to represent the scale of diversity present in the glossopterids. However, division of the glossopterids into two classes is probably an extreme measure, especially considering the apparently conserved nature of the foliar material found associated with, or attached to, the fertile structures. Many other authors (as reflected in Table 4.1.1) have divided the glossopterid fructifications among several orders, but in light of the morphological similarities which have been identified between all the ovuliferous glossopterid fructifications from South Africa in this study, the glossopterids are regarded here as being comfortably accommodated within a single order.

Table 4.1.1. A summary of some of the suprageneric taxonomic schemes that have been applied to the glossopterids in the past.

| Author              | Date  | Division           | Class                                       | Order                        | Families                                                                                                                             |
|---------------------|-------|--------------------|---------------------------------------------|------------------------------|--------------------------------------------------------------------------------------------------------------------------------------|
| Arber               | 1905  | (gymnospermous)    | -                                           | -                            | -                                                                                                                                    |
| White               | 1908  | (gymnospermous)    | (pteridospermous)                           | -                            | -                                                                                                                                    |
| Plumstead           | 1952  | (gymnospermous)    | (pteridospermous)                           | -                            | -                                                                                                                                    |
|                     | 1956a | angiosperm         | ?                                           | -                            | -                                                                                                                                    |
|                     | 1956b | precursors         | Glossopteridae                              | -                            | -                                                                                                                                    |
| Rigby               | 1972  | (gymnospermous)    | Pteridospermae                              | Pteridospermales             | Arberiaceae fam. nov.                                                                                                                |
|                     | 1978  | (gymnospermous)    | Cycadopsida?                                | Dictyopteridiales            | Dictyopteridiumaceae, Scutumaceae, Ottokariaceae                                                                                     |
| Surange & Chandra   | 1975  | -                  | -                                           | Pteridospermales             | Lidgettoniaceae, Denkaniaaceae, Parthaceae                                                                                           |
|                     |       |                    |                                             | Glossopteridales             | Scutumaceae, Dictyopteridiumaceae, Ottokariaceae                                                                                     |
|                     | 1978  | -                  | -                                           | Pteridospermales             | Lidgettoniaceae, Denkaniaaceae, Parthaceae                                                                                           |
|                     |       |                    |                                             | Glossopteridales             | Scutumaceae, Cistellaceae, Hirsutiaceae                                                                                              |
| Lacey <i>et al.</i> | 1975  | (gymnospermous)    | Cycadopsida                                 | Pteridospermales             | Glossopteridaceae                                                                                                                    |
| Schopf              | 1976  | -                  | Glossopteridopsida                          | -                            | -                                                                                                                                    |
| Kovacs-Endrody      | 1976  | -                  | -                                           | -                            | Glossopteridaceae                                                                                                                    |
| Mareshwari          | 1976  | (gymnospermous)    | Glossopteridopsida                          | Lidgettoniales               | -                                                                                                                                    |
|                     | 1990  | (gymnospermous)    | (unknown)                                   | Ottokariales                 | -                                                                                                                                    |
|                     |       |                    |                                             | Ottokariales                 | Dictyopteridiumaceae Surange & Chandra 1975 <i>ex Rigby</i> 1978 <i>emend.</i>                                                       |
| Gould & Delevoryas  | 1977  | -                  | Pteridospermopsida                          | Lidgettoniales               | Eretmoniaaceae Banerjee 1984 <i>emend.</i>                                                                                           |
| Appert              | 1977  | -                  | -                                           | Glossopteridales             | -                                                                                                                                    |
| White               | 1978  | -                  | -                                           | Glossopteridales             | -                                                                                                                                    |
| Smithies            | 1978  | Glossopteridophyta | Glossopteridopsida                          | Ottokariales Maheshwari 1976 | Ottokariaceae Surange & Chandra 1975                                                                                                 |
| Taylor              | 1981  | Pteridospermophyta | -                                           | -                            | -                                                                                                                                    |
| Pant                | 1982  | -                  | (pteridospermous?)                          | Glossopteridales             | -                                                                                                                                    |
| Melville            | 1983a | -                  | Angiospermopsida (subclass: Glossopteridae) | Glossopteridales             | -                                                                                                                                    |
| Banerjee            | 1984  | -                  | Glossopteridopsida                          | Arberiales                   | Arberiaceae                                                                                                                          |
|                     |       |                    |                                             | Lidgettoniales               | Lidgettoniaceae                                                                                                                      |
|                     |       |                    |                                             | Palmetophyllitales           | Palmetophyllitaceae (including <i>Rigbya</i> )                                                                                       |
|                     |       |                    |                                             | Glossopteridales             | Vannusaceae, Ottokariaceae, Scutumaceae, Dictyopteridiumaceae, Plumsteadiaceae, Plumaceae, Austroglossaceae, Isodictyopteridiumaceae |

| Author                       | Date         | Division             | Class                                                         | Order                                                                                | Families                                                                                                                                                                                                              |
|------------------------------|--------------|----------------------|---------------------------------------------------------------|--------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                              |              |                      |                                                               | Senothecales                                                                         | Senotheceaceae                                                                                                                                                                                                        |
|                              |              |                      |                                                               | Kendostrobales                                                                       | Kendostrobaceae                                                                                                                                                                                                       |
| Meyen                        | 1984<br>1987 | Pinophyta            | Ginkgoopsida                                                  | Arberiales                                                                           | Arberiaceae and another unnamed                                                                                                                                                                                       |
| Anderson & Anderson          | 1985         | Pinophyta            | Ginkgoopsida                                                  | Glossopteridiales/<br>Ottokariiales                                                  | Ottokariaceae, Rigbyaceae, Arberiaceae,<br>Lidgettoniaceae                                                                                                                                                            |
|                              | 1997         | -                    | Glossopteridopsida?                                           | -                                                                                    | -                                                                                                                                                                                                                     |
|                              | 2003         | -                    | Ottokariopsida                                                | -                                                                                    | -                                                                                                                                                                                                                     |
| Holmes                       | 1990         | (gymnospermous)      | Gymnospermae                                                  | Glossopteridales                                                                     | Ottokariaceae                                                                                                                                                                                                         |
| McLoughlin                   | 1990a        | Pteridospermophyta   | Glossopteridopsida<br>Sporne 1965                             | Glossopteridales<br>Lakhanpal, Maheshwari &<br>Awasthi 1976                          | Dictyopteridiaceae Rigby 1978 nom. corr.<br>Rigbyaceae Anderson & Anderson 1985<br>Lidgettoniaceae Anderson & Anderson 1985<br>Arberiaceae Anderson & Anderson 1985                                                   |
|                              | 1990b        | Pteridospermophyta   | Glossopteridopsida<br>Lakhanpal, Maheshwari &<br>Awasthi 1976 | Dictyopteridiales Rigby<br>1978 nom. corr.                                           | Scutaceae Rigby 1978 nom. corr.                                                                                                                                                                                       |
|                              | 1995         | Pinophyta Meyen 1984 | ?                                                             | Dictyopteridiales Meyen<br>1984 nom. nov.                                            | Dictyopteridiaceae Surange & Chandra ex Rigby 1978<br>emend. Maheshwari 1990 nom. corr.<br>Arberiaceae Rigby 1972<br>Rigbyaceae Anderson & Anderson 1985                                                              |
| Stewart & Rothwell           | 1993         | -                    | -                                                             | Glossopteridales                                                                     | -                                                                                                                                                                                                                     |
| Taylor                       | 1996         | -                    | (pteridospermous)                                             | Glossopteridales                                                                     | -                                                                                                                                                                                                                     |
| Adendorff et al.             | 2002         |                      |                                                               | Glossopteridales sensu<br>Pant 1982                                                  | Arberiaceae Anderson & Anderson, 1985<br>Rigbyaceae Anderson & Anderson, 1985<br>Lidgettoniaceae Anderson & Anderson, 1985<br>Dictyopteridiaceae Surange & Chandra 1975 ex Rigby<br>1978 emend. Maheshwari 1990       |
| Doweld                       | 2003         |                      | Arberiopsida cl. nov.<br>Dictyopteridopsida cl.<br>nov.       | Arberiales Meyen 1984<br>Dictyopteridiales<br>McLoughlin 1995 ex Doweld<br>ord. nov. | Arberiaceae Rigby 1972<br>Dictyopteridiaceae Rigby 1978 (Dictyopteridiaceae)                                                                                                                                          |
|                              |              |                      |                                                               | Rigbyales ord. nov.<br>Lidgettoniales ord. nov.                                      | Rigbyaceae Anderson & Anderson 1985<br>Lidgettoniaceae Anderson & Anderson 1985;<br>Parthaceae fam. nov., Denkanliaceae fam. nov.                                                                                     |
| Adendorff<br>(current study) | 2004         | Pinophyta Meyen 1984 | Glossopteridopsida<br>Maheshwari 1976                         | Dictyopteridiales Rigby<br>1978 (nom. corr. McLoughlin<br>1990b)                     | Rigbyaceae Anderson & Anderson, 1985<br>Arberiaceae Rigby 1972<br>Dictyopteridiaceae Surange & Chandra 1975 ex Rigby<br>1978 emend. Maheshwari 1990<br>Lidgettoniaceae Surange & Chandra 1975 emend. Banerjee<br>1984 |



By far the most commonly used ordinal name assigned to the glossopterids, has been the Glossopteridales. Anderson & Anderson (1985), whilst acknowledging the common usage of the name, rejected Glossopteridales, which is based on a foliar organ, instead assigning a name derived from an ovuliferous fructification as advocated by Meyen (1984) in his guidelines for the classification of gymnosperms. Anderson & Anderson (1985) chose the name Ottokariales, in preference over Meyen's (1984) Arberiales, as they considered *Ottokaria* to have priority over all other genera of ovuliferous fructifications that have been found in attachment with leaves of *Glossopteris*. However, as noted by McLoughlin (1990b), *Dictyopteridium* was in fact the first ovuliferous glossopterid fructification ever found. Rigby (1978) and McLoughlin (1990b, 1995) both used the name Dictyopteridiales for the order encompassing the glossopterids.

Numerous families have been created over the years for glossopterid fructifications. The most tenable and easily applied familial groupings are probably those created by Anderson & Anderson (1985), viz. the Lidgettoniaceae, Ottokariaceae, Arberiaceae and Rigbyaceae. For the same reasons described in the previous paragraph, McLoughlin (1990b) used Surange & Chandra's (1975) Dictyopteridiaceae rather than Ottokariaceae.



#### 4.1.2 CLASSIFICATION OF THE SOUTH AFRICAN FRUCTIFICATIONS

The classification scheme adopted in this study of the ovuliferous glossopterid fructifications from South Africa, is closely based on those proposed by Anderson & Anderson (1985) and McLoughlin (1995), and is summarised below.

*Division*        **Pinophyta** Meyen 1984

*Class*            **Glossopteridopsida** Maheshwari 1976

*Order*           **Dictyopteridiales** Rigby 1978 (nom. corr. McLoughlin 1990b)

*Families*

**4.1.2.1        Rigbyaceae** Anderson & Anderson 1985 emend.

***Original diagnosis* (Anderson & Anderson, 1985; fructification only):**

'*Fertiliger* – simple polysperm presumably axillary to unmodified *Glossopteris* leaf; *polysperm* – solitary multiovuliferous capitulum, bilaterally symmetrical, flattened dorsiventral; palmate with 6-8 lobes, fused to deeply cleft, each lobe terminating in an elliptical truncate ovuliferous scale; *stalk*- very long slender (to 70 mm); *attachment* – presumably axillary to unmodified glossopterid leaf; *ovules* – 1 per lobe, attached abaxially at base of ovuliferous scales; *detached seed* (known only for *R. arberioides*)- sessile, oval to round, 3-4 mm diam., conspicuously winged.'

***Emended diagnosis:*** Simple, solitary, multiovuliferous polysperm with pedicel terminating in fan-shaped aggregation of dichotomous branches, fused to varying degrees into a fan-shaped receptacle. Ultimate branches terminate in thinned, longitudinally striated scale or wing-like extension with single ovule/ seed scar at base of each scale. Seeds only borne on one surface of fructification; scales continuous with branch termini on sterile surface.

**Emendations:** Anderson & Anderson (1985) included information about associated leaves and a proposed mode of attachment of the fructifications to the plant; this information is probably too speculative to be included within a diagnosis, and has been omitted. The structure of the branch termini is clarified, particularly with reference to the bifacial nature of the fructification and the relationship between the wing/scale and seed-attachment point. Reference to seeds being attached to the abaxial surface of the fructification is omitted, as no attached fructifications are known and it is not possible to conclude which is the abaxial surface. The diagnosis has been expanded slightly to accommodate the Australian genus *Cometia* (McLoughlin, 1990a), the only other recognised member of the family.

**South African genus:** *Rigbya*

#### 4.1.2.2      **Arberiaceae** Rigby 1972 emend.

**Original diagnosis (Rigby, 1972a):** 'Female fructifications of branched or unbranched rachis bearing laterally inserted pinnae which are simple, bifid or multifid with terminal or laterally placed solitary ovules. Pinnules with a lamina, cupules and other sterile structures absent'.

**Emended diagnosis:** Ovuliferous fructifications comprising a primary axis which may be dichotomously branched, and which may bear a single order or multiple orders of branches; termini of ultimate branches bear a solitary ovule, and may have a sterile scale-like structure distal to seed attachment scar; fructifications do not have a fan-shaped arrangement of branches.

**Emendations:** the terms 'rachis', 'pinna' and 'pinnule' were removed, as they are particularly associated with fern fronds and reflect Rigby's (1972a) view that they were pteridospermous structures; the presence of a sterile scale-like feature distal to the seed attachment scar was included. Rigby (1972a) made a point of excluding fertile structures with any form of sterile structures from the family, and restricted its members to those having laterally inserted branches

only. The exclusion of fructifications with a fan-shaped arrangement of branches is to re-enforce the distinction between the Rigbyaceae and Arberiaceae.

**South African genera:** *Arberia*, *Vereenia*.

**4.1.2.3 Dictyopteridiaceae** Surange & Chandra ex Rigby 1978 emend. Maheshwari 1990 (nom. corr. McLoughlin 1995)

**Diagnosis (Maheshwari, 1990):** 'Fructification simple, dorsiventral, axillary, subtended by a normal vegetative glossopterid leaf, stalk adnate and fused with midrib or median veins for some distance. A large number of ovules borne on abaxial surface, adaxial surface with spreading 'venation'. Male counterpart not known definitely'.

**Notes:** a possible addition to this diagnosis would be the inclusion of the presence and details of the wing and its relationship to the marginal rank of seed scars.

**South African genera:** *Bifariola*, *Estcourtia*, *Elatra*, *Ottokaria*, *Scutum*, *Gladiopomum*, *Plumsteadia*, *Gonophylloides*, *Dictyopteridium*.

**4.1.2.4 Lidgettoniaceae** Surange & Chandra 1975 emend.  
Banerjee 1984

**Diagnosis (adapted from Banerjee 1984):** ovule-bearing organs comprising small dorsiventrally flattened sporophylls attached to a reduced, petiolate, leafy bract. Sporophylls bifacial with fertile and sterile surface; margin of sporophyll lobed or dentate. Sporophylls borne on short to long, slender pedicels which are distichous or attached in single row to petiole of leafy bract.

**Notes:** possible emendations would include mention of the (in many cases) campanulate form of cupules, substitution of the term sporophyll with a more neutral term such as capitulum, and clarification of the structure of the capitula,

which are divided into a seed-bearing receptacle and a marginal wing as in members of the Dictyopteridiaceae.

**South African genus:** *Lidgettonia*.

#### **4.1.2.5 The naming of species of glossopterid fructifications**

There have been various schools of thought with regard to the difficult issue of naming glossopterid fructifications. The main themes can be summarised as follows:

- 1) a system of form-genera and species, unrelated to attached *Glossopteris* leaves (e.g. Plumstead, 1952, 1956a,b, 1958; Surange & Chandra, 1975; Rigby, 1978; McLoughlin, 1990a,b, 1995; Pant, 1999);
- 2) use of form-genera, but each fructification adopts the epithet of its attached *Glossopteris* leaf (e.g. Kräusel p. 324 in Plumstead, 1952; Menéndez, 1962b; Lacey *et al.*, 1975);
- 3) inclusion of the fructification in the same genus and species as its subtending leaf (e.g. Mamay p. 324 in Plumstead, 1952); or whichever name has priority (Kovács-Endrödy, 1976);
- 4) inclusion of the leaf and associated or attached organs in the genus and species assigned to the ovuliferous fructification (Anderson & Anderson, 1985).

Each of these systems has its own set of advantages and disadvantages, but the first is the most commonly applied in the literature, and is the one that has been used throughout this study. Glossopterid fructifications are most frequently found detached and dissociated from their subtending leaves. To allow for the description and analyses of these organs, authors have in the past assigned them to their own form-genera. However, in cases where they have been found attached to a known *Glossopteris* leaf, the unfortunate situation has arisen where two organs have different names, despite the fact that they obviously belong to the same plant. As Schopf (1976) noted: 'A purely artificial taxonomic fragmentation should not be introduced in the fossils which show several parts connected. One organically connected plant specimen cannot possibly be

simultaneously assigned to more than one taxon'. He considered this to be a violation of the ICBN (Art. 63), and recommended the avoidance of scientific names altogether, opting instead for a looser classification based on 'types', e.g. *Ottokaria* type, strictoid type etc. This system is useful in recognising broad morphological groupings within the glossopterid fertile structures, but is not practical in more detailed studies and comparisons.

No-one likes using form-genera. It is obviously a very artificial way of classifying organisms. However, there are times when this system offers the most practical and concise manner of dealing with taxonomic quandaries in palaeontology, allowing research to continue, and hopefully leading to a point where we can represent the taxa in a more biologically representative manner. Tying the taxonomy of the fructifications to the species of subtending *Glossopteris* leaf is simply not a practical approach at this time. Whilst we can all appreciate the ideal situation where each plant, with all its organs has a single name, there are many examples of fructifications that have not yet been found in attachment to a *Glossopteris* leaf - perhaps some of them never will. In addition, *Glossopteris* leaf taxonomy is poorly understood and almost always subjective to some degree. Any approach relying on consistent and accurate identification of *Glossopteris* leaves across the globe is probably going to cause more confusion than clarification at present, and will hinder attempts to correlate information from different parts of Gondwana.

Our current knowledge of *Glossopteris* leaves indicates that there is a higher degree of diversity in the fructifications, or that the diversity in the fertile structures is more readily apparent than that of the leaves. This is reflected in the remarkable circumstance where some authors have placed glossopterid fructifications within separate orders, while the associated or attached leaves languish in the single genus *Glossopteris* (e.g. Chandra & Surange, 1975). Apparently a single leaf genus simply does not allow for adequate expression of the diversity exhibited in the polysperms. Traditionally, in botanical studies it is the ovuliferous fertile structures that have served as the basis of taxonomic systems.

Anderson & Anderson (1985) made a bold attempt at portraying a unified, naturalistic view of *Glossopteris*, but perhaps relied too heavily on associative evidence. We really need to study this plant group further before we can confidently identify complete organ groupings.

## 4.2 DICHOTOMOUS KEY

Taxonomic keys are particularly difficult to use in the field of palaeontology since fossils are seldom complete, and each step usually relies on an individual character or dimensional range which may or may not be preserved. However, my hope is that together with the reconstructions and key end-notes provided, this key will be a useful and practical guide to the ovuliferous glossopterid fructifications of South Africa. The key end-notes have been included to provide the user with a clearer understanding of the diagnostic characters of each taxon, thereby reducing the chances of new fructifications being shoe-horned into existing taxa.

**Table 4.2.1. Summary of the families and species of South African glossopterid fructifications included in the key.**

| FAMILY                    | GENUS                  | SPECIES                  | KEY END-POINT               | KEY END-NOTE |
|---------------------------|------------------------|--------------------------|-----------------------------|--------------|
| <b>RIGBYACEAE</b>         | <i>Rigbya</i>          | <i>arberioides</i>       | Step 2 (a)                  | A            |
| <b>ARBERIACEAE</b>        | <i>Arberia</i>         | <i>hlobanensis</i>       | Step 3 (b)                  | B            |
|                           |                        | <i>madagascariensis</i>  | Step 4 (a)                  | C            |
|                           | <i>Vereenia</i>        | <i>leeukuilensis</i>     | Step 4 (b)                  | D            |
| <b>DICTYOPTERIDIACEAE</b> | <i>Bifaria</i>         | <i>intermittens</i>      | Steps 6 (b), 9 (b) & 16 (b) | E            |
|                           | <i>Estcourtia</i>      | <i>conspicua</i>         | Step 8 (b)                  | F            |
|                           | <i>Elatra</i>          | <i>leslii</i>            | Step 9 (a)                  | G            |
|                           | <i>Ottokaria</i>       | <i>transvaalensis</i>    | Step 12 (a)                 | H            |
|                           |                        | <i>hammanskraalensis</i> | Step 12 (b)                 | I            |
|                           |                        | <i>huriadica</i>         | Step 12 (c)                 | J            |
|                           | <i>Scutum</i>          | <i>leslii</i>            | Step 15 (a)                 | K            |
|                           | <i>Gladiopomum</i>     | <i>dutoitides</i>        | Step 17 (a)                 | L            |
|                           |                        | <i>acadarensis</i>       | Step 17 (b)                 | M            |
|                           |                        | <i>elongatum</i>         | Step 17 (c)                 | N            |
|                           | <i>Plumsteadia</i>     | <i>lerouxii</i>          | Step 18 (a)                 | O            |
|                           |                        | <i>gibbosa</i>           | Step 19 (b)                 | P            |
|                           | <i>Gonophylloides</i>  | <i>strictus</i>          | Step 20 (a)                 | Q            |
|                           |                        | <i>waltonii</i>          | Step 20 (b)                 | R            |
|                           | <i>Dictyopteridium</i> | <i>natalensis</i>        | Step 21 (a)                 | S            |
|                           |                        | <i>flabellatum</i>       | Step 21 (b)                 | T            |
| <b>LIDGETTONIACEAE</b>    | <i>Lidgettonia</i>     | <i>lidgettonioides</i>   | Step 22 (a)                 | U            |
|                           |                        | <i>elegans</i>           | Step 23 (a)                 | V            |
|                           |                        | <i>africana</i>          | Step 23 (b)                 | W            |

The species of glossopterid fructifications that have been included in the key are listed in Table 4.2.1. The list is the product of a fairly extensive revision of the taxonomy of the glossopterid ovuliferous fructifications. Each taxon and

each revision that was implemented is discussed in detail in Chapters 5 to 8. The key is based purely on morphological characters, and may or may not reflect phylogenetic relationships between the taxa.

#### **4.2.1 CHARACTERS USED IN KEYING A SPECIMEN**

Wing morphology was probably the single most important character used in the key to distinguish between different genera of the Dictyopteridiaceae. Use of the wing as a primary character takes advantage of the fact that at least part of the wing should be preserved, even in generally poorly represented or incomplete specimens. Other characters that played a central role in the compilation of the key were L:W ratio and shape of the receptacle. Seed scar morphology proved to be an important feature when differentiating between *Plumsteadia* and *Dictyopteridium*. Members of the Arberiaceae were distinguished on the basis of basic branching patterns, seed scar and wing/scale morphology. Scale leaf and cupule morphology were used to separate species of the Lidgettoniaceae.

As with most botanical situations involving the use of morphological parameters, it is important to have a large sample size to be able to reliably assess the degree and direction of variation within a population. Unfortunately, glossopterid fructifications are fairly rare, and often there is only a handful of specimens of any particular taxon available for comparison. This means that steps in the key which rely on quantitative characters may not prove to be as reliable as those involving qualitative distinctions.

When this key is tried and tested, it will no doubt prove to be less than air-tight, not only when new fructifications surface, but also in cases when members of existing taxa are found that do not fall within the morphological or size constraints outlined here. The detailed key end-notes and fossil reconstructions that have been provided should help to circumvent confusion in these cases, enabling the user to make identifications or comparisons at a glance, without placing too much emphasis on quantitative information.



**When keying a specimen, the following measurements and characters may be required:**

(Refer to section 3.1.2 for clarification on the basic morphological features characteristic to each member of the four families of ovuliferous fructifications).

- 1) overall **grouping and positioning of the ovules** or seed scars;
- 2) pattern of **branching** (if applicable);
- 3) **overall size** of the fructification;
- 4) **attached leaf or scale leaf morphology:**
  - a) size;
  - b) shape;
  - c) petiole features;
  - d) position of polysperm attachment;
- 5) **wing or terminal scale morphology:**
  - a) appearance of margin (entire, dentate, lobed etc.);
  - b) is wing continuous around the receptacle, does it vary in width in different places;
  - c) medial and apical width of wing;
  - d) angle and morphology of wing fluting and striations: (i) are fluting and striations perpendicular to the edge of the receptacle or are they apically inclined;(ii) is the fluting only distinct near the edge of the receptacle, or all the way to the margin;
- 6) **receptacle morphology:**
  - a) shape (overall, base and apex);
  - b) size (length and width);
  - c) length to width ratio;
  - d) presence of an apical spine;

7) **pedicel features:**

- a) length;
- b) width;
- c) morphology: is the pedicel considerably expanded at insertion into the receptacle;

8) **seed scar morphology:**

- a) closely spaced, bulbous cushions, or small, isolated tubercles (in impressions);
- b) size and shape;

9) in the case of the Lidgettoniaceae, the following **capitulum features** should be noted:

- a) number of capitula per scale leaf;
- b) size of dorsiventrally compressed capitula;
- c) shape of capitulum (strongly campanulate, spatulate?);
- d) number of ovules (seed scars);
- e) number of wing segments/ teeth;
- f) shape of subtending scale leaf.

**NOTE:** Although the presence of one or two wings is considered to be a major point of divergence in the key, the presence of a dual wing structure is difficult to observe in practice - the double wings in *Bifariala* and *Elatra* remained undetected for 50 years. For this reason, each of the wing morphologies of *Bifariala* has been individually keyed, in addition to the major, double wing dichotomy described in Step 7. The covering and secondary wings of *Elatra* are usually obscured or are very inconspicuous in impression fossils, and have been omitted from the key except for a brief description in the key end-note (H).

## 4.2.2 KEY TO THE REVISED SOUTH AFRICAN TAXA OF GLOSSOPTERID OVULIFEROUS FRUCTIFICATIONS

### STEP 1:

- a) Branched or lobed fructification with ovules (or seed scars) borne singly or in pairs on terminal branches or lobes - STEP 2 [**RIGBYACEAE, ARBERIACEAE**]
- b) Multiple ovules (or seed scars) aggregated onto a central receptacle; or may have multiple receptacles which are reduced in size, and borne on a single scale leaf - STEP 5 [**DICTYOPTERIDIACEAE, LIDGETTONIACEAE**]

### STEP 2:

- a) Planar, flabellate primary axis with peripheral branches along distal margin, or fan-shaped series of dichotomous branches in a single plane; terminal branches with elongated, oval to rectangular, striated wing distal to single seed scar – *Rigbya arberioides* [Table 4.2.2, end-note **A**] [**RIGBYACEAE**].

- b) Primary axis not fan-shaped; branching may be 3-dimensional - STEP 3 [**ARBERIACEAE**]

### STEP 3:

- a) Elongated, expanded, planated lamina or primary axis bearing lateral branches - STEP 4
- b) Primary axis not planated, branching pattern 3-dimensional; bifacial, oval branch termini with narrow wing distal to seed scar(s)- *Arberia hlobanensis* [Table 4.2.2, end-note **B**].

### STEP 4:

- a) Terminus of each ultimate branch with elongated, striated wing distal to seed scar(s); lateral branching may be dichotomous, and may be in 3 dimensions - *Arberia madagascariensis* [Table 4.2.2, end-note **C**].
- b) Terminal section of each branch rounded, slightly expanded, and sharply, laterally recurved towards the edge of the narrowly elliptical lamina; branches in opposite lateral ranks – *Vereenia leeukuilensis* [Table 4.2.2, end-note **D**].

### STEP 5:

- a) Relatively large fructifications (usually >1.5 cm in length); solitary, borne on *Glossopteris* leaves similar to associated vegetative forms – STEP 6 [**DICTYOPTERIDIACEAE**]
- b) Relatively small fructifications (usually <1.5 cm in length); borne in pairs on a specialised, fertile scale leaf that differs significantly from associated vegetative leaves]– STEP 22 [**LIDGETTONIACEAE**]

### STEP 6:

- a) Single striated wing present along periphery of receptacle, or wing absent - STEP 7
- b) Double wing structure present; receptacle narrowly elliptical to broadly lanceolate with two superposed, peripheral wings; overarching, hooded wing absent - *Bifariale intermittens* [see steps 10(b) & 17(b) to confirm two separate wing morphologies] [Table 4.2.2, end-note **E**].

### STEP 7:

- a) Wing striations inclined towards apex of fructification - STEP 8
- b) Wing striations and fluting perpendicular to edge of receptacle, or wing absent - STEP 10

### STEP 8:

- a) Wing broadest at the apex (acute), contracted at base of receptacle - STEP 9
- b) Wing of equal width medially and apically, base contracted and decurrent along short pedicel - *Estcourtia conspicua* [Table 4.2.2, end-note F].

### STEP 9:

- a) Wing apex elongated and acuminate, receptacle circular to transversely elliptical; on closer inspection, complex wing structure present, with hood beneath impression of fertile surface, secondary scutoid wing in base - *Elatra leslii* [Table 4.2.2, end-note G]
- b) Wing apex acute, receptacle ovate to broadly lanceolate [check for evidence of a second wing - see Steps 6(b) & 16(b)] - *Bifariaia intermittens* [Table 4.2.2, end-note E].

### STEP 10:

- a) Wing not divided into lobes, or wing absent - STEP 11
- b) Peripheral wing divided into rounded or truncated lobes (as opposed to dentate or scalloped margin - see definitions), the mid-line of each lobe corresponding to the mid-line of a marginal seed scar; lobes may be partially fused - STEP 12

### STEP 11:

- a) Receptacle width:pedicel width  $\leq 3$ ; wing entire - STEP 12
- b) Receptacle width:pedicel width  $> 3$ ; wing absent, dentate or entire - STEP 13

### STEP 12:

- a) Well-defined wing lobes partially fused at base with blunt, rounded apices, receptacle ovate to obovate, pedicel moderately expanded at insertion - *Ottokaria transvaalensis* [Table 4.2.2, end-note H].
- b) Wing with shallow, truncated lobes (fused for most of length), receptacle circular to transversely elliptical, pedicel moderately expanded at insertion - *Ottokaria hammanskraalensis* [Table 4.2.2, end-note I].
- c) Wing margin entire or with shallow, weakly defined lobes; receptacle ovate to circular, pedicel very broadly expanded at insertion - *Ottokaria buriadica* [Table 4.2.2, end-note J].

### STEP 13:

- a) Seed scars close together and composed of well-defined, elliptical cushions with central tubercle (tubercles may or may not be preserved) - STEP 14
- b) Seed scars comprising small but prominent, widely spaced, tubercles (very weakly developed, low, dough-nut shaped seed cushions may be present) - STEP 21

### STEP 14:

- a) Medial wing width  $\geq 2.5$  mm - STEP 15
- b) Medial wing width  $< 2.5$  mm - STEP 18

### STEP 15:

a) Wing with prominent fluting extending from receptacle edge to wing margin; wing continuous around receptacle except at pedicel insertion - ***Scutum leslii*** [Table 4.2.2, end-note **K**].

b) Wing with ill-defined fluting that is more prominent adjacent to the receptacle; wing contracted at base and apex of receptacle - STEP 16

### STEP 16:

a) Receptacle with a narrow, pointed, striated, apical spine; radially striated wing abruptly contracted at apex on either side of spine, and forms a basal lobe on either side of pedicel insertion - STEP 17

b) Receptacle without an apical spine [check for evidence of a second wing - see Steps 6(b) & 9(b)] - ***Bifariaia intermittens*** [Table 4.2.2, end-note **E**].

### STEP 17:

a) Receptacle elliptical to lanceolate with a L:W ratio of approximately 3:1 - ***Gladiopomum dutoitides*** [Table 4.2.2, end-note **L**].

b) Receptacle lanceolate, extremely elongate oblong to lorate with a L:W ratio of approximately 5:1 - ***Gladiopomum acadarensense*** [Table 4.2.2, end-note **M**].

c) Receptacle elongate to lorate with a L:W of approximately 7:1 - ***Gladiopomum elongatum*** [Table 4.2.2, end-note **N**].

### STEP 18:

a) L:W of receptacle >3.5:1; small seed scars (av. 1.3 mm long), sessile fructification with truncate to slightly hastate base, attached to midrib in the basal portion of a lanceolate to elliptical or oblong *Glossopteris* leaf with a narrowly cuneate base; leaf venation distinctive, perpendicular to midrib with polygonal to rhombic meshes adjacent to midrib becoming linear in the midlaminal to marginal region - ***Plumsteadia lerouxii*** [Table 4.2.2, end-note **O**].

b) L:W of receptacle < 3.5:1 - STEP 19

### STEP 19:

a) Base of receptacle markedly cordate to auriculate -STEP 20

b) Base of receptacle rounded, or very slightly cordate with a receptacle L:W >1.5:1 - ***Plumsteadia gibbosa*** [Table 4.2.2, end-note **P**].

### STEP 20:

a) Sessile, ovate to broadly lanceolate fructification with pronounced, rounded, basal auricles; seed scars small (av. 1 mm, <2 mm long) and numerous; borne on the midrib in the basal half of a long, narrowly elliptical *Glossopteris* leaf with a cuneate base and fine venation that arches gently from the midrib before following a fairly straight path across the mid-laminal and marginal parts of the lamina - ***Gonophylloides strictus*** [Table 4.2.2, end-note **Q**].

b) Pedicellate, ovate fructification, with moderately cordate base; sterile surface often with strong imprints of seed scars - ***Gonophylloides waltonii*** [Table 4.2.2, end-note **R**].

### STEP 21:

a) Receptacle surface smooth between tubercles on fertile surface, where present, cushions are shallow and ill-defined - *Dictyopteridium natalensis* [Table 4.2, end-note **S**].

b) Receptacle surface with distinctive venation pattern on both sterile and fertile surfaces; veins radiate from the base and arch sharply at receptacle margin producing prominent ridges/grooves along the periphery - *Dictyopteridium flabellatum* [Table 4.2.2, end-note **T**].

### STEP 22:

a) Capitula large (guideline: >8 mm in diameter in dorsiventrally compressed specimens); lobes deeply incised with acute apices, campanulate capitula deeply reflexed; 9-13 seed scars; club-shaped scale leaf - *Lidgettonia lidgettonioides* [Table 4.2.2, end-note **U**].

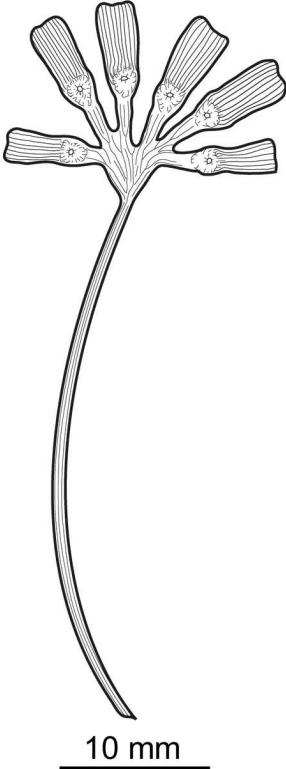
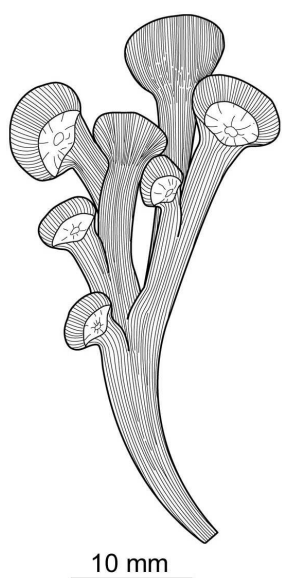
b) Capitula small (guideline: <8 mm in diameter in dorsiventrally compressed specimens); capitula campanulate with moderately scalloped margin, or spatulate - STEP 23

### STEP 23:

a) One to three pairs of small, spatulate capitula (<4 mm diameter), with 2 or 3 seed scars and a distally extended wing that is contracted at pedicel insertion; scale leaf slender and obovate - *Lidgettonia elegans* [Table 4.2.2, end-step **V**].

b) 1 to 4 pairs of capitula >4 mm in diameter, campanulate with scalloped to entire margin; 5-11 seed scars; scale leaf rhomboidal to obovate - *Lidgettonia africana* [Table 4.2.2, end-step **W**].

Table 4.2.2. Key end-notes for ovuliferous glossopterid fructifications of South Africa, listing the most important diagnostic characters and including an impression fossil reconstruction of each taxon.

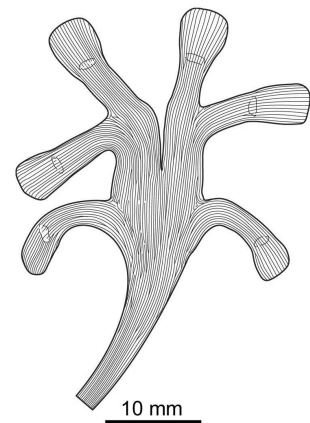
| TAXON                                      | PRINCIPAL DIAGNOSTIC CHARACTERS                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     | RECONSTRUCTION OF IMPRESSION FOSSIL                                                   |
|--------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------|
| A <i>Rigbya arberioides</i><br>Step 2 (a)  | <p>Planar, flabellate primary axis with peripheral branches along distal margin, or fan-shaped series of dichotomous branches in a single plane with five to nine, most frequently seven ultimate branches; fructification bifacial, with seeds only borne on one surface;</p> <p><b>Terminal scale/wing:</b> terminal branches each bear a single 2.5 to 8 mm long, elongate-elliptical to ovate or elongate-spatulate scale/wing distal to single seed scar; wing longitudinally striated with truncate to concave distal margin;</p> <p><b>Sterile surface:</b> continuous, uninterrupted surface with striations continuous from pedicel to distal margins of wing;</p> <p><b>Pedicel:</b> typically long and slender; pedicel, its branches and terminal scales all longitudinally striated;</p> <p><b>Seeds:</b> attached platyspermic seeds flattened, rounded to ovate with lateral wings;</p> <p><b>Subtending <i>Glossopteris</i> leaf:</b> no attached leaves known.</p> |   |
| B <i>Arberia hlobanensis</i><br>Step 3 (b) | <p>Primary axis not planated, branching pattern 3-dimensional and dichotomous; branches longitudinally striated; primary axis gradually tapered towards the base; ultimate branches short, each expanding distally to form a slightly cup-shaped, transversely elliptical scale-like feature;</p> <p>scales bifacial, with striate sterile surface, and fertile surface with 1 or 2 indistinct seed scars at base and weakly differentiated, distal wing which is contracted at the base.</p> <p><b>Other features:</b> attached seeds and leaves unknown.</p>                                                                                                                                                                                                                                                                                                                                                                                                                      |  |

**C** *Arberia Madagascar-  
iensis*  
Step 4 (a)

Dorsiventral, branched axis which may give rise to branches in a plane perpendicular to the primary axis; primary axis is planated, almost laminar, fan-shaped and tapering proximally into a stout pedicel; lateral branching is pinnate in the proximal region, with a single, prominent apical dichotomy; primary axis bears prominent longitudinal striations that continue into the lateral branches;

**Branch termini:** terminus of each ultimate branch with a short, ill-defined, longitudinally striated wing/scale distal to seed scar;

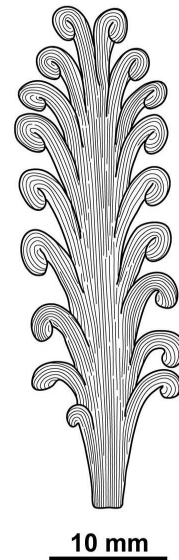
**Other features:** attached seeds and leaves unknown.



**D** *Vereenia  
leeukuilensis*  
Step 4 (b)

Simple, planated, oblanceolate to elliptical ovuliferous fertile axis comprising a laminate primary axis without dichotomies, giving rise to a single order of approximately opposite lateral branchlets; branchlets arise from axis at a steep angle and are as long as the broadest width of the primary axis; termini of the branchlets are pendulous to tightly recurved; terminus of each branchlet is rounded, slightly expanded, and sharply, laterally recurved towards the edge of lamina; base of primary axis extended into a tapering pedicel; all features bear longitudinal striations;

**Other features:** attached seeds and leaves unknown.





**E** *Bifariaia intermittens*  
Steps 6 (b), 9 (b) & 16 (b)

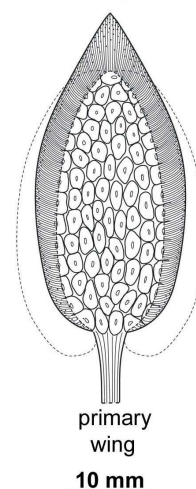
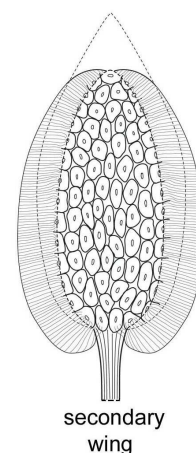
**Wing:** two superposed, peripheral wings present; primary wing with acute apex, tapered base, apically inclined striations; secondary wing scutoid, discontinuous at apex, radial striations and fluting, basal wing lobes; secondary wing flush with fertile surface of fructification, primary wing continuous with sterile surface of receptacle;

**Receptacle:** narrowly elliptical to broadly lanceolate; L:W of ca. 2:1;

**Seed scars:** smooth, elliptical cushions (in impressions), central tubercle present in some cases; marginal rank of rectangular scars;

**Sterile surface:** fine, dichotomising and anastomosing veins arising from pedicel, traversing receptacle in fan-shaped pattern; when veins reach edge of receptacle, they recurve before entering the primary wing and arch slightly towards the apex;

**Subtending Glossopteris leaf:** fructification attached near base of petiole; leaf is oblanceolate with cuneate base and obtuse apex; midrib is persistent and well-defined; veins emerge at acute angle from midrib, arching gently and continuously across lamina, forming fine, narrow, parallel meshes at an angle of about 50° to medio-longitudinal axis.



**F** *Estcourtia conspicua*  
Step 8 (b)

**Wing:** of equal width medially and apically, base contracted and decurrent along short pedicel; striations and fluting weakly developed, and slightly apically inclined;

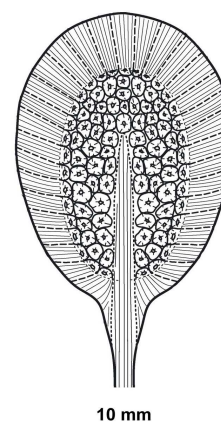
**Receptacle:** oval to elliptical; tapered wedge of tissue extends from pedicel into receptacle;

**Seed scars:** small and densely arranged on receptacle; marginal rank of rectangular scars;

**Sterile surface:** fan-shaped network of broad-meshed venation;

**Other features:** fructification has only been found attached to subtending leaf;

**Subtending Glossopteris leaf:** lanceolate to elliptical, petiolate, cuneate to attenuate base; meshes vary from broad, polygonal near base and near midrib, to elongate polygonal, linear towards apex and margins; vein course straight to moderately curved with a mid-laminal vein angle of approximately 55°; midrib well-defined and persistent.



**G** *Elatra leslii*  
Step 9 (a)

**Wing:** apex elongated and acuminate, tapers towards base of receptacle; campylodromous fluting and striations; on closer inspection, a complex wing structure is present, with hood-like hood lying beneath impression of fertile surface in fossil; secondary scutoid wing with lobes present in base;

**Receptacle:** circular to transversely elliptical;

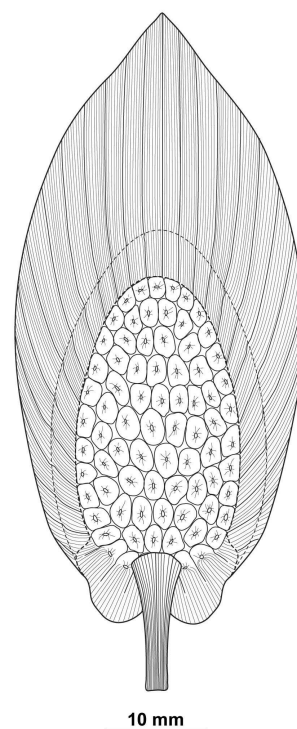
**Seed scars:** large, prominent, circular, elliptical to polygonal, raised cushions with central tubercle;

**Sterile surface:** veins arise from pedicel, in some cases forming a medio-longitudinally oriented bundle in the base of fructification; veins diverge in fan-shaped pattern, dichotomise and anastomose to form meshes; at edge of receptacle, veins recurve sharply before entering primary wing and arching towards apex;

**Pedicel:** striated, moderately expanded at insertion;

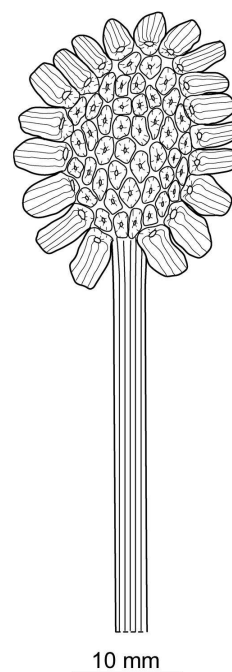
**Other features:** impression of fertile surface of receptacle is carried by a mass of sediment that is discontinuous with the primary wing impression, and can be chipped away to reveal a continuation of the wing as a hood beneath; this is the largest glossopterid fructification known to date, with an overall length of 25.3 (48) 79.3 mm and width of 13.2 (27) 39.3 mm;

**Subtending *Glossopteris* leaf:** regularly found attached in base of narrowly obovate leaf with rounded apex, cuneate to roundly hastate base; midrib prominent, persistent; fine venation with parallel meshes follows a straight to gently curved path to margin at angle of c. 40°.



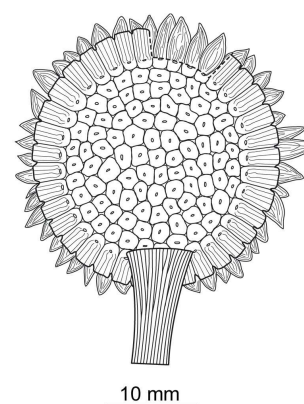
**H** *Ottokaria transvaalensis*  
Step 12 (a)

**Wing:** characterised by deeply lobed margin; degree of lobe fusion is variable within a single specimen - may be separated to base, but in most cases fused in basal quarter to two thirds of lobe length; lobes may be slightly tapered, and have apices that are truncated, slightly pointed, or (most commonly) bluntly rounded; lobes have radial striations;  
**Receptacle:** circular, ovate to obovate;  
**Seed scars:** shallow depressions each bearing a raised elliptical cushion with an apical pit (in impressions);  
**Sterile surface:** fine, fan-shaped network of veins continuing into wing;  
**Pedicel:** long, striated, only moderately expanded at insertion;  
**Other features:** smallest of the South African *Ottokaria* species, 14.3 (21.8) 29.6 mm long, 14.8 (21.2) 30.1 mm wide; subtending leaf type unknown; seeds unknown.



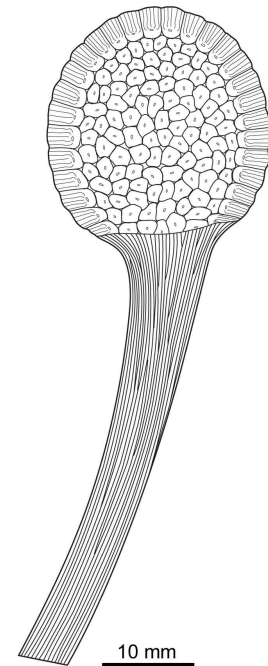
**I** *Ottokaria hammanskraalensis*  
Step 12 (b)

**Wing:** relatively narrow with weak fluting and striations; lobes fused for most of length, giving margin a notched appearance;  
**Receptacle:** sub-circular to transversely elliptical;  
**Seed scars:** each represented by a shallow depression (in impressions) with a central tubercle;  
**Sterile surface:** veined, indistinct;  
**Pedicel:** pedicel long, broad, prominently expanded at insertion, but not as broad as in *O. buriadica*; with prominent longitudinal striations; pedicel insertion is at a slightly oblique angle, above and behind the apparently uninterrupted peripheral wing;  
**Other features:** large fructification, 18.9 (28.5) 40.3 mm long, 15.3 (28.2) 39.4 mm wide;  
**Seeds:** often found with *in situ* seeds, which have an apically extended, pointed wing; the seed wings protrude beyond the edge of the wing, forming a fringe of pointed lobes which may be mistaken for a fructification wing feature;  
**Attached leaves:** subtending leaf type unknown.



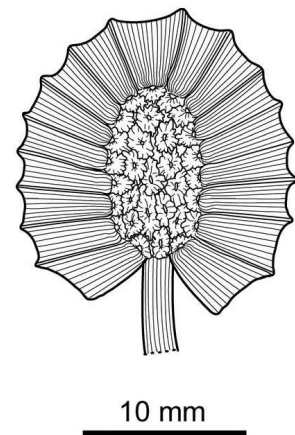
**J** *Ottokaria buriadica*  
Step 12 (c)

**Wing:** narrow, continuous and of fairly even width along entire margin of receptacle; wing margin entire or may be denticulate;  
**Receptacle:** broadly ovate to sub-circular;  
**Seed scars:** roughly circular, low cushions (in impressions) with a central tubercle;  
**Sterile surface:** sterile surface with coarse reticulum of spreading venation;  
**Pedicel:** very broadly expanded at insertion, receptacle width:pedicel width <3; bears prominent longitudinal striations; pedicel insertion is at a slightly oblique angle, above and behind the apparently uninterrupted peripheral wing;  
**Leaf type:** organic connection to a *Glossopteris* leaf has not been unequivocally demonstrated for this taxon, but type specimen is closely associated with a gangamopteroid form;  
**Other features:** large fructification, 21.6 (27.2) 30.9 mm long, 19.5 (25.6) 31.1 mm wide; subtending leaf type unknown.



**K** *Scutum leslii*  
Step 15 (a)

**Wing:** prominent; continuous, of regular diameter, except at point of pedicel insertion where sharply constricted to form a rounded or laterally truncated lobe on either side of pedicel; fine radial striations, and prominent fluting perpendicular to margin of receptacle; margin dentate, undulating, scalloped or entire;  
**Receptacle:** circular, elliptical, obovate or ovate to broadly lanceolate; rounded base and apex;  
**Seed scars:** marginal seed scars square, forming distinctive rank along periphery of receptacle; central seed scars elliptical, longitudinal to long axis of receptacle; scars are raised cushions, each with central depression bearing a tubercle;  
**Sterile surface:** laminate with spreading, reticulate venation radiating from pedicel insertion;  
**Pedicel:** slender, striated, typically of even width;  
**Seeds:** ovate, flattened, typically small, (c.4 mm long, 2.5 mm wide), with narrow to prominent wing;  
**Subtending *Glossopteris* leaf:** polysperm borne proximally on midrib or on petiole; leaf variable; elliptical, oblong to narrowly oblanceolate, with cuneate base tapering into long, narrow petiole, or decurrent base which may be slightly expanded at base into small,



inconspicuous, sagittate lobes; apex moderately acute; veins diverge from well-defined and persistent midrib at steep angle, arching gently across lamina at 40 - 70°; meshes elliptical to elongate polygonal near midrib, becoming linear in mid-laminal and marginal regions.

**L** *Gladiopomum dutoitides*  
Step 17 (a)

**Wing:** broad, margin entire; fine striae and fluting oriented perpendicular to receptacle, flute definition decreasing towards the margin; wing discontinuous at base, forming a truncate to convex lobe on either side of pedicel insertion; tapers abruptly at apex near base of apical spine; wing width: receptacle width = 0.7:1;

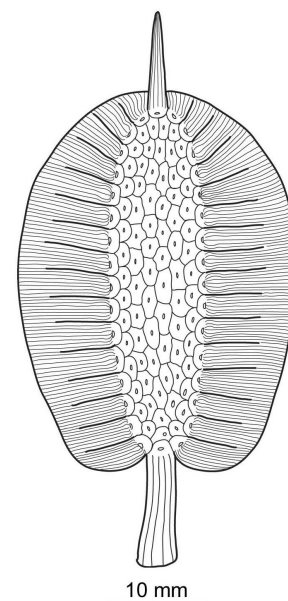
**Receptacle:** oblong, elongate elliptical to lanceolate, with L:W of about 3:1; very pronounced, longitudinally striated, tapered apical spine, ca. 5-10 mm long;

**Seed scars:** numerous, closely spaced;

**Sterile surface:** sterile surface is characterized by a fan-shaped network of bifurcating and anastomosing veins, with strongly parallel venation along the central axis of the receptacle;

**Pedicel:** striated, may be slightly expanded at junction with receptacle;

**Subtending *Glossopteris* leaf:** fructification attached to base of petiole of elongate oblanceolate *Glossopteris* leaf, with obtuse apex, attenuate base and strongly developed, persistent midrib; venation is straight to gently arching with few bifurcations and anastomoses, forming parallel meshes at an angle of approximately 45° to midrib.



**M** *Gladiopomum acadarensense*  
Step 17 (b)

**Wing:** very broad, margin entire; fine striae and fluting oriented perpendicular to receptacle, flute definition decreasing towards the margin; wing discontinuous at base, forming a truncate to convex lobe on either side of pedicel insertion; tapers abruptly at apex near base of apical spine; wing width: receptacle width up to 1.5:1;

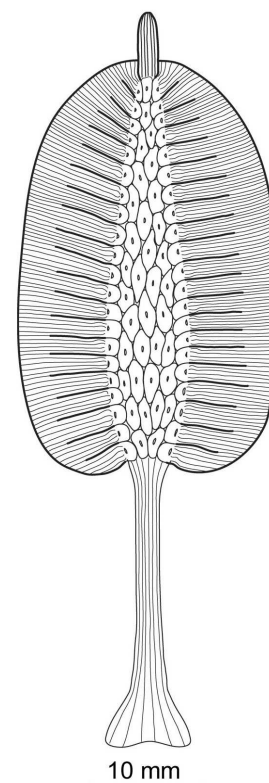
**Receptacle:** lanceolate, extremely elongate oblong, to lorate and in some cases falcate, with a high L:W ratio (up to 5:1); apical spine present, but weakly developed;

**Seed scars:** numerous, closely spaced; elliptical towards centre of receptacle; marginal rank of rectangular scars along periphery of receptacle;

**Sterile surface:** sterile surface is characterized by a fan-shaped network of bifurcating and anastomosing veins, with strongly parallel venation along the central axis of the receptacle;

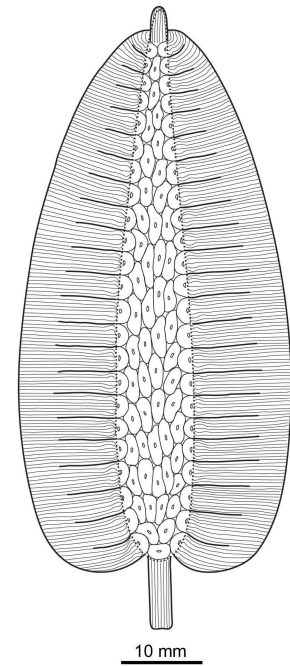
**Pedicel:** long, striated, may be slightly expanded at base and/or at junction with receptacle;

**Other features:** subtending *Glossopteris* leaf unknown.



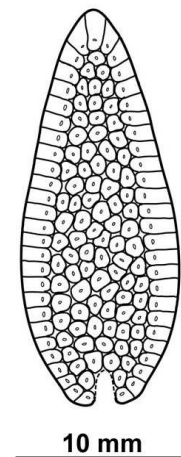
**N** *Gladiopomum elongatum*  
Step 17 (c)

**Wing:** broad, margin entire; fine striae and fluting oriented perpendicular to receptacle, flute definition decreasing towards the margin; wing discontinuous at base, forming a truncate to convex lobe on either side of pedicel insertion; tapers abruptly at apex near base of apical spine; wing width: receptacle width = ca. 1;  
**Receptacle:** unusually long; elongate lanceolate to lorate, with a high L:W ratio (up to 7:1); apical spine present but not well defined;  
**Seed scars:** numerous, closely spaced; marginal rank of rectangular scars;  
**Sterile surface:** sterile surface is characterized by a fan-shaped network of bifurcating and anastomosing veins, with strongly parallel venation along the central axis of the receptacle;  
**Pedicel:** short, striated;  
**Other features:** subtending *Glossopteris* leaf unknown.



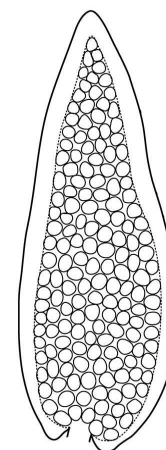
**O** *Plumsteadia lerouxii*  
Step 18 (a)

**Wing:** wing narrow and entire with striations and ill-defined fluting;  
**Receptacle:** narrowly lanceolate with high length to width ratio ( $>3.5$ ; av. 5) and low ratio of wing width to receptacle width; apex acute, tapering; base rounded, truncate or slightly cordate;  
**Seed scars:** small, closely spaced, with well-defined cushions;  
**Other features:** to date, has never been found isolated from subtending leaf;  
**Subtending *Glossopteris* leaf:** fructification sessile, attached to midrib in lower third of elliptical, oblong to elongate-obovate leaf with long, tapering, cuneate base and rounded to obtusely pointed apex; veins follow straight path to margin, nearly perpendicular to well-defined, persistent midrib; meshes coarse, polygonal adjacent to midrib, becoming narrower and more elongated towards margin.



**P** *Plumsteadia gibbosa*  
Step 19 (b)

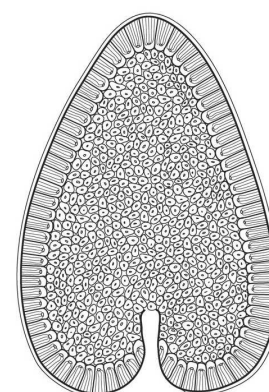
**Wing:** narrow and entire with moderate to pronounced, persistent, radial striations and fluting; may have small basal lobes;  
**Receptacle:** ovate to lanceolate with length to width ratio of 2-3.5; apex acute, base rounded to truncate;  
**Pedicel:** short, longitudinally striated;  
**Seed scars:** major diagnostic character of taxon - prominent and bulbous, may or may not have central tubercle;  
**Other features:** sterile surface obscured by secondary imprints of seed scars in many cases;  
 many specimens have been found with attached seeds; seeds circular to elliptical, slightly pointed at micropylar end; seeds may have a very narrow wing;  
**Subtending *Glossopteris* leaf:** attached near top of petiole of leaf with cuneate base; gently arching venation steeply angled (20°-40°), with elongated polygonal to parallel meshes.



10 mm

**Q** *Gonophylloides strictum*  
Step 20 (a)

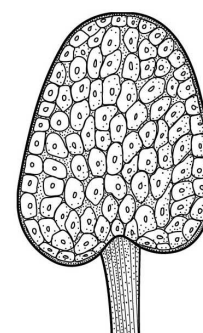
**Wing:** very narrow, fluted wing with entire margin;  
**Receptacle:** ovate to broadly lanceolate; apex rounded to moderately acute; base cordate with pronounced, rounded, basal auricles;  
**Seed scars:** small and numerous, closely spaced;  
**Sterile surface:** fine, anastomosing and bifurcating veins diverging from point of pedicel insertion, radiating across receptacle and recurving into basal lobes;  
**Other features:** sessile; sterile surface ; almost always found attached to leaf;  
**Subtending *Glossopteris* leaf:** borne in lower third of long, narrowly elliptical *Glossopteris* leaf with fine, gently arching to straight venation with mid-laminal angle of approximately 60°, and elongate polygonal to parallel meshes.



10 mm

**R** *Gonophylloides waltonii*  
Step 20 (b)

**Wing:** absent or very narrow, with radial fluting and striations; groove along periphery;  
**Receptacle:** ovate; apex obtusely rounded; base moderately cordate;  
**Pedicel:** short, striated, slightly expanded at insertion;  
**Seed scars:** seed scars large and prominent, sterile surface with strong secondary imprints of seed scars;  
**Other features:** only isolated specimens have been found; venation on sterile surface indistinct.



10 mm



**S** *Dictyopteridium natalensis*  
Step 21 (a)

**Wing:** fairly narrow, continuous along the periphery of receptacle except at pedicel insertion; margin entire or rarely dentate, bearing prominent fluting and fine striations perpendicular to margin of receptacle;

**Receptacle:** ovate-lanceolate with rounded to truncate or slightly cordate base, pointed to obtusely rounded apex; tendency to be asymmetrical (falcate);

**Pedicel:** sessile or with short pedicel;

**Seed scars:** in most cases only represented by small tubercles on a smooth receptacle surface; where present, cushions are shallow and ill-defined, except at margin where they may be prominent and rectangular, corresponding to positions of wing flutes;

**Sterile surface:** veined, with a strong medio-longitudinal density of parallel veins, and a fairly open mesh pattern (only 1 or 2 meshes from longitudinal bundle to wing); veins recurve at receptacle edge, running between marginal scars and traversing the wing, where they delimit consecutive wing flutes;

**Other features:** no attached seeds have been found.

**Subtending *Glossopteris* leaf:** attached to weakly-defined midrib in long,

**Wing:** peripheral wing entire, narrow, continuous except at base, bearing faint striations perpendicular to margin of receptacle; some specimens lack fluting but most possess strong transverse grooves/ridges near the receptacle margin;

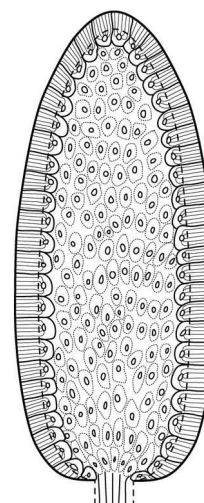
**Receptacle:** narrowly oblong-lanceolate with acute, pointed apex and truncate to rounded base;

**Pedicel:** fructification sessile, or with short pedicel;

**Seed scars:** receptacle surface smooth, with randomly scattered, elliptical to circular, raised tubercles (in impressions), each sharply delimited by a narrow groove in receptacle surface;

**Sterile surface:** veins anastomose and bifurcate, arching at steep angle to margin of receptacle, before traversing wing; medio-longitudinal concentration of veins present;

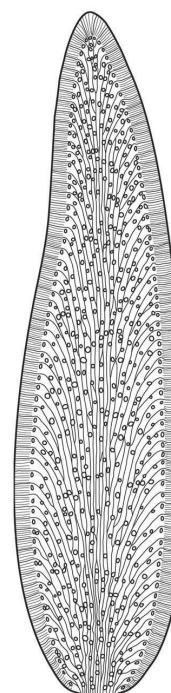
**Other features:** receptacle surface with distinctive venation pattern on both sterile and fertile surfaces; receptacle bears prominent, flabellate pattern of venation on both surfaces, with veins manifesting as ridges on sterile surface, grooves on fertile surface, with intervening areolae



10 mm

narrow cuneate base of a *Glossopteris* leaf with steeply inclined venation following a straight path to margin; meshes larger and more elliptical to polygonal near midrib, becoming narrower and more parallel towards margin.

**T** *Dictyopteridium flabellatum*  
Step 21 (b)



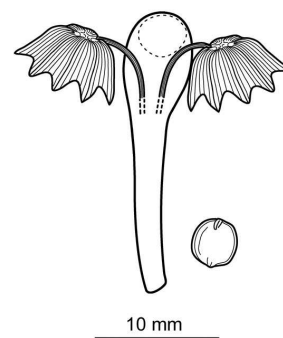
10 mm

particularly prominent along edge of receptacle;  
**Attached leaves and seeds:** unknown.



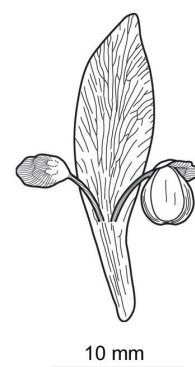
**U** *Lidgettonia lidgettonioides*  
Step 22 (a)

**Capitula:** 2-4 per scale leaf; large (8-13 mm diameter) and deeply campanulate; wing with prominent scallops, and well-defined, acutely pointed teeth;  
**Seeds:** broadly elliptical, 4-4.3 mm long, 3.3-3.7 mm wide, with very narrow lateral wing (<0.4 mm); micropylar and chalazal ends relatively rounded, with short pointed tip or narrow cleft at micropyle;  
**Scale leaf:** small, narrow, club-shaped; apex of scale leaf rounded, with distinct region of localised thickening in distal portion of lamina;  
**Capitular attachment:** capitula each with a long, slender pedicel; attached in opposite pairs at base of expanded portion of scale.



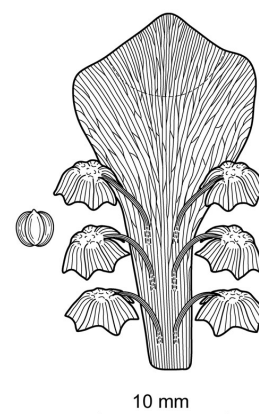
**V** *Lidgettonia elegans*  
Step 23 (a)

**Capitula:** 2-6 (most commonly 2) per scale leaf; small (2.4-3.4 mm long), spatulate to spoon-shaped; receptacle ill-defined, with 2 or 3 seed scars on fertile surface; wing striated, margin entire or weakly scalloped with 3 or 4 obtuse, poorly differentiated teeth; wing reaches maximum breadth distally, tapering away at base of receptacle;  
**Seeds:** small (3-4 mm diameter), sub-circular, with conspicuous lateral wings and truncate micropylar and chalazal ends;  
**Scale leaf:** elliptical to obovate with slightly elongated, tapered base;  
**Capitular attachment:** capitula borne in pairs, in opposite ranks along contracted, basal portion (petiole) of scale leaf.



**W** *Lidgettonia africana*  
Step 23 (b)

**Capitula:** 2-8 per scale leaf; palmate to campanulate, with 6-13 seed scars; wing rarely entire, more commonly moderately scalloped (<1.6 mm deep), producing an obtuse to acutely pointed tooth at the junction between each wing segment;  
**Seeds:** seeds small (1.6-3.7 mm long), transversely elliptical with broad lateral wings (0.6 – 1 mm); micropylar and chalazal ends truncate or slightly recessed;  
**Scale leaf:** obovate to rhombic; highly variable in shape;  
**Capitular attachment:** capitula borne in pairs, in opposite ranks along contracted, basal portion (petiole) of scale leaf.



## CHAPTER 5 RIGBYACEAE Anderson & Anderson 1985 emend.

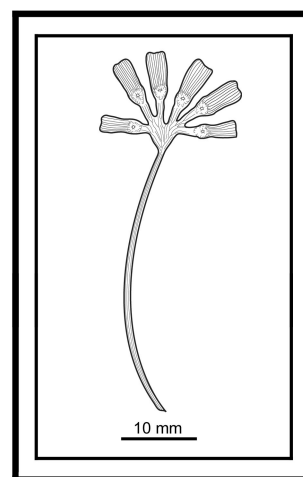
The Rigbyaceae is a small group of fructifications that have been affiliated with the glossopterids on the basis of their consistent association with *Glossopteris* leaves. None has been found in organic attachment to glossopterid leaf material. Only two genera are currently recognised within this family, viz. *Rigbya* and *Cometia*, although the taxon described in section 5.2 (previously assigned to *Arberia allweyensis*; Anderson & Anderson 1985) may eventually necessitate the creation of a third genus within this family.

*Cometia* has only been found in the Bowen Basin of Queensland, Australia (McLoughlin, 1990a), but *Rigbya* appears to have been more widespread, having been found in Antarctica (Plumstead, 1962a; Schopf, 1976), Australia (Rigby, 1972a; White, 1986; McLoughlin, 1995) and South Africa (Lacey *et al.*, 1975).

### 5.1 RIGBYA Lacey, van Dijk & Gordon-Gray 1975 emend.

#### 5.1.1 INTRODUCTION

*Rigbya* was formally described by Lacey *et al.* (1975), but Australian and Antarctic examples of this fructification had been figured in earlier works by Plumstead (1962a; p. 55, pl. 14, figs 11, 12: *Arberia* cf. *minasica*), Rigby (1972a; pl. 26, figs 5, 6, 7) and Schopf (1967; p. 114, fig. 1). Lacey *et al.* (1975) suggested that all these specimens be included within *Rigbya arberioides*.



*Rigbya arberioides*

White (1978; p. 501, figs 69, 70, 72) and Rigby (1978; p. 17, figs 22, 23) figured additional specimens from eastern Australia which they too referred to *R. arberioides*, on the basis of their close similarities to Schopf's 'Antarcticoid capitulum' (1967, 1976). Later, Melville (1983a) described *Mudgea ranunculoides* from the Upper Permian of New South Wales, Australia, which

was transferred to *Rigbya* by McLoughlin (1990a, 1995). McLoughlin (1990a) suggested that at least four species were represented by the specimens grouped at that stage within *R. arberioides*. In 1995 he created *R. ranunculoides* to accommodate those specimens from Antarctica and Australia showing a high degree of fusion of the branches and terminal scales/wings, the scales purportedly also being significantly shorter than those of *R. arberioides*.

*Rigbya* is unique among glossopterid fructifications in having a fan-shaped arrangement of dichotomous branches showing varying degrees of fusion into a flabellate lamina. The termini of the ultimate branches bear a single seed scar and a scale-like wing distal to the scar. The pedicel is typically long and slender.

Lacey *et al.* (1975) considered *Rigbya* to be a 'problematical fructification'. They were unwilling to affiliate it with any particular plant group, but conceded it may be glossopterid. White (1978) was sceptical about *Rigbya*'s affiliation with the glossopterids, but did not offer any alternative suggestions, and Rigby (1978), Anderson & Anderson (1985) and McLoughlin (1990a, 1995) tentatively placed these fructifications within the glossopterids on the basis of associative evidence.

The consistent association of *Rigbya* fructifications with *Glossopteris* or *Belemnopteris* leaves in several continents, and the close structural similarities<sup>3</sup> with other ovuliferous glossopterid fructifications, are considered here to provide strong evidence in support of these fertile structures belonging within the Glossopteridales.

The most recent account of the South African *Rigbya* specimens was given by Anderson & Anderson (1985), who reported occurrences from three Upper Permian localities in South Africa.

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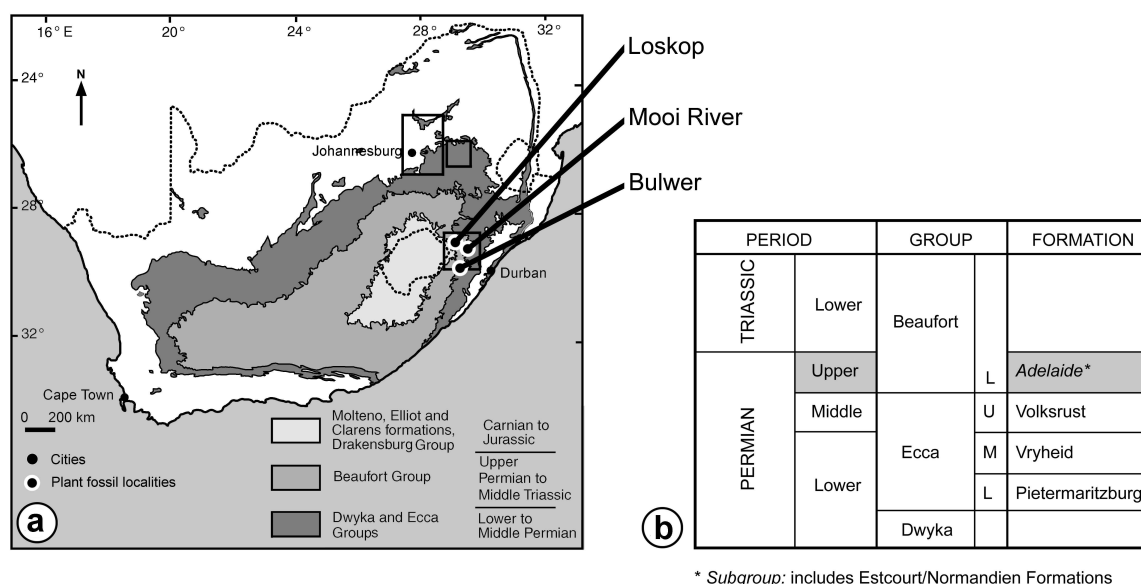
<sup>3</sup> Refer to section 3.1.3 for a discussion on the nature of the structural similarities between *Rigbya* and other members of the Glossopteridales, particularly with regard to the arrangement and morphology of the seed scars and associated wing/ scale-like features (also see pl. 1).

### 5.1.2 FOSSIL MATERIAL

All specimens examined were impression fossils. They are housed in the Natal Museum in Pietermaritzburg and the fossil herbarium of the Bernard Price Institute in Johannesburg (see Appendix I, Table A.I.1).

### 5.1.3 LOCALITY INFORMATION

All specimens examined originated from the Mooi River and Bulwer localities in Kwa-Zulu Natal, north-eastern Karoo Basin, South Africa; Estcourt Formation; Upper Permian (see text-figs 2.2.2, 2.2.4, 5.1.1 a&b). Anderson & Anderson (1985) also recorded the existence of a single specimen from Loskop (also Estcourt Formation), but this specimen was not located.



**Text-figure 5.1.1.** (a) Locality map indicating reported occurrences of *Rigbya arberioides* in South Africa; (b) lithostratigraphic table of the Permian and Lower Triassic deposits in the northern and eastern parts of the Karoo Basin, with shaded areas representing stratigraphic occurrence of *Rigbya* (table adapted from Keyser, 1997).

### 5.1.4 SYSTEMATIC PALAEOBOTANY

#### *Type species*

*Rigbya arberioides* Lacey, van Dijk & Gordon Gray 1975; Upper Permian; Karoo Basin, South Africa.

## ***Etymology***

Named after well-known Australian palaeobotanist, Dr John F. Rigby, in recognition of his extensive contributions to the field of Palaeobotany (Lacey *et al.*, 1975).

## ***Emended generic diagnosis***

Dorsiventrally flattened ovuliferous fructification comprising a pedicel bearing a terminal flabellate aggregation of branches which may be fused to varying degrees. Ultimate branches each terminate in a flattened scale with a single seed attachment point at the base. Seeds only borne on one surface of fructification. Pedicel, its branches and terminal scales all longitudinally striated.

## ***Discussion***

The diagnosis given by Lacey *et al.* (1975) does not comfortably accommodate all of the South African specimens, nor some of those from other parts of Gondwana. Features of McLoughlin's (1995) *R. ranunculoides* such as a rounded distal scale margin and particularly short scales are not easily included within the Lacey *et al.* (1975) diagnosis.

Emendations made here included mainly omissions of details which restricted the diagnosis. If, as McLoughlin (1990a) suggested, there are several species currently grouped within *R. arberioides*, the diagnosis should preclude quantitative parameters, thereby broadening the circumscription of the genus. The description of the scales in particular needed to be expanded to accommodate a variety of shapes and sizes.

The portrayal of the seed scar/wing structural relationship in Lacey *et al.*'s (1975) diagnosis also required emendation. Lacey *et al.* (1975) were uncertain as to whether the terminal scale partially or totally enclosed the basal ovule or was a flattened structure bearing a seed on one side. As this document has hopefully demonstrated (section 3.1), and in line with more recent thinking (McLoughlin, 1990a, 1995), the *Rigbya* fructification is regarded here as a

dorsiventral structure bearing flattened, concavo-convex terminal scales, each bearing a single seed at its base, on one side of the fructification.

Details of the attached seeds were removed from the diagnosis, as these are only known from the South African material.

#### **5.1.4.1      *Rigbya arberioides*** Lacey, van Dijk & Gordon-Gray 1975 emend.

1974 *Rigbya arberioides* Lacey, van Dijk & Gordon-Gray, p. 154, figs NM1669, NM1644.

1975 *Rigbya arberioides* Lacey, van Dijk & Gordon-Gray, p. 409, figs NM1644a,b, NM1646a, NM1669a, NM1650, NM1656.

1978 *Rigbya arberioides* Lacey, p. 186, 188.

1979 *Rigbya arberioides* Lacey, van Dijk & Gordon-Gray; van Dijk, Gordon-Gray, Reid & Lacey, p. 115, pl. 46, figs 17-19.

1984 *Rigbya*; Banerjee, p. 36, text-fig. 9.

1985 *Rigbya arberioides* Lacey, van Dijk & Gordon-Gray; Anderson & Anderson, p. 127, pl. 101, figs 1-6; pl. 102, figs 1-5; text-figs 127.1, 127.2.

1997 *Rigbya arberioides*; Anderson & Anderson, p. 17, fig. 11b.

#### ***Holotype***

Specimen NM1669 (Lacey et al., 1975), an isolated impression fossil; housed in the Natal Museum, Pietermaritzburg [pl. 5, fig. (f)].

#### ***Etymology***

'*arberioides*' - referring to the morphological similarities between this taxon and *Arberia minasica* (White) emend. Rigby 1972 (Lacey et al, 1975).

#### ***Type formation and locality***

Estcourt Formation; Upper Permian; Mooi River locality, eastern Karoo Basin, Kwa-Zulu Natal, South Africa.

### ***Emended species diagnosis***

Pedicle long and slender, with slightly expanded base; expanded at distal end then dividing repeatedly, with close dichotomies, to form a dorsiventral flabellate cluster of five to nine, most frequently seven, ultimate branches. Pedicle may expand to form fan-shaped lamina which gives rise to dichotomising branches, or may bear scales and seed scars directly along distal margin of lamina. Terminal scales 2.5 to 8 mm long, elongate-elliptical to ovate or elongate-spatulate with truncate to concave distal margin. Scales convex in impressions of fertile surface of fructification. Attached platyspermic seeds flattened, rounded to ovate with lateral wings. No attached leaves known.

### ***Description***

(See pls 2-9; Table A.II.1, Appendix II for data summary).

Planar, variously branched, bifacial ovuliferous fructification, with seed attachment points at termini of ultimate branches, each branch terminus flanked distally by an elongated wing. Fructifications (excluding pedicle) are 5.4 (11.6) 16.3 mm long {n=27; SD:3.3} and 8.5 (14.3) 22.6 mm wide {n=14; SD:3.4}.

Pedicle is longitudinally striated and often slightly curved, 12 (35.4) 58 mm long {n=20; SD:12.5} with a basal width of 0.6 (1.0) 1.7 mm {n=26; SD:0.3}, expanding to 0.9 (1.7) 3.2 mm {n=24; SD:0.6} at the first branch or base of lamina.

Fructification may comprise a series of dichotomous branches arising directly from the pedicle which may or may not be slightly expanded proximal to the first bifurcation, or it may consist of a fan-shaped lamina with a distal fringe of ultimate branches. In the latter case, the basal, fan-shaped lamina is 2 (3.6) 4.9 mm long {n=11; SD:1.0} with lateral margins diverging at an angle of 26° (47.8°) 68° {n=15; SD:15.0}, and varies in shape from longitudinally to transversely elliptical. The lamina gives rise to 6 (7.2) 9 {n=13; SD:1} single-order branches along its distal margin, which are 0.6 (3) 5.8 mm long {n=40; SD:1.3}, and 0.5

(0.8) 1.2 mm wide {n=80; SD:0.2}. Longitudinal striations on the pedicel continue onto the lamina where they dichotomise and gently arch across the lamina and onto the single-order branches.

In cases where the fructification comprises a series of dichotomous branches, the primary dichotomy diverges at an angle of 25° (60.1°) 94° {n=14; SD:19.1}, giving rise to two primary branches, 0.8 (2.1) 4 mm long {n=15; SD:1} and 1.3 (1.8) 2.6 mm wide {n=15; SD:0.4}. A second series of dichotomies, or two trichotomies<sup>4</sup>, occur at an angle of 25° (45.3°) 84° {n=13; SD:18.1}, giving rise to secondary branches 0.5 (1.6) 2.7 mm long {n=26; SD:0.7} and 0.4 (1.2) 1.6 mm wide {n=29; SD:0.3}. In rare instances, a third series of branches arise at an angle of 17° (38.9°) 64° {n=12; SD:14.4}, the tertiary branches being 1.1 (3.4) 6.8 mm long {n=26; SD:1.5} and 0.2 (0.8) 1 mm wide {n=23; SD:0.2}. All branches bear longitudinal striations.

The termini of all ultimate branches bear a single ovule/seed scar flanked distally by an elongate-elliptical to ovate or elongate-spatulate, longitudinally striate, scale-like wing. Wing is 2.5 (4.8) 7.6 mm long {n=114; SD:1.1} and 0.8 (2.1) 3.5 mm wide {n=114; SD:0.5}, with a truncate to concave distal margin. The seed scars (in impressions) are circular to elliptical, raised cushions (in impressions) with a central depression, and are 0.8 (1.5) 2.5 mm long {n=34; SD:0.4} and 0.9 (1.3) 1.8 mm wide {n=30; SD:0.2}. On the sterile surface of the fructification, there is no significant differentiation of branch termini, striations on the branch continuing uninterrupted into the slightly expanded wing area.

Attached seeds round to ovate with conspicuous lateral wings [pl. 5, fig. (d)].

### **Comments**

This species displays a wide variety of basic morphological forms (see pl. 9), ranging from a simple, flabellate lamina with terminal branches, to a

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<sup>4</sup> These apparent 'trichotomies' (e.g. pl. 2, fig. (n)) may have resulted from two close and asymmetrical dichotomies, where only one daughter branch of the primary branch dichotomised further, resulting in three ultimate branches per primary branch.



dichotomously branched structure with third or fourth order branches. The specimens from Mooi River (pls 2-6) are more diverse than those from Bulwer (pl. 7), which all have a simple fan-shaped lamina with seed scars and associated scales/wings borne directly along the distal margin, without differentiation of first-order branches. This difference in diversity may be a result of the small sample size from Bulwer, or may reflect regional morphological variation. The Bulwer specimens may belong within McLoughlin's (1995) *R. ranunculoides*.

The specimen figured in pl. 4, figs (d) and (e) is remarkable. Development of the left side of the fructification (the primary branch and three subsidiary branches) appears to have been retarded, as it is approximately a third the size of the right half. In modern plants this type of stunting can result from a viral infection or from damage to the meristem at an early stage in the development of a plant organ.

Lacey *et al.* (1975) described the seeds of *Rigbya* as wingless, but close inspection of the seeds attached to South African *R. arberioides* fructifications [e.g. pl. 5, fig. (g)], revealed them to be platyspermic seeds with a narrow lateral wing. The presence of lateral wings is supported by Anderson & Anderson (1985). The seeds are similar to those of *Lidgettonia africana*, with an ovate to round sclerotesta and rounded lateral wings. In most cases, the seeds are at least partially obscured by the layer of sediment bearing the impression of the fertile surface of the fructification.

#### **5.1.5 DISCUSSION**

In the past, *Rigbya* has only been linked to the glossopterids through its consistent association with *Glossopteris* leaves. Lacey *et al.* (1975) found little in common between *Rigbya* and other glossopterid fructifications such as *Scutum* and *Ottokaria*, citing their dorsiventrally flattened nature and the long slender stalks as the only features they had in common. The taxon is similar to some forms of *Arberia*, particularly those forms of *R. arberioides* which have several orders of dichotomous branches [e.g. pl. 2, fig. (j)]. The basal fan-

shaped lamina seen in many specimens is also reminiscent of members of the Arberiaceae. Recognition of the presence of scale-like features associated with the seed-attachment points in *Arberia* species has strengthened the relationship between this group of fructifications and *Rigbya*. In fact, the only clearly defined characters distinguishing *Rigbya* from *Arberia* are the fan-shaped nature of the primary axis and branching pattern, and the prominence of the terminal scales/wings in the former genus.

A close examination of the structure of *Rigbya* during the course of this study provided unmistakable evidence in support of its glossopterid affinities (see sections 3.1.2 and 3.3). Plate 1 illustrates the similarities in wing and seed scar structure between the different families of glossopterid fertile structures.

Schopf (1967, 1976), Rigby (1972a), White (1978), Melville (1983a,b) all figured *Rigbya* specimens from other parts of Gondwana. As mentioned earlier, McLoughlin (1995) transferred these Australian and Antarctic specimens to a new species, *R. ranunculoides*, along with some additional specimens (p.188, figs 5a-f), on the basis of their high degree of fusion into a fan-shaped lamina, and short, variably fused distal scales/wings. Anderson & Anderson (1985) also considered the specimens described by Rigby (1972a; 1978), White (1978) and Schopf (1967) to be sufficiently different to exclude them from *R. arberioides*. This was a puzzling decision as they themselves noted that *Rigbya arberioides* demonstrates a high degree of morphological variation, which makes the confident characterisation of different species problematic. The silhouette drawings in pl. 9 clearly show the major structural forms of South African *Rigbya* fructifications, and their many intermediates.

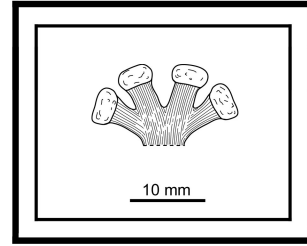
All the specimens of *R. arberioides* from Bulwer have a flabellate lamina bearing scales along the distal margin (pl. 7), and are very similar to those assigned to *R. ranunculoides* by McLoughlin (1995). Although none of the Bulwer specimens exhibited fusion of the scales, they were 2.5 (3.8) 5.8 {n=15; SD: 1.2} mm long, which is close to the size range given by McLoughlin (1995) for *R. ranunculoides* (3-5 mm).

Considering the degree of variability exhibited by *Rigbya* specimens found in the same region and similar time period within South African Upper Permian sediments, the validity of *R. ranunculoides* as a distinct species is questioned here. On the other hand, the complete dominance of this morphological type at the Bulwer locality could support its status as a distinct species.

The occurrence of *Rigbya* appears to have been restricted to the Late Permian in all the Gondwanan continents where it has been found, and is considered to be one of the more reliable biostratigraphic index fossils for this time period (McLoughlin, 1992, 1993a, 1995).

## 5.2 *INCERTAE SEDIS* ('*Arberia allweyensis*'

Anderson & Anderson 1985)



### 5.2.1 INTRODUCTION

This taxon, originally described by Rayner & Coventry (1985) as an 'unknown fructification', is represented by a single, poorly preserved and apparently incomplete specimen from the Lawley locality south of Johannesburg. Rayner & Coventry (1985) suggested it may represent a fragment of either *Arberia* or *Rigbya*.

Anderson & Anderson (1985) named the specimen *Arberia allweyensis* on the basis of their diagnosis for *Arberia*, which incorporated all dichotomously branched, pinnate to paniculose axes bearing a solitary ovule at each branch terminus, and which did not have a protective scale associated with the seed-attachment point.

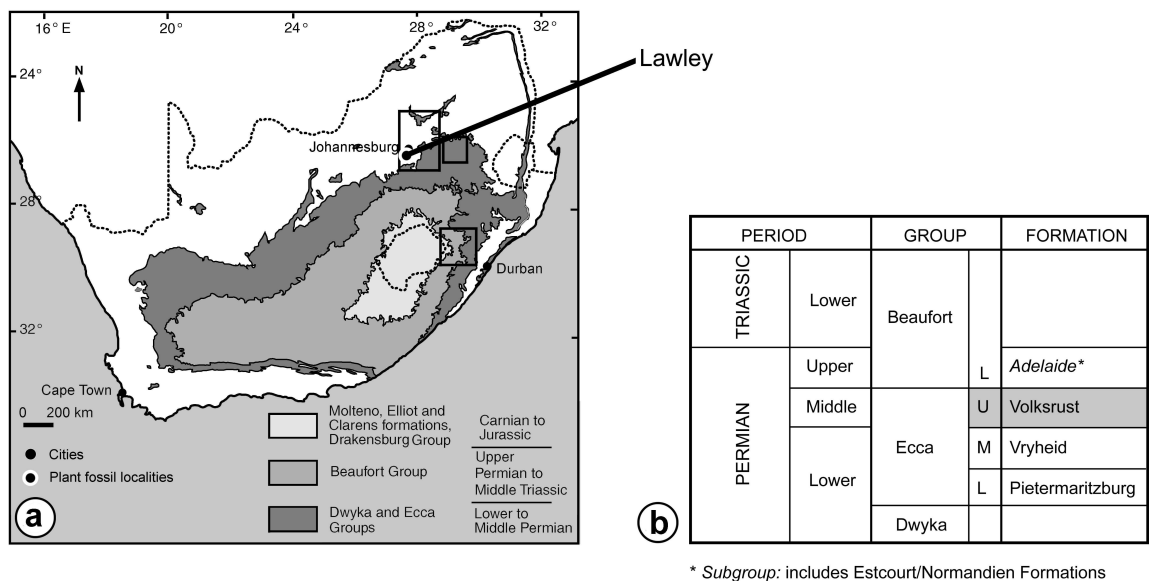
Here, the diagnosis for *Arberia* excludes specimens with a short, simple, fan-shaped primary axis. For this and other reasons explained below, *A. allweyensis* has not been included within the genus *Arberia*, and is instead regarded as a member of the Rigbyaceae.

### 5.2.2 FOSSIL MATERIAL

A single part and counterpart of an impression in soft, pale, kaolinitic clayshale from the Lawley locality. Specimen PRE/F/8380a&b is housed at the National Botanical Institute in Pretoria, South Africa. (See Appendix I, Table A.I.2.)

### 5.2.3 LOCALITY INFORMATION

The specimen was collected from the Lawley locality. The age and stratigraphic position of the Lawley locality is uncertain as the deposits are an outlier of the northern Karoo Basin, but it is thought to be an upper Ecca equivalent (Volksrust Formation, Middle Permian). See text-figs 2.2.2, 2.2.3a & 5.2.1a&b.



**Text-figure 5.2.1.** (a) Locality map indicating reported occurrence of Anderson & Anderson's (1985) '*Arberia allweyensis*' in South Africa; (b) lithostratigraphic table of the Permian and Lower Triassic deposits in the northern and eastern parts of the Karoo Basin, with shaded areas representing stratigraphic occurrence of this taxon (table adapted from Keyser, 1997).

## 5.2.4 SYSTEMATIC PALAEOBOTANY

### 5.2.4.1 Incertae sedis

1985 'Unknown fructification', Rayner & Coventry. p. 30, figs 2 j&k.

1985 *Arberia allweyensis* Anderson & Anderson. p. 131, pl. 110, fig. 10; text-figs 128.8, 131.5.

### **Holotype**

PRE/F/8380a&b [pl. 10, figs (c) & (d)]; housed at the National Botanical Institute in Pretoria, South Africa.

### **Description**

(See plate 10, figs (c) & (d); Table A.II.1, Appendix II).

The single specimen available is the partial part and counterpart of a fertile axis, at least 12 mm long and 18 mm wide. The axis is a fan-shaped, planar structure that bifurcates twice to form four ultimate branches. The gross angle of divergence of the margins of the outer branches of the fructification is 111°; the

interior angle of the major dichotomy is 72° and the ultimate dichotomies occur at angles of 39-50°. The axes bear faint, longitudinal striations. Initial branches are 7-8 mm long and 4-5 mm wide; ultimate branches are 2-3 mm long and 2-3 mm wide, each expanding terminally to form a transversely elliptical structure. The terminal swellings are rough-textured and featureless, measuring 4-5 mm wide and 2-3 mm long, and each probably bore a single seed.

The specimen may be only a fragment of the original fertile structure - the base is clearly missing.

### 5.2.5 DISCUSSION

The transversely elliptical structures borne terminally on the ultimate branches of the Lawley specimen were interpreted by Rayner & Coventry (1985) as seeds. Since the structures are planar, and lie at the same level in the sediment as the main axis of the fructification, it seems more likely that they are the expanded seed-bearing parts of the fructification, much as we see in *Rigbya* and *Arberia*. There are no features to suggest that they are seeds or ovules, although their lack of oxide staining does enhance their differentiation from the axes. Anderson & Anderson (1985) referred to the terminal structures as 'flattened disks'.

The poor state of preservation of the critical seed-bearing termini of the ultimate branches has made any conclusions regarding the affiliations of the taxon equivocal, even at the family level. Anderson & Anderson (1985) recognised that the Lawley specimen could not be comfortably accommodated in *Arberia*, but were reluctant to create a new genus. They suggested that the fructification may represent an intermediate stage between *Rigbya* and the 'more pinnate species' of *Arberia*.

If we assume the Lawley specimen is well enough preserved to represent all the diagnostic features of the taxon, then the absence of any obvious scale-like features associated with the seed-attachment points may be seen as evidence for an affiliation with *Vereenia* (see previous section 6.2). However, the fan-

shaped, planated axis that undergoes several dichotomies is in contradiction with the diagnosis for *Vereenia*, and despite lacking the elongated, elliptical to spatulate scale-like features typical of *Rigbya*, is highly reminiscent of this latter taxon.

White (1908; pl. 8, fig. 8) figured a specimen from Brazil, similar in appearance to Anderson & Anderson's (1985) Lawley fructification, which he placed in *A. minasica*. The specimen is unfortunately not very clearly defined, but appears to have a laminate, fan shaped-axis which undergoes several dichotomies, producing six ultimate branches, each with a slightly expanded terminus.

White (1978; p. 500, fig. 69) figured an unusual specimen of *R. arberioides* from Australia with particularly bulbous seed scars, and no evidence of distal scale/wing-like features. It is possible that these are merely not apparent in the photograph provided, but the image presented is of a fructification very similar to the Lawley specimen, and may warrant closer inspection in this regard. Anderson & Anderson (1985, p.129) noted the occurrence of their *A. allweyensis* in Australia citing White (1978) as the reference. They were probably also referring to this particular specimen.

As already discussed in section 5.1, Rigby (1972a; pl. 25, fig. 7; pl. 25, figs 4 & 7) figured several Australian specimens that appear to be identical to *Rigbya*, but which had very short terminal scales (broader than long). The existence of a form of *Rigbya* with very reduced scales/ wings could be seen as conclusive evidence that '*A. allweyensis*' is more closely affiliated to *Rigbya* than to *Arberia*.

Inclusion of the single Lawley specimen within *Arberia* (Anderson & Anderson, 1985) had far-reaching implications as far as the biostratigraphic range of the genus is concerned. The deposits at Lawley are currently considered equivalent to the Volksrust Formation and are therefore probably Middle Permian in age. However, the deposits represent an outlier of the main Karoo Basin, and we cannot be entirely sure about its lithostratigraphic position. The presence of *Lidgettonia* at Lawley, points to a younger age for the deposits, since this genus

of ovuliferous glossopterid fructifications is an index fossil for the Upper Permian. If the Lawley deposits are Middle Permian in age, Anderson & Anderson's (1985) '*A. allweyensis*' would be the youngest example of *Arberia* in the whole of Gondwana. In light of the close similarities of this fructification to *Rigbya*, and in the absence of convincing evidence that it does in fact belong within the genus *Arberia*, it is recommended that specimen PRE/F/8380a&b be provisionally placed within the Rigbyaceae and not be assigned to any particular genus until more is known about its structure.



## CHAPTER 6 ARBERIACEAE Rigby 1972

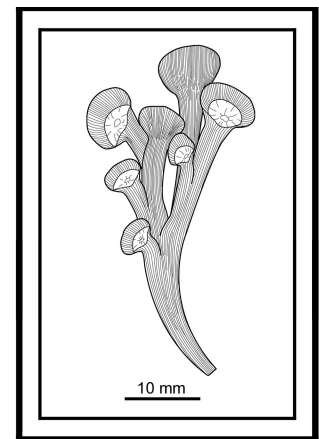
Two South African genera are considered here to belong within this family, viz. *Arberia* and a new genus *Vereenia*. It is possible, in light of the interpretations presented in this work, that a third genus may be required to adequately express the differences between those members of *Arberia* with a laminate primary axis with an apical dichotomy (e.g. *A. minasica* and the South African *A. madagascariensis*), and those specimens with a more three-dimensional branching pattern and lacking a well-developed lamina (e.g. *A. hlobanensis*).

### 6.1 ARBERIA White 1908 emend.

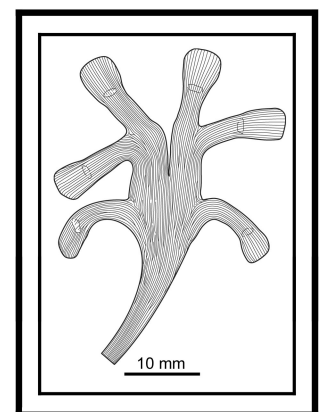
#### 6.1.1 INTRODUCTION

Bunbury (1861) and Feistmantel (1879) both figured strange branched fertile structures from India, but it was only much later that these were described and given a name. White (1908) created the genus *Arberia* to accommodate Feistmantel's specimen (which he called *Arberia indica*) and a similar fertile structure from Brazil (*Arberia minasica*), organs he interpreted as 'deeply incised', 'fertile scale-fronds' which were 'more or less concave-convex'.

Rigby (1972a) emended White's (1908) diagnosis in his comprehensive review of the taxon, interpreting *Arberia* fructifications as a type of pteridospermous megasporophyll of the *Glossopteris* plant. Section 3.3 has dealt with the issues surrounding the structural and diagnostic aspects of members of this genus, but broadly speaking it is a group of simple, branched fructifications bearing a single seed at each branch terminus, with a scale-like feature distal to each seed-attachment point. There may be several orders of branching, and the branches may arise in multiple planes.



*Arberia hlobanensis*



*Arberia madagascariensis*

*Arberia* is geographically wide-spread, and numerous specimens have been described from the Lower Permian of South America (e.g. White, 1908; Lundqvist, 1919; Millan, 1967; Rigby, 1972a), Madagascar (Appert, 1977) and India (Feistmantel, 1881; Surange & Lele, 1956; Pant & Nautiyal, 1965; Maithy, 1970; Chandra & Srivastava, 1981). *Arberia* specimens have also been reported from Australia (White, 1978; McLoughlin, 1995), Antarctica (Plumstead, 1962) and South Africa, but these fructifications are extremely rare in the fossil record.

In 1969 Plumstead (pl. 3, fig. 3) figured a specimen she referred to as a 'strange fructification', which was probably the first record of an *Arberia* fructification from Southern Africa. Anderson & Anderson (1985) later named this specimen *A. hlobanensis*.

Rayner & Coventry (1985) described an 'unknown fructification' which may have been 'a fragment of *Arberia* or *Rigbya*' from the Lawley locality near Johannesburg. Anderson & Anderson (1985) recognised that this taxon may have represented an intermediate form between *Rigbya* and the 'more pinnate species of *Arberia*' and tentatively named it *A. allweyensis*. Here, *Arberia allweyensis* has been tentatively transferred to the Rigbyaceae, on the basis of its compact, fan-shaped branching pattern and planated form (see section 5.2).

Two closely associated fertile structures from the Hammanskraal locality were considered by Anderson & Anderson (1985) to belong in Appert's (1977) *Dolianitia madagascariensis*, which they synonymised with *Arberia* on the basis of its striking similarities with *Arberia* species from India (Surange & Lele, 1956; Maithy, 1970; Chandra & Srivastava, 1981) and South America (Millan, 1967; Rigby, 1972a).

Anderson & Anderson (1985) also described a strange group of planar fertile axes with pinnate branchlets from Vereeniging which they called *A. leeukuilensis*. Although probably closely related to *Arberia*, the ranks of short, opposite branches with distinctive, recurved branch termini apparently lacking any associated scale-like features, were considered here to be sufficiently

distinctive to warrant elevation to a unique generic status, and they have been assigned to a new genus *Vereenia*, within the Arberiaceae (section 6.2).

Anderson & Anderson (1985) created an additional species of *Arberia* (*A. cedarensis*) on the basis of leaf associations alone. Since we cannot be sure that Anderson & Anderson (1985) correctly identified the leaf type belonging to the *Arberia* plant, and since the approach of assigning taxa developed for fertile structures to dissociated leaf types has not been adopted, this species is not recognised here.

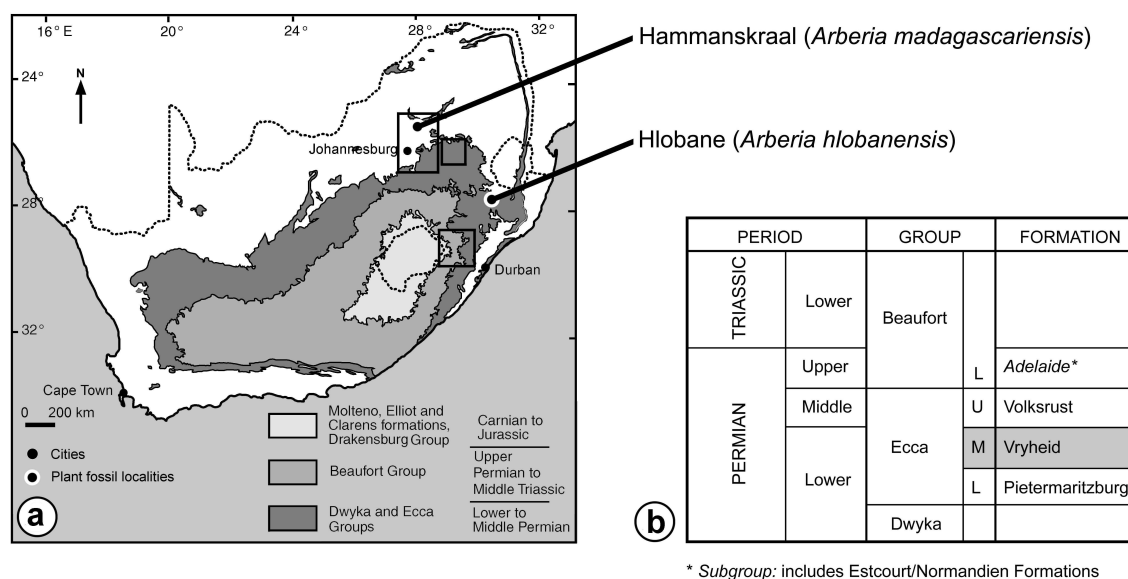
This means that only two South African species are considered to be valid members of *Arberia*, viz. *A. hlobanensis* and *A. madagascariensis*, both from the Lower Permian sediments of the Vryheid Formation.

#### **6.1.2 FOSSIL MATERIAL**

All specimens of *Arberia* reported from South Africa are impression fossils. The specimen of *Arberia hlobanensis* from Hlobane is a part and counterpart (BP/2/15893 & BP/2/15194), and is housed at the Bernard Price Institute, University of the Witwatersrand, Johannesburg. The specimen of *Arberia madagascariensis* (GSP/H/102) from Hammanskraal is housed at the Council for Geosciences in Pretoria. (See Table A.I.3, Appendix I for specimen details).

#### **6.1.3 LOCALITY INFORMATION**

*A. hlobanensis* and *A. madagascariensis* were collected from Hlobane and Hammanskraal respectively, both Lower Permian localities in the northern Karoo Basin of South Africa (Vryheid Formation) (see text-figs 2.2.2, 2.2.3a & 6.1.1a&b).



**Text-figure 6.1.1.** (a) Locality map indicating recognised occurrences of *Arberia* species in South Africa; (b) lithostratigraphic table of the Permian and Lower Triassic deposits in the northern and eastern parts of the Karoo Basin, with shaded areas representing known stratigraphic range of *Arberia* (table adapted from Keyser, 1997).

#### 6.1.4 SYSTEMATIC PALAEOBOTANY

##### *Type species*

*Arberia minasica* White 1908 emend Rigby 1972; Lauro Müller, Santa Catarina, Brazil; Rio Bonito Formation, Parana Basin, Lower Permian.

##### *Etymology*

Named by White (1908) after Professor A.N. Arber, in recognition of his 'important contributions to our knowledge of the Pteridospermic fruits'.

##### *Emended generic diagnosis*

Dichotomously branched to irregularly paniculose polysperm with branches in multiple planes. Primary axis laminar, commonly with a bifurcation in the apex, and with tapered base; subsidiary branchlets arise through series of dichotomies of primary axis, or along margins and on surface of planated primary axis. Primary axis longitudinally striated, striations continuing into lateral branches. Ultimate branchlets terminate in simple scale-like extension with

single ovule attachment point at base of scale. Branch termini bifacial, with smooth, longitudinally striated sterile surface and seed-bearing fertile surface. Striations on lateral branches continuous on sterile surface of scale-like features. Planated primary axis also bifacial in some cases, with lateral branches arising from the axis face corresponding to fertile surfaces of marginal branch termini. Seeds platyspermic, round to ovate, with an acute micropylar notch and narrow lateral wings.

## **Discussion**

The emended diagnosis was adapted in part, from Rigby (1972a). However, Rigby's (1972a) terminology has been changed, since we cannot be sure that these structures are megasporophylls. Terms such as 'rachis', 'pinnae' and 'pinnules' infer speculative homologies.

Rigby (1972a) included within *Arberia* specimens with a forked primary axis and marginal secondary branches, but excluded those specimens lacking a forked primary axis, and having secondary branches both along the margins and arising from the face of the laminate primary axis. In light of the morphological interpretations outlined in section 3.3, a more generalised description of the branching pattern in *Arberia* fructifications has been adopted here in the generic diagnosis, as described by Anderson & Anderson (1985), including mention of branching in three-dimensions.

An examination of the South African specimens of *Arberia*, as well as literature describing specimens from other parts of Gondwana, revealed, in most cases, the presence of a scale-like feature distal to each seed attachment point in these fructifications. Both the diagnoses for the Arberiaceae and for *Arberia* have been emended to accommodate this important feature. Identification of the scale-like features, has led to the recognition of the bifacial nature of the branch termini. The scale-like feature is in essence a thinned extension of the branch terminus, with the longitudinal striations of the branch continuing uninterrupted into the scale on the sterile side, although becoming finer and denser and following a parallel course to the apex of the scale. The fertile side of the branch

terminus bears a seed scar or attached seed/ovule at the base of the scale. Appert's (1977) specimens of *A. madagascariensis* demonstrated that the lateral branches along the margins of the planated primary axis all have their branch termini with fertile surfaces on the same side of the axis. This is the same side of the axis which bears lateral branches perpendicular to the flattened plane of the axis.

The associated organs included by Anderson & Anderson (1985) in their diagnosis were excluded here as associative evidence is not considered sufficient for the establishment of formal biological affiliations. However, details of the *Cordaicarpus*-type seeds of *Arberia* were included, as this kind of seed has consistently been found in organic connection with various species of *Arberia*. A possible exception is McLoughlin's (1995) *A. woolagaensis* which is described as bearing peculiar oblong seeds along the margins of the primary axis. The discovery of more convincing specimens may necessitate further modification of the generic diagnosis with regard to the seeds. It may well transpire that those *Arberia* fructifications with a distinctive fan-shaped lamina with an apical dichotomy and pinnate branches (e.g. *Arberia minasica* and *A. madagascariensis*), need to be separated at the generic level from other forms currently accommodated within *Arberia* which have more radial or spiral branching patterns.

**6.1.4.1      *Arberia madagascariensis*** (Appert 1977) Anderson & Anderson 1985  
emend.

1977 *Dolianitia madagascariensis* Appert, p. 32; pl. 36 figs. 1,2; p. 33, pl. 37, figs 7-9; pl. 38, figs 1-4; pl. 39, figs 1-5; pl. 40, figs 1, 2; text-figs 5-10 [Basionym].

1985 *Arberia madagascariensis* Anderson & Anderson, p. 130; pl.105, figs 1a, 1c; text-figs 130.1, 130.2.

***Holotype***

SA 7/2; Appert (1977), pl. 36, figs 1,2, text-fig. 5.

### ***Paratypes***

SA 7/1 A & B, Appert (1977), pl. 39, figs 2, 3; pl. 40, figs 1, 2; text-figs 8-10.

SA 7/3 A & B; Appert (1977), pl. 38, figs 1-4; pl. 39, fig. 1; text-figs 6, 7.

All specimens are housed at the Geological Institutes at the 'Eidgenössischen Technischen Hochschule' (Swiss Federal Technical University) and the University of Zürich (Appert, 1977; p. 5).

### ***Type formation and locality***

"Couches à charbon à *Glossopteris* et *Gangamopteris*"; Lower Permian; Andranomanintsy, Fundestelle 3, Sakoa Basin, southwestern Madagascar (Appert, 1977; p. 5).

### ***Emended species diagnosis***

Dorsiventrally flattened, branched, fertile axis, 5-7.5 cm long and 2.5 cm wide, with laminar primary axis giving rise to short lateral branches along its margins and across one surface, perpendicular to the plane of the axis. Primary axis laminar, commonly with a bifurcation in the apex, and with tapered base; longitudinally striated, striations continuing into lateral branches. Marginal lateral branches diverge from axis at close to 90° and curve backwards. Ultimate branchlets terminate in simple scale-like extension with single ovule attachment point at base of scale. Branch termini bifacial, with smooth, longitudinally striated sterile surface and seed-bearing fertile surface. Striations on lateral branches continuous on sterile surface of scale-like features. Planated primary axis bifacial, with lateral branches arising from the axis face corresponding to fertile surfaces of marginal branch termini. Attached seeds platyspermic, round to ovate, with an acute micropylar notch and narrow lateral wings.

### **Description of the South African specimen**

(See pl. 10, fig. (e); pl. 11, figs (j)-(k); Table A.II.2, Appendix II for data summary).

Two incomplete, overlapping impressions (GSP/H/102) of branched fertile axes. Specimen in lower right in pl. 10, fig. (e) is 33.7 mm long; primary axis is planate, laminar, fan-shaped, 13.9 mm long and bears prominent longitudinal striations that continue into the lateral branches; primary axis expands towards the apex, reaching 8.7 mm at the first lateral branch; base of primary axis tapers to form a 12 mm long pedicel with a basal width of 2.5 mm. Apex of primary axis is bifurcated, each primary branch giving rise to at least one lateral branch. Branching is pinnate in the proximal region, with lateral branches arising at angles varying from 30° to over 90° to the main axis, in most cases with the branches gently arching back towards the axis. Lateral branches 2 (2.5) 2.8 mm wide {n=4; SD:0.3}, and 7.3 (8.6) 10.1 mm long {n=4; SD:1.2}. Distance between adjacent branches is 4 (4.6) 5.6 mm {n=3}. Lateral branch termini each bear a poorly defined seed scar, and are extended into a longitudinally striated, terminal wing-like scale distal to the seed-attachment point. The scales are approximately 4.5 mm long, 2.7 mm wide and are elliptical to spatulate, with a bluntly rounded apex. They are bifacial, with a striated sterile surface. There are no attached seeds in the South African specimens.

### **Comments**

Appert's (1977) diagnosis for *A. madagascariensis* has been only slightly emended here. His terms 'megastrobilus' and 'sporophyll' have been excluded because of the unproven homologies they infer, and the nature of the terminal scale-like features on the lateral branches has been included. Although Appert (1977) described these in detail, he was unsure what they represented, and did not mention them in the diagnosis (see section 3.3 for a detailed account of Appert's (1977) interpretations).



Anderson & Anderson (1985) placed the Hammanskraal specimens in *A. madagascariensis* because of similarities between the associated seeds and leaves at Hammanskraal and those from the type locality in Madagascar. The seeds included by Anderson & Anderson (1985) within the circumscription of the South African *A. madagascariensis* (p. 287, pl. 112, figs 8-12), although only found in isolation in the Hammanskraal deposits, are very similar to, and fall within the size ranges of, *Cordaicarpus madagascariensis* Appert (1977). Appert (1977) figured several Madagascan specimens of *A. madagascariensis* with these seeds in organic attachment. Appert (1977) described these seeds as 9-14 mm long, 7-11 mm wide, flat, heart-shaped, bilaterally symmetrical, with a lateral wing which is broader in the apex than the base. The apex of the seed has a narrow, triangular notch, corresponding to the micropyle.

Despite this associative evidence, in morphological terms the link between the Hammanskraal specimens and Appert's (1977) *A. madagascariensis* is a somewhat tenuous one.

Both South African specimens have smooth primary axes bearing uninterrupted longitudinal striations across their surfaces. Based on Appert's (1977) observations of lateral branches arising from one of the faces of the lamina primary axis, we would need to assume that both South African impressions were of the sterile, unbranched surface of the fructification.

The specimens from Madagascar figured by Appert (1977) bore a large number of lateral branches, which became more closely spaced towards the apex. In the specimens he figured, 3-7 pairs of marginal lateral branches were present. The Hammanskraal specimens (GSP/H/102) have far fewer lateral branches, although both specimens are clearly incomplete and it is possible that the original fructifications were considerably longer and bore more lateral branches than indicated in the reconstruction on pl. 10, fig. (j). It is also possible that the bifurcation in the apex has been exaggerated in this reconstruction – the specimen upon which it was based was slightly laterally compressed prior to preservation, making this feature difficult to observe. None of the Madagascan

specimens conclusively illustrated a bifurcated apex, since the apices were in all cases missing or incomplete.

It is possible that the South African specimens may be better placed within another species, perhaps *A. minasica*, but until more informative specimens are recovered from the Hammanskraal locality, Anderson & Anderson's (1985) classification has been upheld.

#### **6.1.4.2      *Arberia hlobanensis* Anderson & Anderson 1985 emend.**

1969 'strange fructification', Plumstead; p. 44; pl. 13, fig. 3

1985 *Arberia hlobanensis* Anderson & Anderson; p. 129; text-figs 128.1, 129.2; pl. 103, fig. 1.

#### ***Holotype***

BP/2/15893; an impression fossil in soft, poorly laminated, light brown to pinkish buff shale, with some carbonaceous residues. The specimen is housed in the Bernard Price Institute, University of the Witwatersrand, Johannesburg, South Africa.

#### ***Type formation and locality***

Vryheid Formation (Ecca Group); Lower Permian (Artinskian); Hlobane, northern Karoo Basin.

#### ***Emended species diagnosis***

Irregularly branched fertile axis with single major dichotomy; primary axis is gradually tapered towards the base; branches bear longitudinal striations, and arise in multiple planes. Ultimate branches are short; each expands distally to form a slightly cup-shaped, transversely elliptical scale-like structure; scales are bifacial, with a striate sterile surface, and a fertile surface with one or two indistinct seed scars at the base and a weakly differentiated, distal wing that is contracted at the base.

## **Description**

(See pl. 10, figs (a), (b); pl. 11, figs (g)-(i); Appendix II, Table A.II.2 for data summary).

Part and counterpart of a single, branched, fertile axis, 40.7 mm long, 22 mm wide. The 17.6 mm long pedicel is 5 mm wide at the first branch, tapering proximally to 2 mm. The pedicel is longitudinally striated, striations continuing into all lateral branches. Branching appears to be irregular and in multiple planes, branches typically diverging at 30° to 35°. Main lateral branches are 13-19 mm long, with basal width of 3.3 (3.6) 3.9 mm {n=2}, and subsidiary lateral branches are 2.2 (5.3) 8.7 {n=8; SD:2.7} mm long. Ultimate branches are 1.8-(2.9)-3.7 mm wide {n=3}. The terminus of each ultimate branch is broadly expanded to form a scale-like structure. The slightly cup-shaped scale-like features are transversely elliptical, 4.4-(5)-6.3 mm long {n=5} and 4.3-(6.4)-8.1 mm wide {n=5}. The scales are bifacial, with a fertile surface bearing 1 or 2 indistinct seed scars at the base, and a striate, sterile surface, the longitudinal striae continuing from the pedicel across the scale. The distal portion of the fertile surface of the scale is differentiated into a striated wing, which has a lateral width of 1.9 mm and a distal width of 2.1 mm, and which is discontinuous at the base of the scale.

## **Comments**

Even though this fructification is a multidimensional structure, the seed-bearing termini of the branches are clearly bifacial, with a sterile and a fertile surface and a distal wing-like feature, as in the other ovuliferous glossopterid organs. In the impressions, the seed scars are slightly raised, indistinct cushions, and the scale is convex. This means that in the original plant specimen, the seed scars were depressions, and the wing curved towards the seed-bearing surface of the scale, forming a weakly developed hood.

Although Anderson & Anderson (1985) did not confuse the expanded branch termini with seeds, they reconstructed them as bulbous features. Here the

diagnosis has been emended to accommodate the bifacial nature of the scale-like features, and the differentiation of a wing-like feature distal to the seed-attachment points.

#### 6.1.5 DISCUSSION

Several authors (eg. Feistmantel, 1881; Millan, 1967; Schopf, 1976; Appert, 1977) have suggested, on the basis of associative evidence, that *Arberia* represents the ovuliferous fertile structure of the leaf genus *Noeggerathiopsis*. White (1908), Millan (1967) and Appert (1977) recognised a possible affinity with *Noeggerathiopsis* on the basis of similarities in the attached seeds (of the *Cordaicarpus* type), to those usually associated with cordaitalean plants. McLoughlin and Drinnan (1996) also supported a cordaitalean alliance. Although there does appear to be an association between *Arberia* and *Noeggerathiopsis*, no fructification has ever been found in direct, organic attachment to this or any other leaf type. Rigby (1972a) suggested a link between *Arberia* and gangamopteroid forms of *Glossopteris*.

Anderson & Anderson (1985) favoured an association with *Glossopteris* rather than *Noeggerathiopsis*, but their reasoning was partly circular. They noted that the Ermelo locality was the only one of six middle to upper Ecca assemblages in South Africa, in which there was 'no sign of *Arberia*' (or members of the Arberiaceae as described here), and yet it yielded an abundance of *Noeggerathiopsis* leaves. However, at two of the six middle to upper Permian localities they listed, the only '*Arberia*' specimens present were *Glossopteris* leaves that they had assigned to *Arberia* on the basis of their morphological similarities to leaves associated with *Arberia madagascariensis* at Hammanskraal. *Arberia*, and other members of the Arberiaceae from South Africa, are probably too rare to confidently demonstrate any associative relationship with any particular leaf-type.

Surange & Lele's (1956) *A. umbellate* and Chandra & Srivastava's (1981) *Arberia surangei* are similar to *A. madagascariensis* and *A. minasica*, but have a more elliptical to circular primary axis, and may lack an apical bifurcation. The

specimen figured by Chandra & Srivastava (1981) in pl. 1, figs 1&2 bears numerous indentations on the face of the primary axis, comparable to those seen in Appert's (1977) specimens, which are here interpreted as the bases of lateral branchlets on the fertile face of the primary axis (see section 3.3).

Maithy (1965) recorded a specimen of *Arberia* cf *A. umbellate* from the Karharbari Stage of India, but Chandra & Srivastava (1981) did not consider this specimen to be a valid member of the genus. Maithy's (1970) *Dolianitia karharbarensis*, however, appears to be a legitimate member of *Arberia*, comparable to *A. minasica*, with a prominent apical dichotomy and pinnate lateral branches. The primary axis is particularly broad and robust. Chandra & Srivastava's (1981) *A. surangei* has a more obovate primary axis without an obvious apical dichotomy, and the lateral branches each undergo a dichotomy almost at the margin of the primary axis. The specimen they figured in text-fig. 1 (p. 42) shows evidence of lateral branches arising from the fertile face of the primary axis, as occurs in *A. madagascariensis* (see section 3.3).

Rigby (1972a) noted some similarities between Pant & Nautiyal's (1965, 1966) specimens of 'Ottokaria-like fructifications' and *Arberia*, and synonymised some of them with *Arberia minasica*. Pant & Nautiyal (1984) later defended their status as members of *Ottokaria* and referred them to a new species *Ottokaria zeilleri*. While some of the fructifications figured by Pant & Nautiyal (1984) are distinctly ottokarioid, others have a more fan-shaped, laminar form with an unmistakable apical dichotomy and opposite lateral branches (e.g. pl. 5, fig 35, 37; pl. 8, figs 60, 61; pl. 9, fig. 63), and could comfortably be accommodated within *Aberia*.

Lundqvist (1919) figured several specimens from Brazil (pl. 1, figs 25-29) of laminar, longitudinally striated axes with dichotomous and pinnate branching patterns, and expanded branch termini, although it is not clear in all cases whether the expanded portions are scale-like features or seeds/ovules. In figs 25 and 29 these features are strongly suggestive of the samaropoid seeds typically found in attachment to *Arberia*. Lundqvist (1991) called these fructifications *Arberia* (?) *brasiliensis*, and referred to the seeds as

'*Cardiocarpon* sp.'. Lindqvist's (1919) specimens are similar to the *A. indica*, *A. minasica*, *A. hammanskraalensis* group of fructifications, but the apical dichotomy is not as pronounced.

Millan (1967) described several arberiid fructifications from the Bainha outcrop, Santa Catarina, Guatá Group, Tubarão series of Brazil. He created a new genus, *Dolianitia* to accommodate the branched, ovuliferous fertile axes. Most of the planated axes have a clearly defined, single, dichotomous branch in the apex, and all bear either alternate or opposite lateral branches along their margins. In some specimens these lateral branches undergo a second dichotomy. Millan (1967) identified three species of '*Dolianitia*': *D. opposita* and *D. crassa*, both with a dichotomic main axis and opposite lateral branches, and *D. alternata*, with a main axis lacking a dichotomy, and with alternate lateral branches. The termini of the ultimate branches are each expanded into a short, truncated scale-like feature. The axes are longitudinally striated, and the striations continue uninterrupted into these scale-like features. They are particularly well illustrated in Millan's (1967) pl. 1, fig. 1&1a, pl. 2, figs 2&3 and pl. 4, fig. 2. Two of the specimens he illustrated have a large, single seed attached to a branch terminus. The seeds are of the *Cordaicarpus* type, with a narrow marginal wing, and are quite distinct from the sterile, scale-like structures seen in other branch termini.

Millan's (1967) reasons for separating *Dolianitia* from *Arberia* are not clear, and Rigby (1972a) later synonymised the genera, tentatively assigning most of Millan's (1967) species to *Arberia minasica*. Appert's (1977) decision to uphold Millan's (1967) genus *Dolianitia* rather than assign the specimens he found in Madagascar to *Arberia* are also unclear.

Rigby (1972a) figured a variety of arberiid fructifications from Brazil, some of which are strikingly similar to *Arberia madagascariensis*. The specimens illustrated in his pl. 24, figs 1, 4, 6, 7 and 8 all have a laminar primary axis which undergoes at least one major dichotomy at the apex, and bears small, pinnate lateral branches along its margins. The specimen he figured in pl. 24, fig. 5 is very similar in appearance to *Arberia hlobanensis*, with its more paniculose

structure, and lack of the typical apical dichotomy seen in *Arberia minasica* and *Arberia madagascariensis*. The elliptical, cup-like terminal scales are also highly reminiscent of *A. hlobanensis*.

Rigby (1972a) also included figures of specimens he considered comparable to *Arberia* (pl. 26, figs 5, 6 & 7), which are here regarded to be examples of *Rigbya*. They clearly have the elongated wing/ scale-like structures and the fan-shaped lamina typical of *Rigbya*. The fructification figured in pl. 25, fig. 7 as *Arberia minasica* (Rigby, 1972a), may also represent an unusual example of *Rigbya*, with very short terminal scales. The single report of *Arberia* from Antarctica, by Plumstead (1962a), also appears to be an account of planated, fan-shaped fructifications attributable to *Rigbya* rather than to *Arberia*.

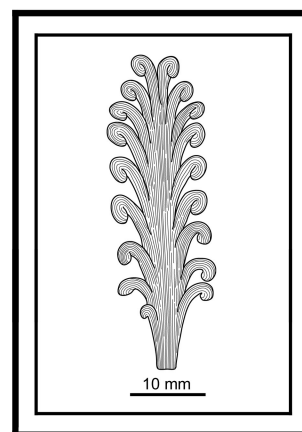
The most recent contribution to the genus was made by McLoughlin (1995), when he described a new species of *Arberia* from the Irwin River Coal Measures of Western Australia. *Arberia woolagaensis* does not closely resemble any other species of *Arberia*. The primary axis is narrowly obovate, lacks an apical dichotomy, and bears peculiar oblong seeds which are either sessile or borne on short lateral branches. The only other report of *Arberia* from Australia is a specimen figured by White (1961), and referred to *A. minasica* by Rigby (1972a), but which almost certainly represents a specimen of *Rigbya*.

Anderson & Anderson (1985) considered the planated *Arberia* species described from South America (Millan, 1967; Rigby, 1972a), Madagascar (Appert, 1977) and India (Surange & Lele, 1956; Maithy, 1970, Chandra & Srivastava, 1981) to all represent a 'single polymorphic species' or 'a rather narrowly defined genus'. These specimens may need to be re-examined in light of the morphological interpretations proposed here, and taxa with bifacial axes, bearing lateral branches across one surface of the laminar primary axis, may need to be distinguished from others that have only pinnate branches or paniculose branching structures.

## 6.2 VEREENIA gen. nov.

### 6.2.1 INTRODUCTION

The type species of *Vereenia* was first described by Anderson & Anderson (1985) as *Arberia leeukuilensis*. This was in accordance with their concept of the genus *Arberia*, incorporating polysperms comprising a simple, variously branched axis bearing a single, unprotected ovule at the terminus of each ultimate branch. As discussed in the previous section (section 6.1), this diagnosis has been emended here to include the presence of a terminal scale associated with each seed-attachment site, and also acknowledges the three dimensionality and dichotomous nature of the branching structure seen in many members of the genus. *Vereenia* however, apparently lacks protective scales at its branch termini which are characteristically recurved. The organ is a planated structure with a laminar primary axis giving rise to a pinnate fringe of lateral branches in the same plane. These features were considered to be distinctive enough to warrant the segregation of this taxon in a new genus within the Arberiaceae.



*Vereenia leeukuilensis*

The name '*Vereenia*' was proposed by Dr Steve McLoughlin (pers. comm.<sup>5</sup>), and is used here with his permission. The taxon will be formally published in a collaborative venture at a later stage.

### 6.2.2 FOSSIL MATERIAL

Six impression fossils from the Vereeniging locality, all from the collections of the Bernard Price Institute, University of the Witwatersrand, Johannesburg, South Africa. (See Table A.I.4, Appendix I for specimen details).

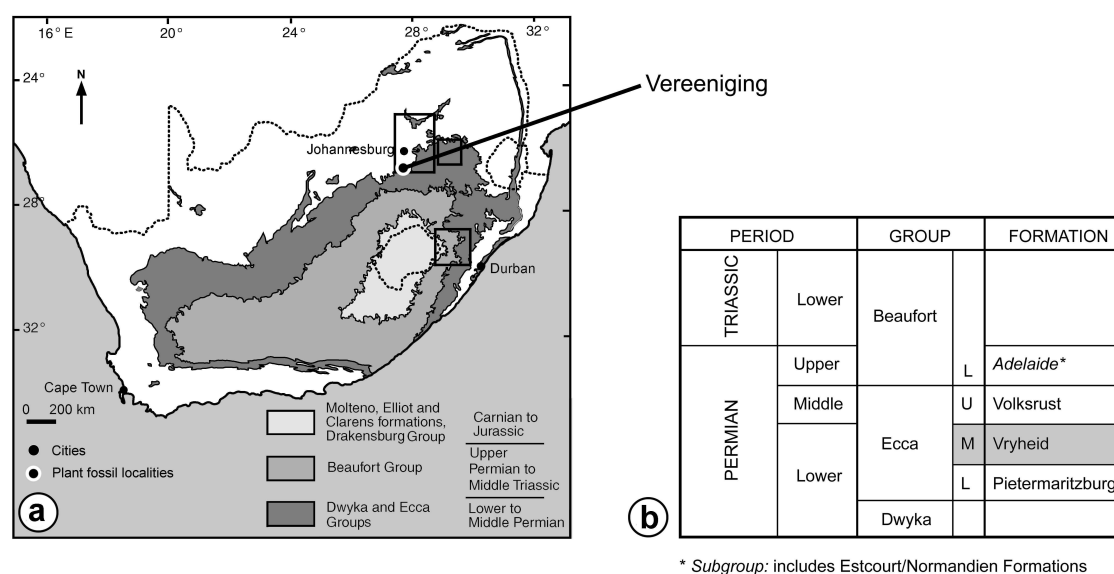
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<sup>5</sup> Department of Resource Sciences, Queensland University of Technology, Brisbane, Queensland, Australia; email: s.mcloughlin@qut.edu.au



### 6.2.3 LOCALITY INFORMATION

*Vereenia* has only been found at the Leeukuil Quarries in Vereeniging, Gauteng Province, in the Karoo Basin, South Africa, in sediments of the Vryheid Formation (middle Ecça Group), of Lower Permian (Artinskian) age (see text-figs 2.2.2, 2.2.3a, 2.2.4 & 6.2.1). According to Le Roux & Anderson (1977), most of the specimens were collected from the Shale Quarry, and a few from the Old Sandstone Quarry (see text-fig. 2.2.5).



**Text-figure 6.2.1.** (a) Locality map indicating reported occurrences of *Vereenia leeuquilensis* in South Africa; (b) lithostratigraphic table of the Permian and Lower Triassic deposits in the northern and eastern parts of the Karoo Basin, with shaded areas representing stratigraphic occurrences of *Vereenia* (table adapted from Keyser, 1997).

### 6.2.4 SYSTEMATIC PALAEOBOTANY

#### *Type species*

*Vereenia leeuquilensis* (Anderson & Anderson 1985) comb. nov. McLoughlin & Adendorff (unpubl.); Lower Permian; Karoo Basin, South Africa.

#### *Etymology*

‘*Vereenia*’ - after the Vereeniging locality in South Africa.

### **Combined diagnosis**

(Adapted from Anderson & Anderson, 1985).

A simple, oblanceolate to narrowly elliptical, planated fertile axis without dichotomies, bearing a single order of ovuliferous branchlets in opposite lateral ranks. Branchlets are short and unspecialised, with rounded, pendulous, slightly expanded and strongly recurved termini.

### **Discussion**

*Vereenia* is a branched fertile axis with a pinnate branching pattern, an individual seed apparently borne at each lateral branch terminus. These are characters that supported the placement of this taxon within the same family as *Arberia*. The specimens are not preserved in sufficient detail to understand the nature of the seed attachment points, but they appear to be fairly unspecialised, rounded and barely expanded, as opposed to the scale-like structures seen in most members of *Arberia*. The lack of any dichotomous branching in *Vereenia* is also a feature that may be used to differentiate the two genera.

#### **6.2.4.1      *Vereenia leeukuilensis* (Anderson & Anderson 1985) comb. nov.**

1985 *Arberia leeukuilensis* Anderson & Anderson 1985  
1997 *Arberia leeukuilensis* Anderson & Anderson, p. 15, fig. 6b.

### **Holotype**

Impression of an isolated fructification, BP/2/14285; housed at the Bernard Price Institute, University of the Witwatersrand, Johannesburg; Anderson & Anderson (1985) pl. 107, fig. 9; this document, pl. 10, fig. (f); pl. 11, fig. (a).

### **Etymology**

'*leeukuilensis*' - after the Leeukuil Quarries at Vereeniging, where the specimens were found.

### ***Type formation and locality***

Vryheid Formation (middle Ecca Group); Lower Permian (Artinskian); Vereeniging, northern Karoo Basin.

### ***Description***

(See pl. 10, figs. (f)-(i); pl. 11, figs (a)-(c); Table A.II.2, Appendix II for data summary).

Planated ovuliferous fertile axis comprising a laminate primary axis without dichotomies, giving rise to a single order of approximately opposite lateral branchlets. Fructifications are 35 (41) 45 mm {n=4; SD: 4.5} long and 9.3 (11.1) 12 mm {n=5; SD: 1.1} wide. Primary axis is narrowly elliptical to oblanceolate with a maximum width of 4 (4.9) 5.5 mm {n=6; SD: 0.6}. Base of primary axis is extended into a 7 (7.5) 8 mm {n=4; SD: 0.4} long pedicel that is 4.5 (5.2) 6 {n=4; SD: 0.7} mm wide at the first lateral branch, tapering to 1.7 mm at the base. Pedicel is finely striated, the striations bifurcating and continuing onto the primary axis and into the secondary, lateral branches. Outer margins of the primary axis diverge in the proximal to medial region at 22°-29°. Up to 18 branchlets diverge from the primary axis at a fairly steep angle of 15° (28.9°) 54° {n=20; SD: 10.4} to the long-axis of the fructification, then arch away from the primary axis, curving proximally. Distance between bases of consecutive branchlets is 2.7 (3.9) 5.6 mm {n=22; SD: 0.9}, with branchlets tending to be closer together towards the base and apex of the fructification. Branchlets are 2.2 (5.1) 7.5 mm long {n=34; SD: 1.2}, tending to be shorter near the base of primary axis, and are 1.3 (1.5) 1.7 mm {n=14; SD: 0.2} wide. Branchlets are expanded at the apex to form weakly differentiated seed-bearing structures that are rounded, pendulous to tightly recurved. The terminal swellings are 1.5 (2.3) 5 mm {n=19; SD: 0.5} long and 1.3 (1.8) 2.7 mm {n=19; SD: 0.4} wide, and may be angled slightly away from the plane of the axis, i.e. turned in towards the lamina [see BP/2/14284, pl. 10, fig. (i)]. Indistinct, seed-like features are

associated with the branchlet termini in specimen BP/2/14283 [pl. 10, fig. (h)]; these are 2.9 to 3.2 mm long, 3.6 to 3.9 mm wide.

No clear examples of attached seeds, or attached leaves have been found.

### **Comments**

The entire surface of the fructification bears fine striations, which run from the pedicel into the lamina, where they follow a path predominantly parallel to the long axis of the fructification, diverging sharply at intervals into the lateral branches. The striations (which probably represent veins) bifurcate, but it is unclear whether or not they anastomose.

### **6.2.5 DISCUSSION**

Although beautiful in their simplicity, the lack of detail in the specimens belonging to this taxon has not allowed for more than a superficial evaluation of their structure and affinities. *Vereenia* has features reminiscent of *Arberia*, but it either lacks the seed scar/ scale arrangement seen in all the other glossopterid fructifications, or these details are obscured in all the specimens available.

The striated, laminar primary axis with lateral branches is similar to that of *Arberia madagascariensis* from Hammanskraal. The *Arberia* specimen, however, has ultimate branch termini with a protective scale-like feature distal to the seed scar, and the lamina also undergoes a primary dichotomy in the apical region. In addition, *A. madagascariensis* gives rise to branches which diverge from the plane of the laminar primary axis (see section 6.1).

There do not appear to be any reports of fructifications attributable to *Vereenia leeuukuilensis* from other parts of Gondwana, although there are some examples which may be comparable at the generic level. Surange & Lele (1956) described an unusual fructification from the Lower Permian Talchir beds of India, which they named *Arberia umbellata*. They described it as a megasporophyll-like organ, 15 x 12 mm in size, with a flattened, expanded head bearing several

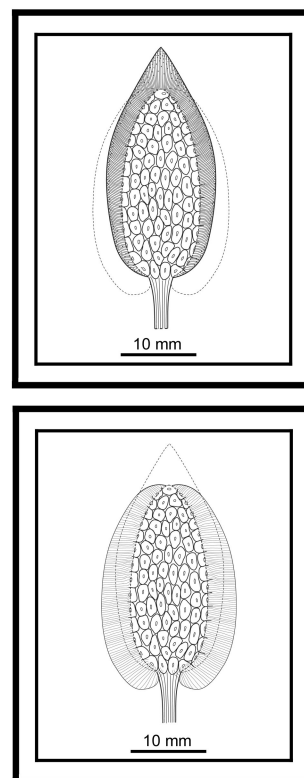
strongly recurved processes. This taxon is very similar in appearance to the laminate *Arberia* species such as *A. minasica*, *A. indica* and *A. madagascariensis*, but the strongly recurved lateral branches are highly reminiscent of *Vereenia*. It is impossible to tell from the photograph provided by Surange & Lele (1956), whether there is a scale-like extension of the branch terminus distal to the seed-attachment point, or whether the branches terminate in simple, unspecialised swellings as seen in the South African specimens of *Vereenia*.

## CHAPTER 7 DICTYOPTERIDIACEAE Surange & Chandra ex Rigby 1978 emend. Maheshwari 1990 (nom. corr. McLoughlin 1990b)

### 7.1 *BIFARIALA* gen. nov.

#### 7.1.1 INTRODUCTION

*Bifariala* is the name suggested here for a group of fructifications initially described by Plumstead (1958a) under the name *Hirsutum intermittens*. These fructifications were the driving force behind Plumstead's insistence that the Vereeniging fructifications were bisexual, bearing pollen-bearing organs in addition to seeds. A close examination of these polysperms revealed a morphology unlike any other glossopterid fructification described, and helped to explain some of Plumstead's convictions.



*Bifariala intermittens*

See section 3.2 for a detailed historical account of this genus, and for an explanation of the morphological interpretations used in the following diagnosis.

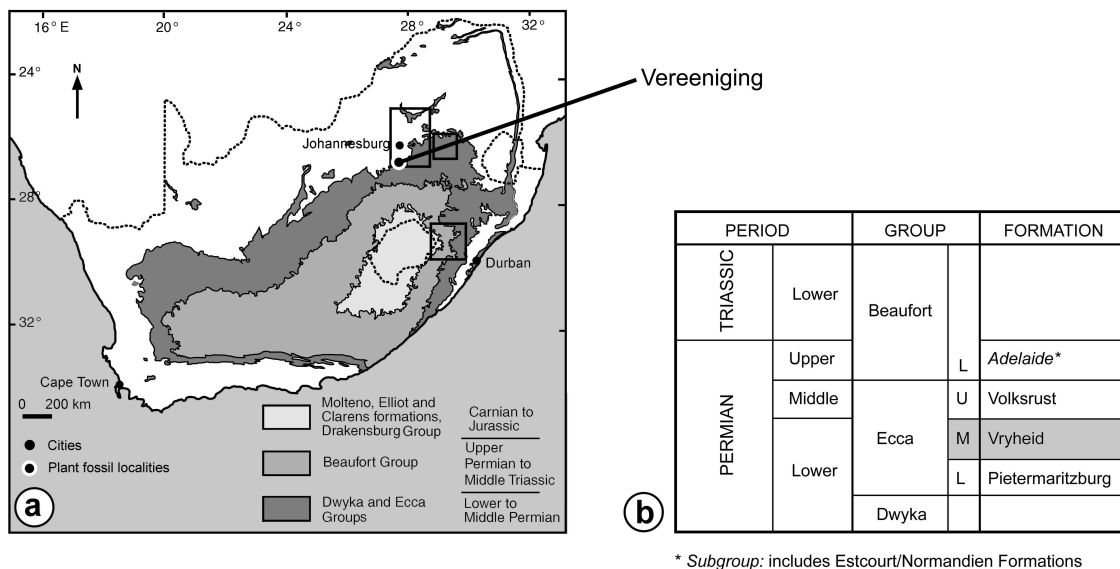
#### 7.1.2 FOSSIL MATERIAL

A total of 42 impression fossils of *Bifariala* were examined; all are housed at the Bernard Price Institute for Palaeontology (BPI) at the University of the Witwatersrand in Johannesburg and the Vaal Teknorama Museum (VM) in Vereeniging (see Table A.I.5, Appendix I).

#### 7.1.3 LOCALITY INFORMATION

*Bifariala* has only been found at the Leeukuil Quarries in Vereeniging, Gauteng Province, in the Karoo Basin, South Africa, in sediments of the Vryheid Formation (middle Ecca Group), of Lower Permian (Artinskian) age (see text-

figs 2.2.2, 2.2.3a, 2.2.4 & 7.1.1). According to Le Roux & Anderson (1977), most of the specimens were collected from the Old Sandstone Quarry and the Shale Quarry (see text-fig. 2.2.5). This genus has not been reported from other parts of Gondwana.



**Text-figure 7.1.1.** (a) Locality map indicating reported occurrences of *Bifaria intermittens* in South Africa; (b) lithostratigraphic table of the Permian and Lower Triassic deposits in the northern and eastern parts of the Karoo Basin, with shaded areas representing stratigraphic occurrences of *Bifaria* (table adapted from Keyser, 1997).

#### 7.1.4 SYSTEMATIC PALAEOBOTANY

##### Type species

*Bifaria intermittens* (Plumstead 1958) comb. nov., emend; Lower Permian; Karoo Basin, South Africa.

##### Etymology

Latin: 'bifariam' – in two parts; 'ala' – wing; referring to the dual wing structure.

##### Combined diagnosis for genus and type species

Isobilateral, dorsiventral, pedicellate, ovuliferous organ comprising a spoon-shaped, narrowly elliptical to lanceolate receptacle with L:W of about 2:1, and two superposed, peripheral wings.

Robust, primary wing continuous with sterile surface of fructification; bears finely arched striae curving towards apex. Primary wing is broadest in apical region, with acute to acuminate apex; base is narrowly tapered towards pedicel.

Secondary wing arises immediately adjacent to the seed scars on fertile surface of receptacle; wing contracted and discontinuous at the apex, but forms a rounded lobe on either side of pedicel at base of receptacle. Secondary wing is finely striated; may show poorly-defined fluting corresponding to positions of marginal seed scars. Fluting and striae oriented perpendicular to edge of receptacle in secondary wing.

Attached near base of petiole of oblanceolate *Glossopteris* leaf with cuneate base and obtuse apex. Midrib is persistent and well-defined; veins emerge at acute angle from midrib, arching gently and continuously across lamina, forming fine, narrow, parallel meshes at an angle of about 50° to medio-longitudinal axis.

#### **7.1.4.1      *Bifariaia intermittens* (Plumstead 1958) comb. nov., emend.**

- 1952    *Scutum dutoitides* Plumstead, pars, p. 289, pl. 45, figs 2, 3. non pl. 45, fig. 1; text-fig. 2.  
1956    *Scutum dutoitides* Plumstead; Plumstead, pars, p. 8, 12, pl. 7, figs 1-3, pl. 10, fig. 3; text-fig 2b,c.; non pl. 6, figs 1-2; text-fig. 2a. [1956a].  
1958    *Scutum sewardii* Plumstead, pars, p. 59, pl. 13, figs 1, 1a; non. fig. 2. [1958a]  
1958    *Hirsutum intermittens* Plumstead, p. 60, pl. 14, figs 1-3, pl. 15, figs 1-5. [1958a].  
1985    *Hirsutum intermittens* Plumstead; Anderson & Anderson, p. 120, text-figs. 4-8, pl. 78, figs 1-11, 16-18, pl. 95, fig. 12.

#### ***Holotype***

Two syntypes designated L.II.70 and L II 71 by Plumstead (1958a; pl 15, fig. 1; pl. 14, fig. 3); re-registered as BP/2/14003 and BP/2/13974 respectively in the collections of the Bernard Price Institute, School of Geosciences, University of the Witwatersrand, where they are currently housed; BP/2/14003 cited by Anderson and Anderson as the holotype [1985; pl 78, fig. 8; this document: pl. 12, fig. (a)].



### ***Type formation and locality***

Vryheid Formation (middle Ecca Group); Lower Permian (Artinskian); Vereeniging, northern Karoo Basin.

### ***Description***

(See plates 12 – 18; Table A.II.3, Appendix II for data summary).

Fructifications are 6.2 (28.1) 42 mm long (excluding the pedicel) {n=33; SD: 6.4} and 10.5 (14.9) 21.3 mm wide {n=40; SD:2.5}, with overall L:W of 1.3 (1.9) 2.9 {n=33; SD:0.4}. Pedicel bears longitudinal striations and is 2.8 (10.1) 22.3 mm long {n=28; SD:4.3}. Pedicel tends to be of fairly even width, but may broaden slightly near junction with receptacle. Maximum pedicel width measured was 1.6 (2.6) 4 mm {n=29; SD:0.6}, minimum 1.2 (2) 3.2 mm {n=22; SD:0.5}.

The narrowly elliptical to lanceolate receptacle is a spoon-shaped structure with convex fertile surface and concave sterile surface (in impressions). Receptacle is 11 (21.7) 33.6 mm long {n=36; SD:5.1}, 6.5 (9.5) 13.8 {n=42; SD:1.9} wide, has a L:W of 1.6 (2.3) 3.8 {n=36; SD:0.5} and an area of 59 (159) 260 mm<sup>2</sup> {n=34; SD:55.5}. Receptacle is bifacial with sterile and fertile surface. Fertile surface bears 31 (57.5) 93 {n=17; SD:19.6} elliptical seed scars at a density of 5 (8.6) 15 scars per 25 mm<sup>2</sup> {n=17; SD:2.5}. Seed scars are 1.6 (2.5) 3.8 mm long {n=145; SD:1.45}, 0.7 (1.5) 2 mm wide {n=130; SD:0.2}, smooth, raised cushions which may have a central tubercle or depression. Marginal scars tend to be more rectangular, forming a regular rank along receptacle edge; medial scars are longitudinally oriented along axis of fructification.

Two superposed wings are borne along periphery of receptacle. Primary wing is continuous with sterile surface of fructification; secondary wing is continuous with fertile surface.

Primary wing is narrowly tapered to 0.5 (0.8) 1 mm {n=5; SD:0.2} at the base of receptacle, expanding in width towards apex where it is most broadly developed. Primary wing has medio-lateral width of 1.4 (2.5) 4 mm {n=38;

SD:0.7}, apical width of 2.5 (5.3) 8.4 mm {n=38; SD:1.5}. Apex is acute and may be slightly acuminate; margin is entire. Wing bears uniform, closely spaced striae or veins that enter the wing at an angle approximately perpendicular to edge of receptacle, and then curve distally to intersect margin at about 10° to long-axis of fructification. The primary wing may be slightly retroflexed, curving away from the fertile surface of the receptacle.

Secondary wing is contracted and discontinuous at apex of receptacle, and forms a rounded lobe on either side of pedicel at base of receptacle. Medio-lateral wing width is 2.1 (4.1) 6.3 mm {n=20; SD:1.3}; basal width is 1.5 (3.6) 5.6 mm {n=22; SD:1.1} and secondary wing width : receptacle width is 0.3 (0.4) 0.8 {n=21; SD:0.1}. Wing is finely striated with faint fluting that corresponds to positions of marginal seed scars on fertile surface of receptacle. Fluting is more prominent immediately adjacent to edge of receptacle, fading towards wing margin. Both striae and flutes are radially oriented, perpendicular to receptacle margin. Fine striae of secondary wing converge at cicatrix of each marginal seed scar on receptacle. Secondary wing margin is entire.

Fructification attached to midrib approximately 10 mm above base of 142.6 mm long {n=1}, 22.4 mm wide, narrowly elliptical *Glossopteris* leaf with cuneate base and tapering but blunt apex. Midrib narrow but persistent, 2.2 to 0.8 mm wide {n=1}. Veins fine with narrow, parallel meshes and marginal density of 22 veins per 10 mm {n=1}; arise at steep angle to midrib, arch gently and continuously across lamina, with a mid-laminal angle of 37.7° {n=3} and marginal angle of 63° {n=3}.

### **Comments**

As a result of the primary wing being continuous with the sterile surface of the receptacle, there is a distinct groove, or 'crack' as Plumstead (1958a) referred to it, between the margin of the fertile surface of the receptacle and the primary wing in the impression fossil [e.g. pl. 12, figs (d), (e); pl. 13, figs (h), (i); pl. 15, fig. (b); pl. 17, fig. (a)]. Conversely, in impressions of the sterile surface, the overlying secondary wing is always at a higher level than the veined surface of the receptacle.

The secondary wing appears to have been thin and delicate. Exposure of this wing through removal of the impression of the primary wing in impressions of the fertile surface of the fructification, proved to be very difficult (pl. 16), as the cleavage plane along this structure was weakly developed. Impressions of the secondary wing tend to be much fainter than those of the primary wing, which explains why it has been overlooked in the past. Oddly enough however, the secondary wing is most clearly preserved and prominent in the holotype specimen (pl. 12, fig. a).

Because the 'preferred' plane of cleavage in impressions of *B. intermittens* is apparently through the more robust primary wing of the polysperm, there are few specimens with large parts of the secondary wing exposed. Some specimens have the secondary wing exposed along one side of the receptacle [e.g. pl. 12, fig. (c); pl. 14, fig. (i); pl. 15, fig. (k)], but most commonly, the secondary wing is only visible in the base of the fructification where the primary wing has tapered away towards the pedicel. The holotype [pl. 12, fig. (a)] was prepared by Plumstead (1952) to expose the secondary wing along the left side of the fructification. There are no clear examples of fructifications with the secondary wing exposed along the entire periphery of the receptacle. A possible exception, as discussed further in section 7.6.6 is the type specimen of *Gladiopomum dutoitides*.

#### **7.1.5 DATA ANALYSIS**

There is a fair degree of overlap in the dimensional ranges of *B. intermittens* and *Gladiopomum dutoitides*, but text-fig. 7.1.2 illustrates the tendency for *B. intermittens* to have shorter receptacles than specimens of *G. dutoitides* of comparable width, i.e. *B. intermittens* generally has a smaller receptacle length to width ratio. In text-fig. 7.1.3, *B. intermittens* has a smaller ratio of wing width to receptacle width, a reflection on the narrower wing in this taxon. The controversial type specimen of *G. dutoitides* is perhaps more closely affiliated with the data points for *G. dutoitides* than *B. intermittens*, but could also quite

A scatter plot showing the relationship between Receptacle Width (mm) on the x-axis and Receptacle Length (mm) on the y-axis. The x-axis ranges from 0 to 15 mm with major ticks every 5 units. The y-axis ranges from 0 to 45 mm with major ticks every 5 units. Two data series are plotted: *Gladiopomum dutoitides* (represented by open triangles) and *Bifariaia intermittens* (represented by solid circles). The *G. dutoitides* data points are generally located at higher receptacle widths (between 6 and 14 mm) and higher receptacle lengths (between 15 and 41 mm). The *B. intermittens* data points are more widely distributed, covering receptacle widths from approximately 6.5 to 14 mm and receptacle lengths from approximately 11 to 34 mm. There is a notable overlap between the two species in the region of 8-12 mm width and 15-30 mm length.

| Species                       | Receptacle Width (mm) | Receptacle Length (mm) |
|-------------------------------|-----------------------|------------------------|
| <i>Gladiopomum dutoitides</i> | 6.2                   | 17                     |
| <i>Gladiopomum dutoitides</i> | 6.8                   | 20                     |
| <i>Gladiopomum dutoitides</i> | 7.5                   | 15                     |
| <i>Gladiopomum dutoitides</i> | 9.8                   | 39                     |
| <i>Gladiopomum dutoitides</i> | 11.2                  | 31                     |
| <i>Gladiopomum dutoitides</i> | 12.5                  | 34                     |
| <i>Gladiopomum dutoitides</i> | 13.2                  | 41                     |
| <i>Gladiopomum dutoitides</i> | 13.8                  | 33                     |
| <i>Bifariaia intermittens</i> | 6.8                   | 11                     |
| <i>Bifariaia intermittens</i> | 7.2                   | 15                     |
| <i>Bifariaia intermittens</i> | 7.5                   | 16                     |
| <i>Bifariaia intermittens</i> | 7.8                   | 17                     |
| <i>Bifariaia intermittens</i> | 8.2                   | 18                     |
| <i>Bifariaia intermittens</i> | 8.5                   | 19                     |
| <i>Bifariaia intermittens</i> | 8.8                   | 20                     |
| <i>Bifariaia intermittens</i> | 9.2                   | 21                     |
| <i>Bifariaia intermittens</i> | 9.5                   | 22                     |
| <i>Bifariaia intermittens</i> | 9.8                   | 23                     |
| <i>Bifariaia intermittens</i> | 10.2                  | 24                     |
| <i>Bifariaia intermittens</i> | 10.5                  | 25                     |
| <i>Bifariaia intermittens</i> | 10.8                  | 26                     |
| <i>Bifariaia intermittens</i> | 11.2                  | 27                     |
| <i>Bifariaia intermittens</i> | 11.5                  | 28                     |
| <i>Bifariaia intermittens</i> | 11.8                  | 29                     |
| <i>Bifariaia intermittens</i> | 12.2                  | 30                     |
| <i>Bifariaia intermittens</i> | 12.5                  | 31                     |
| <i>Bifariaia intermittens</i> | 12.8                  | 32                     |
| <i>Bifariaia intermittens</i> | 13.2                  | 33                     |

A scatter plot showing the relationship between Receptacle Length (Y-axis, 0 to 45) and Medial Wing Width: Receptacle Width (X-axis, 0.0 to 1.2). The plot compares two species: *Gladiopomum dutoitides* (represented by triangles) and *Bifariola intermittens* (represented by circles). The data points for *G. dutoitides* are generally higher on the Y-axis than those for *B. intermittens*, indicating a larger receptacle length for a given medial wing width. The legend is located below the plot.

| Species                       | Medial Wing Width: Receptacle Width | Receptacle Length |
|-------------------------------|-------------------------------------|-------------------|
| <i>Gladiopomum dutoitides</i> | 0.40                                | 34                |
| <i>Gladiopomum dutoitides</i> | 0.45                                | 31                |
| <i>Gladiopomum dutoitides</i> | 0.60                                | 41                |
| <i>Gladiopomum dutoitides</i> | 0.65                                | 34                |
| <i>Gladiopomum dutoitides</i> | 0.93                                | 39                |
| <i>Gladiopomum dutoitides</i> | 0.93                                | 17                |
| <i>Gladiopomum dutoitides</i> | 1.01                                | 20                |
| <i>Bifariola intermittens</i> | 0.25                                | 18                |
| <i>Bifariola intermittens</i> | 0.28                                | 20                |
| <i>Bifariola intermittens</i> | 0.28                                | 19                |
| <i>Bifariola intermittens</i> | 0.32                                | 17                |
| <i>Bifariola intermittens</i> | 0.32                                | 13                |
| <i>Bifariola intermittens</i> | 0.35                                | 27                |
| <i>Bifariola intermittens</i> | 0.38                                | 17                |
| <i>Bifariola intermittens</i> | 0.38                                | 11                |
| <i>Bifariola intermittens</i> | 0.40                                | 26                |
| <i>Bifariola intermittens</i> | 0.42                                | 20                |
| <i>Bifariola intermittens</i> | 0.45                                | 25                |
| <i>Bifariola intermittens</i> | 0.48                                | 26                |
| <i>Bifariola intermittens</i> | 0.55                                | 29                |
| <i>Bifariola intermittens</i> | 0.72                                | 15                |
| <i>Bifariola intermittens</i> | 0.75                                | 15                |

### 7.1.6 DISCUSSION

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(section 7.6.6) and Appendix IV. There is a possibility that this specimen may belong in *Bifariala intermittens* rather than *Gladiopomum*. The secondary wing of *B. intermittens* is very similar to the wing seen in *Gladiopomum dutoitides*. In both polysperms, the wing is contracted at the apex with basal lobes. Wings in both taxa bear radial striations and fluting which is only developed near the receptacle, fading towards the entire wing margin. The taxa have indistinguishable seed scar morphologies and have narrow, lanceolate receptacles. For these reasons, specimens of *Bifariala* with fully exposed secondary wings would closely resemble members of *G. dutoitides*. It is possible that the holotype of *Gladiopomum* is a specimen of *B. intermittens* with only the extreme apex of the primary wing exposed, giving the appearance of a longitudinally striated apical spine. Text-figs 7.1.2 & 7.1.3 illustrate similar but distinct scatter plots for *Bifariala intermittens* and *Gladiopomum dutoitides*, with the type specimen of *G. dutoitides* falling within the ranges for both taxa.

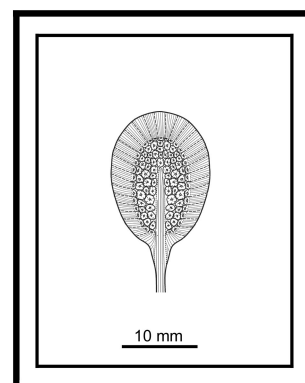
Taxonomically, *Bifariala* is quite distinct from *Gladiopomum* in having a dual wing structure. However, in light of the similarities between the two genera, it is conceivable that the apical spine in *Gladiopomum* represents a reduced primary wing, restricted to the extreme apex of the fructification. The only other glossopterid fructification that has a double wing is *Elatra leslii*, although the wing system is more elaborate, as discussed earlier in section 3.2. The primary wing of *Bifariala* is similar to the primary wing of *Elatra*, in that it bears apically inclined striations, is tapered towards the base of the receptacle and is extended into a point at the apex. However, in *Bifariala* the secondary wing is continuous along the entire periphery of the receptacle except at the base and apex, and is not only developed in the base of the fructification as in *Elatra*. *Bifariala* also lacks a hood.

There have been no reports of taxa from other parts of Gondwana with a dual wing structure, and not even of fructifications with a wing similar to the primary wings of *Bifariala* and *Elatra*.

## 7.2 *ESTCOURTIA* (Lacey *et al.*) Anderson & Anderson 1985 emend.

### 7.2.1 INTRODUCTION

Only three specimens of this very rare fructification have been found. They were discovered and described by Lacey *et al.* (1975) as *Scutum conspicuum*. Unlike other members of *Scutum*, however, the wing of this fructification is smooth, entire and the base is decurrent along the pedicel. In addition, the seed scars are small and close together, and the subtending leaf differs significantly from those attached to *S. leslii*. Anderson & Anderson (1985) placed this taxon in a new genus, *Estcourtia*, and made the taxonomically invalid decision to change the species name from '*conspicuum*' to '*vandijkii*'. In light of the significant morphological differences exhibited between the two taxa, this Upper Permian taxon has been kept separate from *Scutum*, as per Anderson & Anderson (1985).



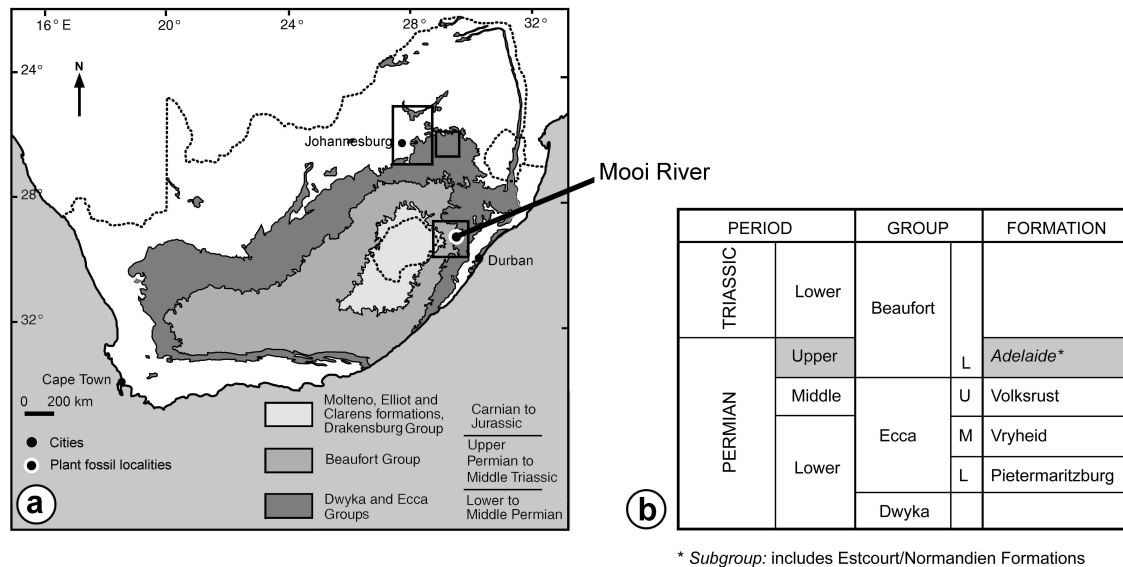
*Estcourtia conspicua*

### 7.2.2 FOSSIL MATERIAL

The three specimens from the Mooi River locality are all housed at the Natal Museum, Pietermaritzburg (see Table A.I.6, Appendix I.). Anderson & Anderson (1985; Table 2.5, p 33; p125) reported the occurrence of an *Estcourtia* fructification from the upper Beaufort locality, Glandisrock near Inhluzane. This specimen could not be located in the collections at the BPI. All specimens are impression fossils.

### 7.2.3 LOCALITY INFORMATION

The only confirmed occurrence of this species are the three specimens described by Lacey *et al.* (1975) from the Mooi River locality in Kwa-Zulu Natal, South Africa, in sediments of the Estcourt Formation, Lower Beaufort Group (Upper Permian). See Text-figs 2.2.2, 2.2.4 and 7.2.1a&b.



**Text-figure 7.2.1** (a) Locality map indicating reported occurrences of *Estcourtia conspicua* in South Africa; (b) lithostratigraphic table of the Permian and Lower Triassic deposits in the northern and eastern parts of the Karoo Basin, with shaded areas representing stratigraphic occurrences of *E. conspicua* (adapted from Keyser, 1997).

## 7.2.4 SYSTEMATIC PALAEOLOGY

### *Type species*

*Estcourtia conspicua* (Lacey *et al.*) Anderson & Anderson 1985 comb. nov., emend.; Upper Permian; Karoo Basin, South Africa.

### *Etymology*

'*Estcourtia*' - from the town Estcourt, near the Mooi River locality where the type specimen was found.

### *Emended combined diagnosis*

Isobilateral, dorsiventral, capitate ovuliferous fructification consisting of a receptacle with a peripheral wing and a short pedicel. Receptacle oval to elliptical, bearing circular to elliptical seed scars; scars small (1-1.4 mm long) and densely packed on fertile surface. Wing moderately broad, with a smooth margin; fluting and striations very faint, apically inclined and only vaguely defined near the edge of receptacle. Wing is continuous around receptacle

except at pedicel insertion, and of regular width apically and medially, although contracted at the base; the wing base is decurrent along the short pedicel. A tapered wedge of strengthening tissue extends from the pedicel into the receptacle. Sterile surface of the receptacle is characterised by a fan-shaped network of broad-meshed venation. The fructification is attached to the midrib in the basal third of a *Glossopteris* leaf, the seed-bearing surface of the receptacle facing the subtending leaf. The leaf is lanceolate to elliptical, petiolate, with a cuneate to attenuate base and meshes that vary from broad, polygonal near the base and near the midrib, to elongate polygonal and linear towards the apex and margins; vein course straight to moderately curved from midrib to margin, with a mid-laminal vein angle of approximately 55°; midrib well-defined and persistent.

### ***Discussion***

*Estcourtia* is a fairly typical capitate glossopterid ovuliferous fructification, in that it is an isobilateral, dorsiventrally flattened polysperm, with a central, seed-bearing receptacle surrounded by a fluted, striated wing. As with other genera such as *Scutum*, *Bifaria*, *Dictyopteridium* and *Elatra*, the fructifications are borne on the midrib of a relatively large, apparently unspecialised *Glossopteris* leaf. The primary distinguishing features of the genus relate to its wing. The wing is continuous and of even width around the entire receptacle, except at the base where it is contracted. The margin is entire and the wing has a smooth appearance, the slightly apically inclined striations and fluting being particularly faint. The most unusual feature of the wing, which is perhaps unique to this taxon, is the decurrent base. The wing extends down the short pedicel, forming a tapering flange on either side.



**7.2.4.1      *Estcourtia conspicua*** (Lacey *et al.* 1975) Anderson & Anderson 1985  
comb. nov., emend.

1974 *Scutum conspicuum* Lacey, van Dijk and Gordon-Gray, p. 154; fig. NM 1276, p. 155.

1975 *Scutum conspicuum* Lacey, van Dijk and Gordon-Gray, p. 394-5, pl. NM 1276a, 1276b.

1978 *Scutum conspicuum* Lacey, p. 187.

1985 *Estcourtia vandijkii* Anderson & Anderson, p. 126, pl. 95, fig. 8; pl. 96, figs 1a,b, 2-4; text-figs 126.1-6.

***Holotype***

NM/1276a,b; Lacey *et al.* 1975, p. 394-5; Anderson & Anderson 1985, p. 126, pl. 96, figs 1a,b; pl. 19 (this document). Impression fossil; incomplete part and counterpart of a fertiliger. The specimen is housed at the Natal Museum, Pietermaritzburg.

***Etymology***

'*conspicua*' - after *Glossopteris conspicuum*, the taxon that Lacey *et al.* (1975) assigned to the subtending leaf of this fructification.

***Type formation and locality***

Estcourt Formation (Lower Beaufort Group); Upper Permian; Mooi River, eastern Karoo Basin.

***Description***

(See plates 19-22; Appendix A.II.3 for data summary).

The fructifications are 21.3 mm {n=1} long and 13.1 (15.1) 17.1 mm {n=2} wide, with a gross length to width ratio of 1.4 {n=1}. Each polysperm is attached to a subtending *Glossopteris* leaf by means of a short, featureless pedicel. The pedicel is 1.7 (2.6) 3.5 mm {n=2} wide at insertion.

Receptacle is oval to elliptical, 9.7 (11.1) 12.5 mm {n=2} wide and 18.5 mm {n=1} long, and has a length to width ratio of 1.5 {n=1}. There is a wedge of

longitudinally striated tissue that extends from the top of the pedicel approximately a third of the way into the receptacle. This wedge is most easily seen in the type specimen [pl. 19; pl. 22, fig. (c)].

Receptacle is surrounded by a smooth, entire, peripheral wing, continuous except at point of pedicel insertion. Faint striations are visible on surface of the wing, and there is some evidence of fluting near the receptacle margin, corresponding to the positions of the marginal seed scars. Fluting and striations are slightly inclined towards the apex [see line drawings in pl. 22, figs (b) and (c)]. Wing is of even width medially [1.9 (2) 2.1 mm {n=2}] and apically [2.1 mm {n=1}] but is contracted at base to 0.4 (0.6) 0.8 mm {n=2}. The ratio of the medial wing width to receptacle width is 0.2 {n=2}. The wing base extends along either side of the short pedicel, the decurrent wing flanges being 3.4 – 4 mm {n=2} long, with a proximal width of approximately 1.2 mm {n=1}.

The fertile surface of the bifacial receptacle has a surface area of 86 (135) 184 mm<sup>2</sup> {n=2}, and bears 131 (205.5) 280 {n=2} small, irregular to elliptical seed scars at a density of 38 per 25 mm<sup>2</sup> {n=2}. The peripheral seed scars tend to be circular to square and are 0.7 (1.0) 1.1 mm in diameter {n=4; SD: 0.2}, while the more central seed scars tend to be more irregular in shape, with a length of 0.9 (1.1) 1.4 mm {n=8; SD: 0.2} and a width of 0.8 (0.9) 1.1 mm {n=8; SD: 0.1}.

The sterile surface of the receptacle is not well represented in the fossil material available, but in specimen BP/2/8172b [pl. 20, fig. (d)], a coarse-mesh network of bifurcating and anastomosing veins can be seen.

Each polysperm is attached to the midrib of a lanceolate to elliptical, petiolate *Glossopteris* leaf, over 100 mm long and 19.7 (24.7) 29.6 mm {n=2} wide, with a cuneate to attenuate base. Attachment is in the basal third of the leaf, with the fertile surface of the receptacle facing towards the leaf. The midrib is 3.7 to 0.3 mm {n=3} wide and it persists to the leaf apex. The leaf is petiolate, with a petiole width of 1.9 {n=1}, and length of 13 mm {n=1}. Leaf venation is variable, with broad, open, polygonal meshes in the basal part of the leaf and near the midrib, becoming narrower and more linear towards the margins and apex of the

leaf. The marginal vein density is 11 (13.7) 16 {n=3; SD: 2.5} per 10 mm in the medial part of the leaf. Vein angles tend to be larger towards the base (approximately 70°), decreasing in the medial part of the leaf to 46° (54.3°) 70° {n=7; SD: 10.8} (mid-laminal) and 46° (52.6°) 64° {n=7; SD: 6} (marginal). The veins follow a straight to gently arching course from the midrib to the margin.

### **Comments**

The 'wedge of strengthening tissue' that extends up into the receptacle from the pedicel, could be interpreted as a region of fusion of the fructification to the subtending *Glossopteris* leaf. None of the polysperms show any sign of lateral displacement prior to preservation, and there is no clear delimitation between the pedicel (taken as the ridge of vascular tissue with wing flanges) and the midrib. In other fructifications, such as *Scutum*, the pedicel is clearly distinct from the vascular tissues of the subtending leaf, and there is often a pronounced abscission area visible at the base of the pedicel. *Scutum* polysperms also usually exhibit some degree of lateral displacement relative to the leaf. It is feasible that just the pedicel of *Estcourtia* is adnate, and the strengthening tissue is an imprint of the midrib of the subtending leaf. However, when there is secondary imprinting of leaf structures on impressions of fructifications, some background detail of the original impression details usually remains. In the specimens of *Estcourtia*, the seed scars terminate abruptly at the junction with the wedge-shaped area that extends from the pedicel. We will have to wait for further examples of this taxon to surface in order to clarify this detail.

The wing striations are most clearly seen in specimen BP/2/8172a&b (pl. 20). In the type specimen, NM/1276 (pl. 19) there are strong secondary imprints originating from the venation of the subtending leaf, which are easily confused with wing features, and which have the effect of exaggerating the degree of apical inclination of the wing striations. These secondary imprints can be distinguished from the wing striations by matching them up with the leaf venation along the periphery of the fructification. The clarity of the secondary imprints creates a sense of the wing having been very thin.

The type specimen, NM/12076a&b is an incomplete fertiliger. The apical half to two-thirds of the leaf and the apex of the attached fructification are missing. No specimens have been found with attached seeds.

All three *Estcourtia* specimens have only partial leaves in attachment, and these leaves show a fair degree of variation. The type specimen (pl. 19) has a leaf with coarse, polygonal meshes, whereas BP/2/8172a&b has meshes that are finer and more regular, becoming linear [pl. 20, figs (a)-(d)]. There would appear to be a change in the pattern of venation from a broader, more open mesh shape in the base of the leaf and close to the midrib, to a more linear, closely spaced arrangement in the distal and marginal areas of the leaf lamina. Lacey *et al.* (1975) considered the attached leaves to be *Glossopteris conspicua* Feistmantel. However, according to Feistmantel's diagnosis for *G. conspicua*, the coarse meshes that are characteristic of the species, are continued right to the leaf margin, although they may become smaller in size away from the midrib. Judgement on the specific affiliations of the leaves has been reserved until further, more complete specimens are found.

### 7.2.5 DISCUSSION

When Lacey (1974) created the binomial *Scutum conspicuum*, he was clearly not comfortable about using two, separate sets of form genera and species to describe a single fertiliger. Apparently as a compromise, he retained the practice of assigning a different genus to the glossopterid fructification, but assigned to it the same specific epithet as applied to its subtending leaf (*G. conspicua*), an approach recommended by Schopf (1976). When Anderson & Anderson (1985) later transferred the taxon from *Scutum* to *Estcourtia*, they changed the specific epithet from '*conspicuum*' to '*vandijkii*'. They did not explain their decision to change the species name, but it would appear that their circumscription of the *E. vandijkii* 'palaeodeme' did not reliably encompass Feistmantel's diagnosis for *Glossopteris conspicua*, particularly the leaves with cordate bases that they included within the taxon. This substitution of a species name is not in accordance with the ICBN (Greuter, W. *et al.*, 1994), which

requires clearly substantiated reasons for a change of name, even if the name in question reflects inaccuracies, or is not entirely appropriate. The specific epithet '*conspicua*' is therefore conserved.

*Estcourtia* is most similar to *Scutum*, where it originally resided when first described by Lacey *et al.* (1975). However, *Scutum* typically has a wing with a dentate margin, very well-defined, radial fluting and a lobed base. The slightly apically inclined fluting and contracted base seen in *Estcourtia* could affiliate it with taxa originally placed in the genus *Hirsutum*, viz. *Elatra* (Plumstead, 1956a, 1958a; Appert, 1977) or *Bifaria* (Plumstead, 1956a, 1958a). However, unlike either of these taxa, the apex of the wing is not broad and drawn into a point, and there is no evidence to suggest the presence of a dual wing structure. Lacey (1978) noticed strong similarities between *Estcourtia* and *Venustostrobus diademus* (Chandra & Surange, 1977a). Both are attached to petiolate, coarse-meshed *Glossopteris* leaves in a similar size range and with cuneate bases. There are differences in the venation, but given the variability observed even within a single locality, the disparities are relatively minor. Like *Estcourtia*, *Venustostrobus* is very rare, with only six specimens having emerged from the extensively collected Jambad Colliery in the Raniganj Coalfield. Chandra and Surange (1977a) adopted Plumstead's (1952, 1956a, 1958a) 'bivalve' interpretation of the capitate fructifications of *Glossopteris*, including *Venustostrobus*. They illustrated the part and counterpart of two of the specimens, and there is no evidence to suggest that the impressions do not simply represent the two surfaces of a single, bifacial organ. The receptacle is circular in shape, with a moderately broad, fluted wing with an entire margin. From the line drawings provided by Chandra and Surange (1977a) however, the base of the wing does not appear to be decurrent along the pedicel. Chronostratigraphically, the Raniganj Stage and Estcourt Formation are probably comparable, as discussed by Lacey *et al.* (1975), and certainly seem to yield similar floral elements.

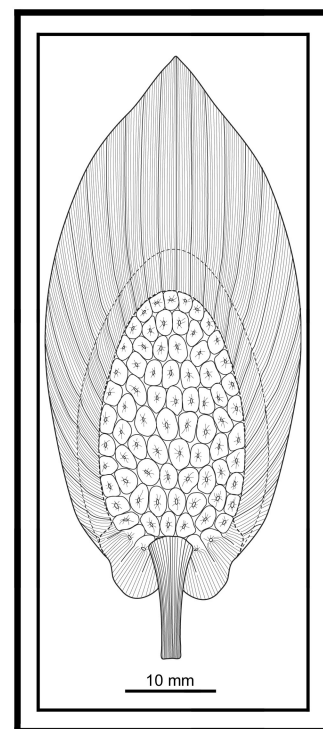
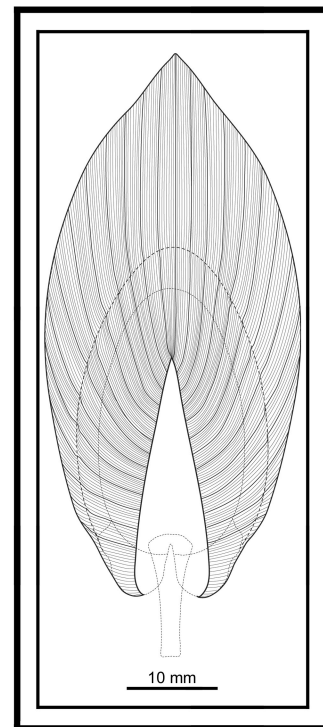
### 7.3 **ELATRA** Appert 1977 emend.

#### 7.3.1 INTRODUCTION

In 1921, a single specimen of 'an *Ottokaria*- like fructification' was described from the Vereeniging locality, by Thomas. Unwilling to erect a new genus on the basis of a single specimen, Thomas (1921) tentatively named it *Ottokaria leslii*. Despite intensive collecting conducted at the Vereeniging locality by S.F. LeRoux and Edna P. Plumstead, further examples of this fructification were never found. Then, in 1969, Plumstead briefly mentioned two large, unnamed fructifications from the Hammanskraal locality that bore a strong resemblance to the specimen described by Thomas (1921). The first detailed descriptions of these polysperms were compiled by Smithies (1978), in her M.Sc. dissertation. She recognised the link between the new specimens from Hammanskraal, and Thomas' type specimen of *Ottokaria leslii* residing in the Natural History Museum in London.

The taxon was described by Smithies (1978) as a tripartite fructification called *Hirsutum leslii*. Later a more conventional, streamlined diagnosis was published by Smithies in Anderson & Anderson (1985), where the fructifications were portrayed as simple, dorsiventrally flattened structures with an apically extended wing bearing recurved striations that converged on the apex.

Smithies (1978, 1985) did not make reference to a paper by Appert (1977), in which he describes specimens almost identical to those of *H. leslii*, from



*Elatra leslii*

Madagascar. These fructifications, which he assigned to a new genus *Elatra*, differed only in having a shorter wing with a lobed apex, as opposed to the entire-margined, elongated to acuminate wing seen in the Hammanskraal specimens (see section 3.2.3, text-fig. 3.2.12). Since the genus *Hirsutum* has been abandoned (Adendorff *et al.*, 2002; see Appendix IV), the specimens currently residing in *H. leslii* are treated here under the new combination *Elatra leslii*.

For a detailed explanation of the morphological interpretations used in the diagnosis and descriptions below, please refer to sections 3.1 and 3.2.

### **7.3.2 FOSSIL MATERIAL**

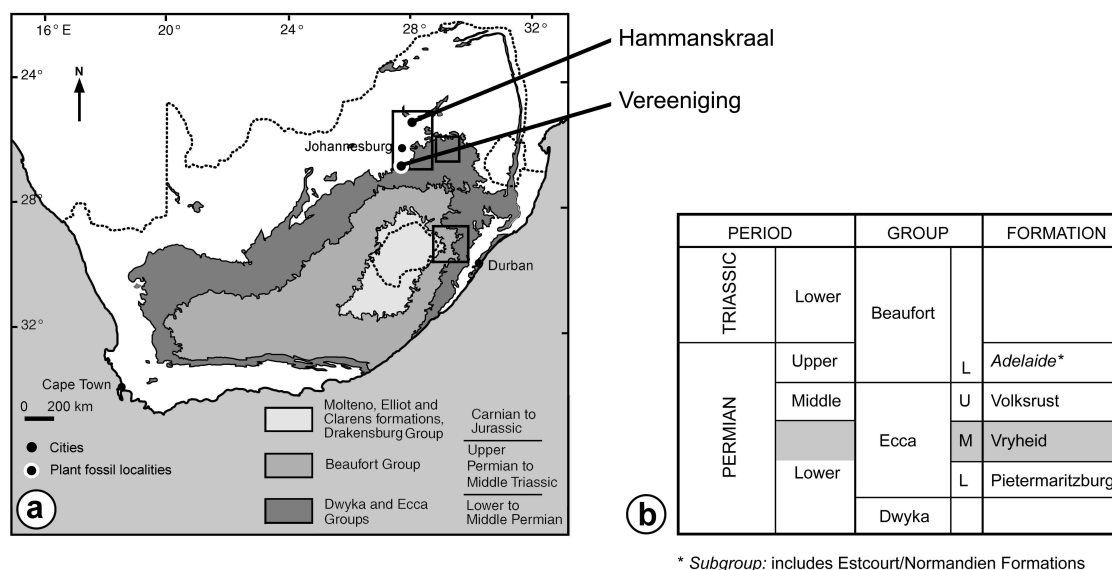
A single specimen of *Elatra leslii* was found at the Vereeniging locality by Thomas in 1921, and no further examples have been recovered from this site. This specimen resides in the collections of the BPI, and its counterpart is housed in the Natural History Museum in London. Numerous specimens have been found at the Hammanskraal locality, and over 50 of these were examined in detail. The Hammanskraal specimens are all compression/ impression fossils, and are housed at the Bernard Price Institute for Palaeontology (Johannesburg), the National Botanical Institute (Pretoria) and the Council for Geosciences (Pretoria).

[See Table A.I.7, Appendix I for lists of specimen numbers].

### **7.3.3 LOCALITY INFORMATION**

The single specimen from the Vereeniging locality was found by Thomas (1921) at the Klip River Quarry, described by Le Roux and Anderson (1977) (text-figs 2.2.2, 2.2.3a, 2.2.5 & 7.3.1). All other specimens were collected at the Hammanskraal locality. Sediments at the Vereeniging locality are considered to belong to the Vryheid Formation (middle Ecca Group) of the northern Karoo Basin, which places them in the Lower Permian (Artinskian). The

Hammanskraal sediments are Bushveld Basin deposits, thought to be Vryheid Formation equivalents.



**Text-figure 7.3.1.** (a) Locality map indicating reported occurrences of *Elatra leslii* in South Africa; (b) lithostratigraphic table of the Permian and Lower Triassic deposits in the northern and eastern parts of the Karoo Basin, with shaded areas representing stratigraphic occurrences of *Elatra* (table adapted from Keyser, 1997).

## 7.3.4 SYSTEMATIC PALAEONTOLOGY

### *Type species*

*Elatra bella* Appert 1977; "Couches à charbon à *Glossopteris* et *Gangamopteris*"; Lower Permian; Andranomanintsy, Fundestelle 3, Sakoa Basin, southwestern Madagascar.

### *Etymology*

'elatra' - 'wing' in Malagasy.

### *Emended generic diagnosis*

Dorsiventral, isobilateral, pedicellate fructification comprising a multi-ovuliferous, receptacle with a peripheral primary wing, a basal secondary wing, and a covering hood which partially encloses the seed-bearing surface and is continuous with the primary wing.



Receptacle circular, elliptical, transversely elliptical to ovate, with rounded to truncate base. Receptacle is bifacial, with multiple seed scars on fertile surface, and veined sterile surface with broad, elliptical to elongate meshes.

Campylodromous venation arches from pedicel insertion to margin of receptacle where it recurves and proceeds to the apical wing margin at a steep angle.

Primary wing with fine striations and fluting, corresponding to positions of marginal seed scars. Wing tapers at base, may be expanded into small lobe on either side of pedicel insertion; broadest in apex; apex pointed, acuminate to bluntly rounded; margin entire or with weakly developed scallops in apical section.

Covering hood with basal aperture; diverges from primary wing near receptacle edge and arches over fertile surface.

Secondary wing developed in basal region with gently rounded to sharply pointed lobes; margin entire; fine striations and fluting corresponding to positions of marginal seed scars; fluting only developed near receptacle edge.

### ***Discussion***

Appert's (1977) diagnosis has been emended to accommodate a new model for the fructification as a dorsiventral, isobilateral fructification with an elaborate, three-part wing structure. Although the holotype assigned by Appert (1977) does not have any part of the covering hood exposed, its presence can be inferred from Appert's (1977) descriptions (see section 3.2.3, p. 92), and the discontinuity of the impressions of the fertile surface and the primary wing. The part and counterpart of the Madagascan type specimen, show characteristics identical to those of fructifications from Hammanskraal in every respect apart from the morphology of the primary wing, which is shorter in *Elatra bella* and is gently undulating towards the apex, ending in a few blunt teeth. Since the hood is obscured in *E. bella*, details of the morphology of this wing have been omitted from the generic diagnosis.

Appert (1977) also included an associated scale leaf in his diagnosis. This has been excluded from the emended diagnosis, as associative evidence is not regarded here as a valid source of diagnostic information.

#### **7.3.4.1      *Elatra leslii* (Thomas, 1921) comb. nov., emend.**

1921 *Ottokaria leslii* Thomas, p. 285-288; fig. 1, p. 285; fig. 2, p. 286.  
1969 'new and significant fructifications of Glossopteridae?', Plumstead, p. 44; pl. 13, figs 6 & 7.  
1976 fructification; Kovács-Endrödy, pl. III, fig. c.  
1978 *Hirsutum leslii* Smithies (MSc dissertation, unpublished); figs 89-129.  
1985 *Hirsutum leslii* Smithies (in Anderson & Anderson); p. 121; text-figs 118.4, 118.8, 121.1, 121.6, 121.7.; pl. 81, figs. 1-11; pl. 95, fig. 10.  
1991 fructification; Kovács-Endrödy, p. 102, pl. 5.25, figs 13, 15, 16.

#### ***Etymology***

'*leslii*' - after Thomas Nicolas Leslie (1858-1942), an amateur palaeobotanist who made large collections of fossil plants at the Vereeniging locality, and who discovered the type specimen described by Thomas (1921).

#### ***Holotype***

An indistinct impression fossil in fine-grained sandstone; NHMV20742, housed at the Natural History Museum, London; Thomas (1921), fig. 1, p. 285, fig. 2, p. 286; counterpart BP/2/15701, housed at the Bernard Price Institute for Palaeontology, Johannesburg; this document, pl. 23, fig. (a).

#### ***Type formation and locality***

Vryheid Formation (middle Ecca Group); Lower Permian (Artinskian); Vereeniging, northern Karoo Basin, South Africa.

#### **Emended species diagnosis**

Primary wing with entire margin, drawn into long, acuminate apex. Secondary wing expanded to form a gently rounded to sharply pointed, sagittate lobe on

either side of pedicel. Covering hood an extension of the primary wing, arching over fertile surface of receptacle, with tent-like, triangular basal aperture spanning basal two thirds (approximately) of receptacle.

Attached seeds elliptical to ovate with narrow wing, ca. 6x4 mm.

Subtending *Glossopteris* leaf narrowly obovate with rounded apex and cuneate to roundly hastate base; fine venation with parallel meshes follows a straight path to margin at an angle of ca. 40°.

### **Description**

(See pls 23-42; Table A.II.3, Appendix II for data summary).

Isobilateral, dorsiventral, ovuliferous fructification comprising a bifacial, seed-bearing receptacle with a tri-partite wing structure. Fructification is 25.3 (48) 79.3 mm long {n=41; SD: 14.2}, 13.2 (27) 39.3 mm wide {n=51; SD: 6.3}, and is attached to midrib of a *Glossopteris* leaf. Seed-bearing surface of receptacle faces the leaf.

Receptacle is 13.7 (26) 45.8 mm long {n=48; SD: 7.8}, 10 (20.4) 28.8 mm wide {n=51; SD: 4.7}, with an area of 147 (484) 718 mm<sup>2</sup> {n=12; SD: 198.3} and a L:W of 0.8 (1.3) 2.1 {n=48; SD: 0.3}. Receptacle is variable in shape from circular to elliptical, ovate, obovate or transversely elliptical. Base is rounded, truncate or slightly cordate. Approximately 40 (55.3) 85 {n=10; SD: 17.7} seed scars are borne on the fertile surface at a density of 1.5 (3.3) 7 scars per 25 mm<sup>2</sup> {n=10; SD: 1.6}. Scars are elliptical to polygonal, becoming more rectangular along marginal rank, and are represented by a low cushion, 2.1 (4) 5.5 mm long {n=66; SD: 4}, 1.4 (2.4) 3.3 mm wide {n=58; SD: 0.5}, with a central, circular tubercle.

Sterile surface of receptacle bears striations continuing from the pedicel into the receptacle in a narrow band of robust central veins ca. 10 mm long, which then evanesce and gently recurve across receptacle surface. Some bifurcations and anastomoses are evident, creating coarse, elliptical to elongated meshes. At the

receptacle margin, veins continue into the primary wing but arch distally, and converge towards the wing apex.

The primary wing is distally expanded and is drawn into an elongated, in some cases acuminate, and pointed apex, reaching a maximum width of 6.5 (20.8) 37.3 mm {n=40; SD: 8.7}, with a transverse apical wing width of 2.6 (24) 35.1 mm {n=42; SD: 6}. Wing narrows medially to a width of 1.3 (2.9) 5.2 mm {n=45; SD: 1.2}, tapering further towards the base of the receptacle. Primary wing is striated and deeply fluted, flutes delimited by adjacent veins; most commonly reflexed away from the impression of the sterile surface and hence away from the fertile surface in the original plant.

Hood is continuous/ fused with the primary wing along proximal margin, arching over fertile surface of receptacle to form a hood like covering with basal aperture. Wing is 7.6 to 12 mm wide at the apex (n= 2), tapering gradually towards the base, to create the triangular, tent-shaped opening over the basal portion of the receptacle. Distal margins of the wing, along the aperture, diverge at an angle of approximately 45° (n=1). Aperture reaches a maximum width of approximately 12 mm (n=1) near base of fructification, and has an overall length of about 20 mm (n=1). Fluting and striations on the primary wing continue uninterrupted into the hood.

Secondary wing only evident in the base of the fructification; comprises two gently rounded to sharply pointed, sagittate basal lobes, 3.5 (4.6) 5.5 long {n=5; SD=0.71}, which overlap pedicel, meeting at midline. Secondary wing is scutoid in structure, with radial striations and fluting corresponding to positions of basal seed scars. Fluting is only apparent close to margin of receptacle.

Pedicel is longitudinally striated, 6.2 (11.7) 21.9 mm long {n=30; SD: 4.1}, with a basal width of 1 (2.8) 4.6 mm {n=22; SD: 0.9}, expanding slightly to 2.2 (5) 6.7 mm {n=28; SD: 0.8} near junction with receptacle.

Attached seeds found in majority of specimens; impressions or compressions of multiple seeds are found in intervening sediment between impression of fertile surface of receptacle and impression of hood. Seeds elliptical to ovate, 4.2 (5.6)

7.6 mm long {n=20; SD: 1.2}, 2.3 (4.0) 5.4 mm wide {n=21; SD: 0.9} with narrow, 0.4 (0.5) 0.7 mm wide {n=5; SD: 0.1} wing. Micropylar end pointed, chalazal end rounded.

The fructification is attached to midrib, very close to the base of subtending *Glossopteris* leaf (fructification is probably axillary with pedicel adnate to midrib). Leaf is narrowly obovate with cuneate to broadly rounded, laterally expanded base (roundly hastate), and rounded apex. Midrib is 0.8 to 6 mm wide {n=5}; prominent and persistent. Venation is fine with parallel meshes, following gently curved to straight course across lamina; mid-laminal vein angle 24° (39.1°) 50° {n=13; SD: 9.6}; marginal vein density 22 (26.4) 32 veins per 10 mm {n=5; SD:4.3}. See plates 38-40 for examples of attached leaves.

### **Comments**

The impression of the fertile surface of the receptacle, bearing multiple seed scars, was preserved on a wedge of sediment nested beneath the impression of the hood, and surrounded by, but not continuous with, the primary wing. This resulted in the edge of the impression of the receptacle being uneven and at a higher level than the surrounding primary wing, e.g. pl. 23, figs. (b), (d); pl. 24, figs (b), (d); pl. 30, figs (c)-(f). When this overlying wedge of sediment bearing the impression of the fertile surface of the receptacle was removed, the hood-like extension of the primary wing was exposed beneath. The impression of the hood was clearly continuous with that of the primary wing, indicating that the proximal margin of the hood was fused with, or rather an extension of, the primary wing. Dissections of two fructifications, to reveal the hood are illustrated in pls 33, 34. Specimens in pl. 28, fig. (d); pl. 36; pl. 37, fig. (c) and possibly pl. 37, fig. (a) represent fully exposed views of the hood. Specimen BP/2/7146a in pl. 36 is a particularly illuminating specimen, as it demonstrates the three-dimensional nature of the primary wing and hood-like extension. One can follow the phytolite as it arches away from the receptacle. This specimen provides evidence to suggest that the outer margin of the secondary wing may be continuous with the hood. The exact relationship between the primary and secondary wings and the hood in the base of the fructification has not yet been

resolved, despite careful dissection of several specimens. It is possible that all three wings are elements of the same three-dimensional wing structure.

Impressions of the sterile surface of the fructification were continuous, uninterrupted surfaces, with venation continuing uninterrupted from the receptacle surface into the impression of the primary wing. In all specimens, however, there was a gentle step or groove near the periphery of the receptacle, which probably traces the base of the hood along the line of its divergence from the primary wing. This feature is particularly well represented in pl. 23, figs (c), (e); pl. 25, figs (a), (b).

The secondary wing lobes tended to be angled away from the fertile surface of the receptacle, into the sediment. In most specimens, the base of the receptacle in the impression of the fertile surface appeared to be fairly rounded to truncate. It was only after removal of the overlying sediment near the base of the fructification, that the basal, secondary wing lobes were exposed. The secondary wing is particularly evident in the type specimen [pl.23, fig. (a)], and in pl. 23, fig. (b); pl. 26, fig. (a), pl. 28, fig. (b).

In many specimens, compressions and impressions of seeds are present within the wedge of sediment bearing the impression of the fertile surface. These seeds are clearly illustrated in pl. 29, figs (a), (b); pl. 30, figs (a), (b).

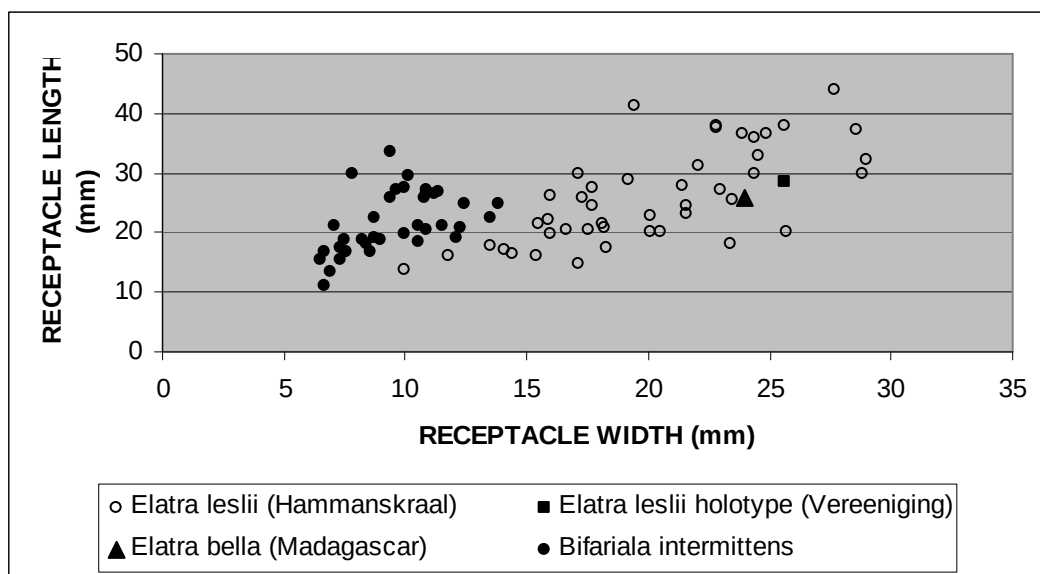
As with specimens of *Ottokaria*, the pedicel is aligned with the sterile surface of the receptacle, with striations continuing directly from pedicel into base of receptacle, but lies at a higher level in the sediment than, as is discontinuous with, the impression of the fertile surface, extending slightly over the base of the receptacle. This indicates that there was a slight protrusion of the receptacle below the point of pedicel insertion.

Specimen BP/2/7401, as illustrated in pl. 32, provides an interesting view of the *E. leslii* fructification. The fructification is still attached to its subtending leaf, but only remnants of the leaf material remain in the fossil. The darkly shaded area in the line drawing of the specimen in fig. (a) illustrates the sediment bearing an

impression of the subtending leaf. There is typical *Glossopteris* venation in this impression, and a broad, well-developed midrib. The medium grey shading in fig. (a) highlights an impression of the hood, and the light grey is the primary wing and sterile surface of the fructification. Note the carbonaceous phytolite or compressions between the layers of sediment bearing impressions of the various structures.

### 7.3.5 DATA ANALYSIS

In text-fig. 7.3.2, the holotype of *Elatra leslii* from Vereeniging, as well as Appert's (1977) type of *Elatra bella* both fall within the dimensional ranges of the Hammanskraal fructifications. *Bifariaia intermittens*, the only other fructification known to have a complex wing structure, has a similar range of receptacle lengths to *E. leslii* but the receptacle widths are much smaller since these fructifications have a more oblong to lanceolate shape.



**Text-figure 7.3.2.** Receptacle lengths and widths for Appert's (1977) *Elatra bella* from Madagascar, *Elatra leslii* from Hammanskraal and *Bifariaia intermittens* from Vereeniging.

### 7.3.6 DISCUSSION

*Elatra leslii* is very similar to Appert's (1977) *E. bella*, but is distinguished here on the basis of wing morphology: the wing of *E. bella* does not appear to be drawn into a long, acuminate point in the apex, as we see in *E. leslii*. *Elatra bella*

also has a dentate apical wing margin. Since Appert (1977) only described a single specimen, we cannot assess the morphological variability of the taxon, and it is possible that the Madagascan and South African species may be synonymous.

As discussed in section 3.2.3 (p. 92, text-fig. 3.2.18), White (1978, p. 499, figs 63, 64; 1986, p. 114, figs. 146, 147) described a single specimen which appears to have a similar body plan to that seen in the Hammanskraal specimens, and which may therefore belong within the genus *Elatra*.

*Elatra* has much in common with *Bifariola intermittens*, and the taxa were probably closely related phylogenetically. Both polysperms have a dual wing structure, the primary wing with an extended, pointed apex and tapered base, and apically inclined striations and fluting. The secondary wing, although only partial in *Elatra*, exhibits radial striations and weakly developed fluting (only clearly evident near the margin of the receptacle) in both genera, and is contiguous with the seed scars on the fertile surface of the receptacle. It is the strange hood seen in *Elatra* that distinguishes this genus from *Bifariola*. The continuity of the striations and fluting in the primary wing and the hood, suggest that the hood is somehow derived from the primary rather than the secondary wing. This is supported by the apparent separation of the covering and secondary wing in the base of the fructification.

Although attached seeds are rare or unknown in other taxa of glossopterid fructifications, many of the specimens of *Elatra leslii* contained *in situ* seeds, which were preserved in the sediment trapped between the fertile surface of the receptacle and the hood. The seeds were elliptical to ovate with a very narrow wing. These factors suggest that the fertile structure may have been dispersed as a unit, rather than being a static seed-bearing platform for the dispersal of individual seeds. However, the tent-like opening within the base of the hood would have allowed for pollination and for the dispersal of seeds prior to abscission of the polysperm. Perhaps the elongated wing apex caught the breeze, shaking the fructification and dislodging the seeds.

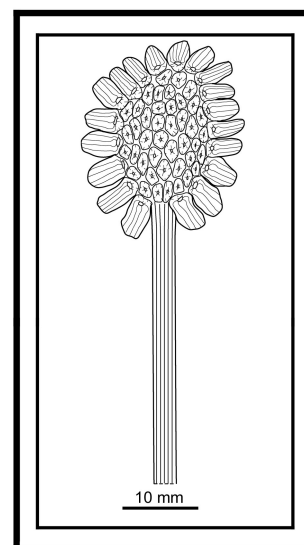


## 7.4. OTTOKARIA Zeiller 1902 emend.

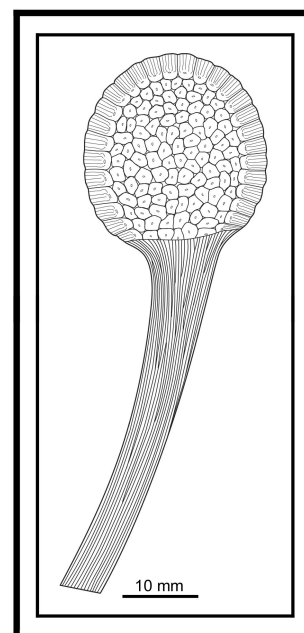
### 7.4.1 INTRODUCTION

Zeiller (1902, pp. 34-36) found the type specimen for this genus in the Karharbari Coalfield, Damodar River Basin, in India. He postulated that the structure was leaf-like, and named it *Feistmantelia bengalensis*. He subsequently (in an addendum to his 1902 paper) changed the name to *Ottokaria bengalensis* after determining that the former designation was preoccupied.

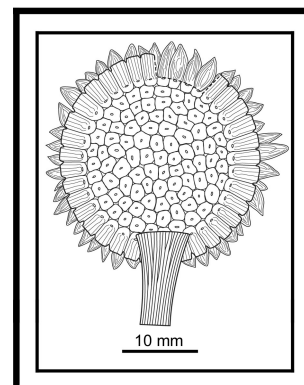
Zeiller's (1902) original Latin diagnosis described *Ottokaria* as a rounded leaf with a long petiole, a dentate margin, and with divergent, fan-shaped, dichotomous venation. Its fertile nature was recognised later, by authors such as White (1908, p. 533), Seward (1917, p. 354), Seward & Sahni (1920) and Thomas (1921, p.287). The type specimen of *O. bengalensis* was preserved in close proximity to a *Glossopteris indica* leaf, and although Zeiller (1902) acknowledged the association, he did not consider there to be organic attachment between the organs. It was only after Plumstead's (1952, 1956a,b, 1958a) landmark papers that a definitive link was established between *Ottokaria* and *Glossopteris* leaves, and it is now generally accepted that Zeiller's (1902) specimen was in fact the earliest glossopterid ovuliferous fructification to have been found in organic connection to a glossopterid leaf (e.g. Bose, Harris in Plumstead, 1956b; Pant & Nautiyal, 1966, 1984, Schopf, 1976; Maheshwari, 1976; Chandra & Surange, 1979).



*Ottokaria transvaalensis*



*Ottokaria buriadica*



*Ottokaria hammanskraalensis*

Differences in structural interpretations of fructifications assigned to *Ottokaria* have resulted in several emendations of the genus in the past.

Plumstead (1956b) emended the diagnosis to conform to her ideas on the bipartite, bisexual nature of the Vereeniging material. Schopf (1976) considered the fructifications to be dorsiventral, bifacial structures, and Banerjee (1978) considered the fructifications to be bipartite, comprising a scale-like bract with a lobed margin, and a separate, flabellate system of fine axes with ultimate branches terminating in megasporangia. Surange & Chandra (1975) and Rigby (1978) reconstructed *Ottokaria* as having a strobiloid receptacle with a funnel-shaped, peltate basal scale. Pant & Nautiyal (1984) and Anderson & Anderson (1985) concurred with Schopf's (1976) dorsiventral, bifacial reconstruction of the fructifications.

The first tentative record of an *Ottokaria*-like fructification from South Africa was made by Thomas (1921). This unusual ovuliferous structure from Vereeniging was later placed in *Hirsutum leslii* by Smithies (1978), and is here recognised as *Elatra leslii* (see section 7.3). Plumstead (1956b) described two species of *Ottokaria* from the Vereeniging locality, viz. *O. transvaalensis* and *O. buriadica*, both associated with gangamopteroid *Glossopteris* leaves. The only other species to have originated from South Africa is *O. hammanskraalensis*, originally described by Smithies (1978) and later officially published with emendations in Anderson & Anderson (1985).

#### **7.4.2 FOSSIL MATERIAL**

All specimens examined were impression/compression fossils, housed at the Bernard Price Institute, the Council for Geosciences, Pretoria and the Vaal Teknorama Museum, Vereeniging.

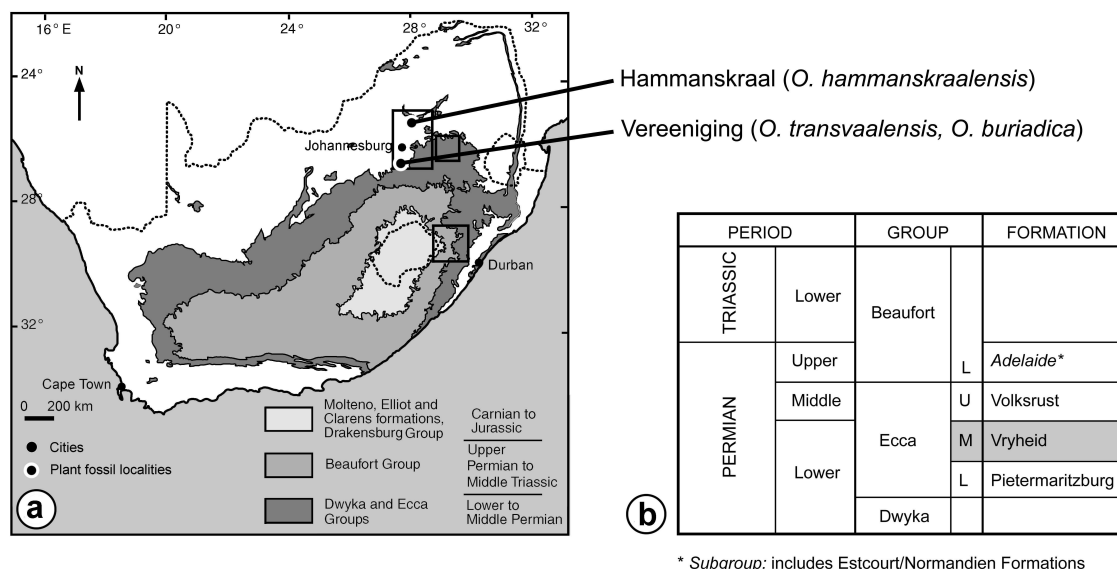
[See Table A.I.8, Appendix I for specimen numbers].

### 7.4.3 LOCALITY INFORMATION

Specimens of *O. buriadica* and *O. transvaalensis* originated from the Leeuukuil Quarries in Vereeniging, Gauteng Province (text-figs 2.2.2, 2.2.3a; 7.4.1a&b). According to Le Roux & Anderson (1977), specimens of both species were found at the Old Sandstone Quarry, the Shale Quarry and the River Quarry (text-fig. 2.2.5). The Vereeniging deposits are in the northern Karoo Basin, and belong to the Vryheid Formation (middle Ecça Group).

Specimens of *O. hammanskraalensis* were recovered from the Hammanskraal refractory clay quarry, which is part of the Bushveld Basin. The sediments are considered to be Vryheid Formation equivalents (text-figs 2.2.2, 2.2.3a; 7.4.1a&b).

Deposits at both localities are considered to be Lower Permian in age (Artinskian).



**Text-figure 7.4.1.** (a) Locality map indicating reported occurrences of *Ottokaria* in South Africa; (b) lithostratigraphic table of the Permian and Lower Triassic deposits in the northern and eastern parts of the Karoo Basin, with shaded areas representing stratigraphic occurrences of *Ottokaria* (table adapted from Keyser, 1997).

#### 7.4.4 SYSTEMATIC PALAEOBOTANY

##### ***Type species***

*Ottokaria bengalensis* Zeiller 1902; Karharbari Basin, India

##### ***Etymology***

*Ottokaria* - after Ottokar Feistmantel, in recognition of his contribution to Gondwanan palaeobotany.

##### ***Emended generic diagnosis***

Solitary, dorsiventrally flattened, isobilateral, pedicellate fructification, comprising round to obovate receptacle with lobed to entire peripheral wing.

Receptacle round to obovate, with rounded apex and truncate, rounded or tapered base. Receptacle bifacial with veined, sterile surface and fertile surface with numerous circular to elliptical seed detachment scars. Sterile surface with dense, reticulate venation radiating from pedicel insertion.

Peripheral wing either surrounds receptacle or is discontinuous at pedicel insertion. Wing may be entire, dentate or denticulate, but is most commonly dissected into partially fused or deeply incised lobes, each lobe corresponding to the position of a marginal seed scar along periphery of receptacle. Lobes may be pointed to truncate or bluntly rounded, and bear fine striations perpendicular to receptacle margin.

Pedicel is longitudinally striated and in most cases, markedly expanded at junction with receptacle. Pedicel may be laterally or obliquely inserted.

## **Discussion**

Pant & Nautiyal's (1984) diagnosis is considered here to be most representative of the genus. However, although they acknowledged the dorsiventral, bifacial nature of the fructification, they also included cuticular features and details of seed anatomy. Since the vast majority of *Ottokaria* specimens are impression fossils, or compression fossils without cuticle preservation, these features were not considered to be practicable and were removed in this emendation.

*Ottokaria* may be a fairly diverse group of fructifications, and the lobed wing margin alone is an inadequate basis for distinction of the genus. Although this feature is well-represented in Zeiller's (1902) original specimen and in the South African species *O. transvaalensis*, the wing is almost entire, or only notched in other species such as *O. buriadica* and *O. hammanskaalensis*. The other important diagnostic character defining the genus is the very long pedicel which expands significantly near insertion into the receptacle, and which may give the receptacle base a broad, fan-shaped appearance.

### **7.4.4.1      *Ottokaria transvaalensis* Plumstead 1956 emend. Anderson & Anderson**

1985

1956 *Ottokaria transvaalensis* Plumstead, p. 214; pl. 33; pl. 34, figs 1, 2; pl. 35, figs 1-4; text-figs a, b; [Basionym]. [1956b].

1956 *Ottokaria buriadica* Plumstead, pars, p. 216, pl. 37, figs 1, 2. non pl. 37, figs 3-4. [1956b].

1978 *Ottokaria transvaalensis* Plumstead; Banerjee, p. 132.

1985 *Ottokaria transvaalensis* Plumstead; Anderson & Anderson, p. 114, pl. 61, figs 1-19; pl. 95, fig. 4; text-figs 114.1, 114.2, 111.4, 111.5.

## **Holotype**

An impression fossil, BP/2/13607a,b, housed at the Bernard Price Institute for Palaeontology, Johannesburg (pl. 43, figs (a) & (b) this document).

## **Paratypes**

Assigned by Plumstead (pl. 35, figs 1-4; 1956b): BP/2/13600a&b, BP/2/13622, BP/2/13647, BP/2/- (specimen described as 'O5' by Plumstead; not found in the BPI collections) (pl. 43, fig. (d); pl. 44, figs (h) & (i) this document).

## ***Etymology***

'*transvaalensis*' - after the old South African province, the Transvaal (now divided into the Northern Province, Mpumalanga and Gauteng - see text-fig. 2.2.2).

## ***Type formation and locality***

Vryheid Formation; Lower Permian (Artinskian); Leeukuil Quarries, Vereeniging, Karoo Basin, South Africa.

## ***Species diagnosis***

(Adapted from Anderson & Anderson, 1985).

Small (approx. 21 mm diameter) with circular to obovate receptacle and long (up to 45 mm) pedicel of even width; wing with deeply incised, bluntly rounded lobes.

## ***Description***

(See pls 43-44; pl. 48, fig. (a); Table A.II.4, Appendix II for data summary).

Isobilateral, dorsiventral ovuliferous fructification with a long pedicel. Receptacle with a lobed, peripheral wing. Overall dimensions (excluding pedicel) are: 14.3 (21.8) 29.6 mm long {n=22; SD: 3.7} and 14.8 (21.2) 30.1 mm wide {n=21; SD: 2.9}.

Receptacle is 10.7 (15.6) 20.1 mm long {n=21; SD: 2.7}, 9.4 (13.7) 17 mm wide {n=19; SD: 2.2}, with an area of 88 (166.4) 231 mm<sup>2</sup> {n=19; SD: 45.1} and a L:W of 0.9 (1.2) 1.4 {n=20; SD: 0.2}. Receptacle is sub-circular, obovate, elliptical to transversely elliptical, and is bifacial, with a sterile, veined surface and a seed-bearing fertile surface. Sterile surface bears anastomosing and bifurcating veins that form a coarse, fan-shaped mesh; veins bifurcate near the

receptacle margin producing prominent striae that continue onto the wing, where they delimit the edges of the wing lobes on either side of each marginal seed scar. Fertile surface has 35 (62.2) 87 {n=5; SD: 22.3} seed scars, at a density of 8 (9.8) 11 scars per 25 mm<sup>2</sup> {n=6; SD: 1.2}. In impression fossils, scars consist of a shallow depression bearing a raised elliptical cushion with an apical pit; 1.4 (2.2) 3.2 mm long {n=38; SD: 0.3}; 0.9 (1.5) 2 mm wide {n=35; SD: 0.3}.

Wing is divided into contiguous, longitudinally striated lobes, oriented perpendicular to receptacle margin; medial lobes are 2.4 (3.6) 4.6 mm long {n=23; SD: 0.5}, 1.6 (2.5) 3.7 mm wide {n=72; SD: 0.6}, apical lobes are slightly smaller with a length of 2.4 (3.4) 5 mm {n=24; SD: 0.6}, and a width of 1.3 (2.3) 3.6 mm {n=62; SD: 0.2}. Degree of lobe fusion is variable within a single specimen - may be separated to base, but usually fused in basal quarter to two thirds of lobe length. Lobes may be slightly tapered, and have apices that are truncated, slightly pointed, or (most commonly) bluntly rounded. Ratio of medial lobe length to receptacle width is 0.2 (0.3) 0.4 {n=22; SD: 0.1}.

Pedicel is longitudinally striated, 9.5 (26.3) 44.7 mm long {n=20; SD: 12.1}, with a basal width of 2.8 (3.6) 4.5 mm {n=17; SD: 0.5}, in some cases expanding slightly at insertion to 3.4 (4.5) 6.8 mm {n=19; SD: 0.9} where the ratio of receptacle width to pedicel width is 2.2 (3.1) 4.5 {n=17; SD: 0.7}. Impression of pedicel may overlap impression of fertile surface, which lies at a slightly lower level in the sediment.

No attached leaves or seeds have been found.

### **Comments**

This is the best represented species of South African *Ottokaria*, with over 25 well-preserved specimens in our collections.

The most important distinguishing feature of the species is the division of the peripheral wing into blunt, well-defined, deeply incised lobes, each lobe corresponding to a marginal seed scar.

The receptacle displays a great degree of variability in shape, from circular [e.g. pl. 44, figs (b), (c) & (f)] to obovate [e.g. pl. 44, figs (g), (h) & (i)].

*O. transvaalensis* is the smallest of the South African *Ottokaria* species, and unlike the other species, it does not have a pedicel that is prominently expanded near the receptacle.

Anderson & Anderson (1985) hypothesised, on the basis of associative evidence, that the fructification is axillary to a gangamopteroid scale leaf. However, no specimens have been found in organic attachment to a foliar organ.

#### **7.4.4.2      *Ottokaria hammanskraalensis* Anderson & Anderson 1985 emend.**

1985 *Ottokaria hammanskraalensis* Anderson & Anderson, p. 113, pl. 60, figs 1-7; pl. 95, fig. 3; text-figs 111.3, 113.1.

1997 *Ottokaria hammanskraalensis*; Anderson & Anderson, p. 15, fig. 3a.

#### ***Etymology***

'*hammanskraalensis*' - originating from the Hammanskraal locality.

#### **Holotype**

Part and counterpart of an impression fossil, GSP/H1/152a,b, housed at the Council for Geoscience, Pretoria.

#### ***Type formation and locality***

middle Eccra Group equivalent; Artinskian; Hammanskraal quarry, outlier of the Karoo Basin, Mpumalanga Province, South Africa.



### ***Emended species diagnosis***

Large (approx. 20 mm wide) sub-circular to transversely elliptical receptacle with narrow peripheral wing divided into shallow, blunt lobes; pedicel broadly expanded at insertion; seeds elliptical with distally elongated, narrowly ovate wing tapering to a point.

### ***Description***

Isobilateral, dorsiventrally flattened, pedicellate, ovuliferous polysperm comprising a central, seed-bearing receptacle with a lobed, peripheral wing.

Receptacle sub-circular to transversely elliptical, 14.7 (20.4) 23.4 mm long {n=4; SD: 4.0} and 11.3 (19.8) 25.4 mm wide {n=4; SD: 6.2} with a L:W of 0.9 (1.1) 1.3 {n=4; SD: 0.2} and an area of 290 (386) 440 mm<sup>2</sup> {n=3; SD: 83.4}.

Receptacle is bifacial, with a veined sterile surface (indistinct) and a fertile surface that bears circular seed scars, each represented by a shallow depression (in impressions) with a central tubercle; scars are 2.1 (2.5) 2.8 mm long {n=7; SD: 0.3} and 1.9 (2.1) 2.2 mm wide {n=4; SD: 0.1}.

Wing relatively narrow with weak radial fluting and striations; wing lobes fused for most of length, giving margin a notched appearance. Lobes correspond to positions of marginal seed scars on fertile surface of receptacle. Medial wing width is 2.8 (3.3) 3.7 mm {n=4; SD: 0.4}, with lobes 0.9 (1.3) 1.5 mm wide {n=5; SD: 0.2}, broadening in the apical region to 1.2 (1.9) 2.5 mm wide {n=6; SD: 0.5}. Ratio of medial wing width to receptacle width is 0.1 (0.2) 0.3 {n=4; SD: 0.1}. Wing is continuous along entire periphery of receptacle.

Pedicel bears prominent longitudinal striations, and is 13.1 (21.1) 31.5 mm long {n=4; SD: 7.7} with a basal width of 2.5 (3.3) 4.2 mm {n=5; SD: 0.8}, expanding at insertion to 4.3 (5.8) 7.1 mm {n=4; SD: 1.2}, where the ratio of receptacle width to pedicel width is 3.3 (3.6) 3.9 {n=3}. Pedicel insertion is at a slightly oblique angle, above and behind the apparently uninterrupted peripheral wing.

Impression of pedicel may overlap impression of fertile surface, which lies at a slightly lower level in the sediment.

Seeds have a long, narrowly ovate, striated wing tapering to an acute apex; they are fairly elliptical in overall shape. Seed dimensions are approximately 7 x 3.5 mm. All fructifications were isolated, with no attached leaves on record.

### **Comments**

Only a few, poorly preserved specimens of this taxon have been found. In several specimens it was difficult to determine whether the pointed projections along the periphery of the receptacle were attached, winged seeds, or pointed wing lobes. However in pl. 47, fig. (d), what appears to be the true wing is visible in the top right of the fructification (the top left in the counterpart [fig. (e)]). The wing is similar to that of *O. buriadica*, although it is notched, the notches delimiting very shallow, blunt lobes. The pointed structures visible along most of the periphery of the fructification are seed wings protruding beyond the edge of the wing. Note how they are at a lower level in the sediment than the receptacle or the wing fragments in the impression of the fertile surface [pl. 47, fig. (e)]. *O. hammanskraalensis* is similar to *O. buriadica* as far as receptacle size and shape are concerned, as demonstrated in text-fig. 7.4.5.

#### **7.4.4.3      *Ottokaria buriadica* Plumstead 1956**

1956 *Ottokaria buriadica* Plumstead, pars, p. 216, pl. 36, figs 1,2; pl. 37, figs 3-4.

non pl. 37, figs 1-2. [1956b].

1956 *Ottokaria buriadica* ?; Plumstead, p. 216, pl. 38, figs 1-4. [1956b].

1962a fructifications; Plumstead, p. 595, fig. 1.

1969 *Ottokaria buriadica* Plumstead; Plumstead, pl. 12, fig. 1.

1973 *Ottokaria buriadica* Plumstead; Plumstead, pl. 3, fig. 6.

1978 *Ottokaria ? buriadica* Plumstead; Banerjee, p. 133.

1985 *Ottokaria buriadica* Plumstead; Anderson & Anderson, p. 112, pl. 56,  
figs 1-12; pl. 95, fig. 2; text-figs 111.1, 111.2, 112.2, 112.3.

### ***Etymology***

'*huriadica*' – after *Gangamopteris huriadica* Feistmantel, which Plumstead (1956b) considered to be the subtending leaf of this fructification.

### ***Holotype***

Part and counterpart of an impression fossil, BP/2/13635a,b, housed at the Bernard Price Institute for Palaeontology, Johannesburg.

Plumstead (1956) assigned a specimen of *O. transvaalensis* as a paratype for *O. huriadica* - this has been excluded here.

### ***Type formation and locality***

Vryheid Formation; Lower Permian (Artinskian); Leeukuil Quarries, Vereeniging, Karoo Basin, South Africa.

### ***Species diagnosis***

(Adapted from Plumstead, 1956b).

Large (approx. 21 x 23 mm), round to ovate receptacle with a relatively narrow wing (wing width: receptacle width of 0.1); pedicel long, broad, prominently expanded at insertion, with a receptacle width to pedicel width ratio of three or less; wing margin entire or rarely denticulate.

### ***Description***

(See pls 45; 46; 47, figs (a)-(c); Table A.II.4, Appendix II for data summary).

Isobilateral, dorsiventral, ovuliferous fructification, 21.6 (27.2) 30.9 mm long {n=13; SD: 3.2} (excluding pedicel) and 19.5 (25.6) 31.1 mm wide {n=12; SD: 3.4}, comprising a seed-bearing receptacle with a peripheral wing, borne on a prominent pedicel.

Receptacle is broadly ovate to sub-circular, 17.2 (22.9) 27.9 mm long {n=13; SD: 3.2}, 15 (20.8) 25.6 mm wide {n=13; SD: 3.1}, with a L:W of 1.0 (1.1) 1.4 {n=13; SD: 0.1}, and an area of 200( 384.8) 573 mm<sup>2</sup> {n=13; SD: 101.8}. It is bifacial, with a sterile surface bearing a coarse reticulum of spreading venation, and a fertile surface bearing 79 (105) 138 {n=3; SD: 30.1} seed scars at a density of 5 (5.7) 6 scars per 25 mm<sup>2</sup> {n=3; SD: 0.6}. Seed scars are roughly circular, low cushions (in impressions) with a central tubercle and are 2 (2.7) 3.3 mm long {n=13; SD: 0.4} and 1.4 (1.8) 2.5 mm wide {n=11; SD: 0.4}.

Wing is continuous and of fairly even width along entire margin of receptacle. It is not contracted at pedicel insertion. Wing is fairly narrow relative to receptacle width, with medial width of 1.9 (2.7) 3.6 mm {n=14; SD: 0.6}, and a ratio of wing width to receptacle width of 0.1 (0.1) 0.2 {n=13; SD: 0.0}. Wing bears radial striations and fluting, and margin is entire, gently undulating or in some cases possibly denticulate.

Pedicel is 26.6 (41.8) 55.6 mm long {n=11; SD: 8.8}, and 4.1 (4.8) 5.8 mm wide {n=12; stdev:0.6} at base, expanding to 5.7 (8.9) 13.2 mm wide {n=12; SD: 2.3} at insertion, and bears prominent longitudinal striations. Ratio of receptacle width to maximum pedicel width is 1.6 (2.4) 3.1 {n=11; stdev: 0.5}, pedicel is therefore, on average, a half to a third as broad as receptacle. Pedicel insertion is at slightly oblique angle, above and behind the apparently uninterrupted peripheral wing.

Organic connection to a *Glossopteris* leaf has not been unequivocally demonstrated for this taxon, although the positioning and orientation of the polysperm relative to a closely associated leaf in the holotype (BP/2/13635a&b) is highly suggestive of attachment [see pl. 45, figs (b) & (c)]. The leaf in question is a gangamopteroid form of *Glossopteris*, with a broad region of well-defined veins in the medial portion of the lamina. Only the base of the leaf is preserved, but it is at least 41.4 mm wide, tapering into a broad, striated petiole (8.2 mm wide at base). The fructification appears to be attached to the top of the petiole, but may be axial. Veins dichotomise and arch away from the medial part of the lamina at a steep angle and then gently arch to the margin, with a

mid-laminal vein angle of 23° (23.3°) 24° {n=3; SD: 0.6}, and a marginal vein angle of 55° (58°) 61° {n=2; SD: 4.2}. Veins bifurcate and anastomose to form fine, elongate to falcate meshes, and have a marginal density of 24 veins per 10 mm.

### **Comments**

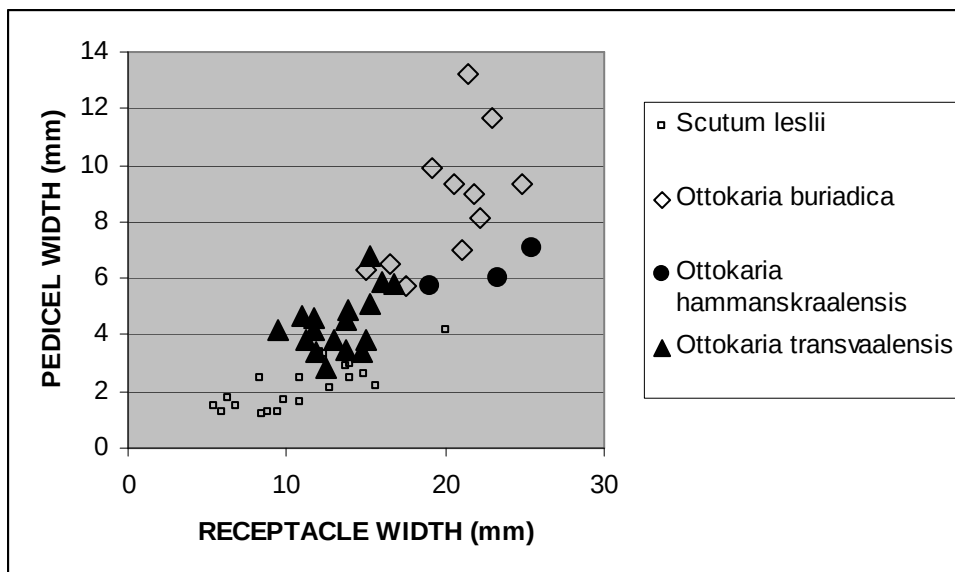
The main differences between *O. buriadica* and *O. transvaalensis*, as outlined by Plumstead (1956b), are that the former tends to be larger, with a smaller ratio of wing width to receptacle width, and it has a pedicel which is markedly expanded at insertion.

Unlike most other members of the genus, *O. buriadica* does not have well-defined wing lobes, and in most cases the wing margin appears to be entire. The taxon has been placed in *Ottokaria* on the basis of other diagnostic features, such as the long, broad pedicel that is prominently expanded at insertion, and the rounded receptacle. Scatter plots (see text-figs 7.4.2 - 7.4.4 below) clearly illustrate the close similarities between the other South African species of *Ottokaria* and *O. buriadica*, with respect to their receptacle and pedicel dimensions. As discussed below, it is possible that a more detailed characterisation of *O. buriadica* and *O. hammanskraalensis*, perhaps with the discovery of additional specimens, may result in the two taxa being synonymised in the future.

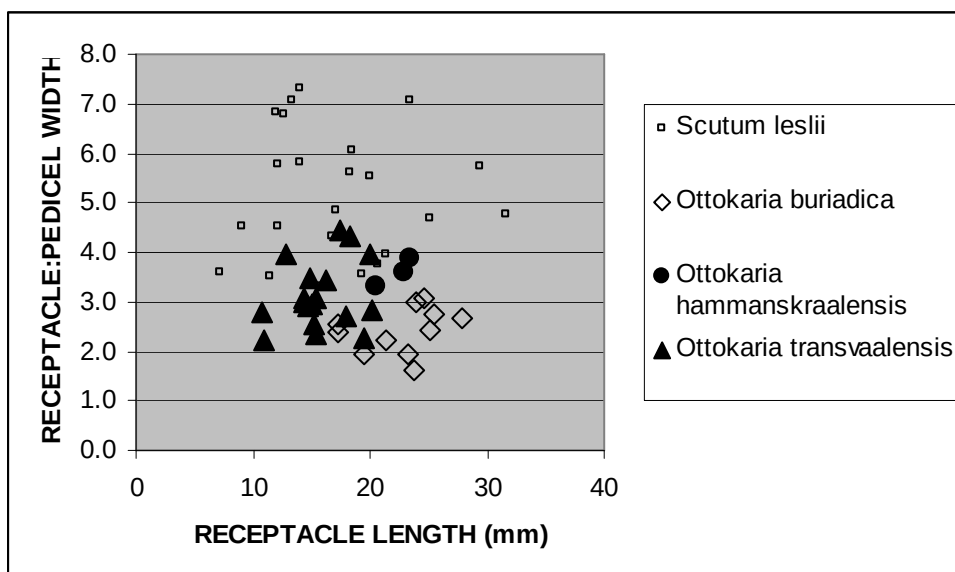
The impression of the pedicel of *O. buriadica* overlaps the impression of the fertile surface of the receptacle, which lies at a slightly lower level in the sediment. This overlapping is the result of the slightly eccentric insertion of the pedicel into the receptacle, and the continuation of the wing along the entire periphery of the receptacle.

#### 7.4.5 DATA ANALYSIS

Text-fig. 7.4.2 illustrates, as expected, that there is a positive correlation between receptacle width and pedicel width - the larger the fructification, the larger the pedicel. There is a slight overlap in the ranges of some of the taxa, but they each form a fairly distinct cluster, *Ottokaria buriadica* and *O. hammanskraalensis* being the largest specimens, and with *O. buriadica* having by far the largest pedicel widths.

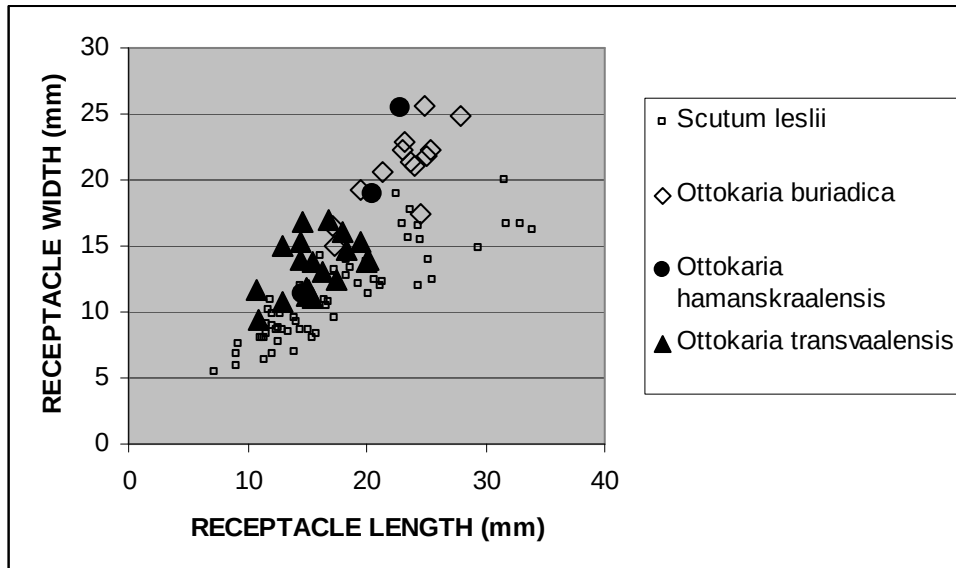


**Text-fig 7.4.2.** Scatter plot of receptacle widths against proximal pedicel widths of *Scutum leslii* and the three South African species of *Ottokaria*.



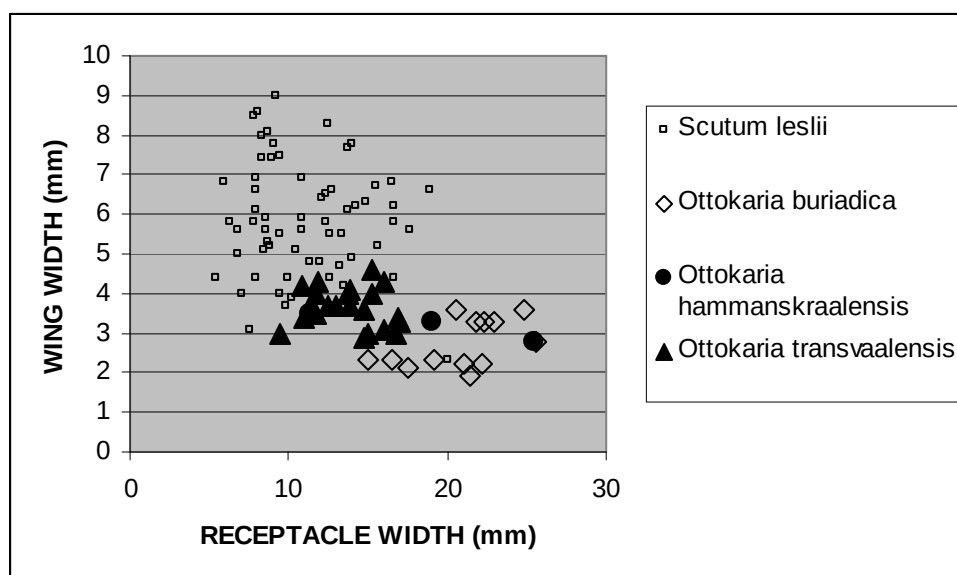
**Text-fig 7.4.3.** Scatter diagram of the ratio of receptacle widths to proximal pedicel widths, versus receptacle length, for *Scutum leslii* and the three South African species of *Ottokaria*.

Using the ratio of the receptacle diameter to the pedicel width, enables us to look at proportional rather than size differences. In text-fig. 7.4.3, all three species of *Ottokaria* are seen to have broad pedicels relative to their receptacle widths, and are fairly tightly clustered, compared with *Scutum*, which displays a greater degree of variability.



**Text-fig 7.4.4.** Scatter plot of receptacle dimensions for *Scutum leslii* and the three South African species of *Ottokaria*.

The differing linear correlations of the receptacle lengths to widths of *Ottokaria* and *Scutum leslii* in text-fig. 7.4.4 are a reflection of differences in shape - the species of *Ottokaria* tend to have rounder receptacles than *Scutum* specimens of the same size. Data points for *O. hamanskraalensis* and *O. buriadica* are clustered together, as a result of the similarities in size and shape of their receptacles. *Ottokaria transvaalensis* displays the same linear relationship between receptacle length and width, although the specimens are smaller. The receptacle lengths and widths of *Scutum leslii* do show a linear relationship, but it is not as tightly constrained as in the species of *Ottokaria*, and reflects a greater degree of diversity in receptacle shape, especially amongst larger specimens. Text-fig. 7.4.5 illustrates how *O. buriadica* and *O. hamanskraalensis* share similar size ranges, with *O. transvaalensis* being significantly smaller. The wing of *O. buriadica* tends to be narrower than in the other two species, but there is considerable overlap in their ranges. Note the high degree of variability in *Scutum leslii*.



**Text-fig 7.4.5.** Scatter diagram of receptacle width versus wing width of *Scutum leslii* and the three South African species of *Ottokaria*.

#### 7.4.6 DISCUSSION

Zeiller's (1902) type specimen of *O. bengalensis*, is very similar in appearance to *O. transvaalensis*, with a well-defined, rounded receptacle with a sterile and a fertile surface, and a peripheral wing which is divided into deeply incised lobes. It is attached by means of a long, slender pedicel to the midrib of a *Glossopteris* leaf, and the pedicel expands at insertion into the receptacle. Insertion is oblique, the fructification being eccentrically peltate.

Plumstead (1956b) discussed the close similarities between some of the Vereeniging specimens and *O. bengalensis*, but decided to place them in a new species, *O. transvaalensis*, 'in view of the great distance which separates the continents at present'. This in itself is not adequate reason for distinguishing between taxa, but since there are other differences such as the broader, blunter lobes and the less oblique insertion of the pedicel in *O. transvaalensis*, and the more fan-shaped appearance of *O. bengalensis*, these fructifications are probably best left in separate species.

Plumstead (1956b) seemed slightly disgruntled about the possibility of Zeiller's (1902) type specimens being in organic attachment to the midrib of a closely associated *Glossopteris* leaf. Both Plumstead (1956b) and Anderson &



Anderson (1985) considered *Ottokaria* to represent the fertile structure of gangamopteroid *Glossopteris* leaves (previously assigned to *Gangamopteris*). Lacey and Huard-Moine (1966) described examples of *Ottokaria*-like fructifications very similar to *O. bengalensis* and *O. transvaalensis* from Zimbabwe, which were found in close association with gangamopteroid leaf forms. The contradiction of a single genus of fructification attached to very different foliar types may be an indication that *Ottokaria* is not a well-constrained genus, or it may simply challenge our perceptions that diversity in the fertile structures of plants is usually greater than that expressed in vegetative parts such as the leaves.

*Ottokaria hammanskraalensis* is probably the least satisfactorily explained species of *Ottokaria* from South African. Smithies (1978) expressed considerable doubt regarding the morphology of this taxon, particularly with respect to the nature of the wing. She too considered the pointed features visible along the periphery of the receptacle to represent *in situ* winged seeds, and noted that in some specimens an 'entire denticulate or irregularly dentate rim' was visible. She reconstructed the fructification with this 'rim' as a narrow peripheral wing, such as that found in *O. buriadica*. Unfortunately, in the formal, published diagnosis of *O. hammanskraalensis* (in Anderson & Anderson, 1985) the pointed seed wings were taken to represent the deeply lobed wing of the fructification. Here Smithies' (1978) original description of the fructification is considered to be more accurate. In fact, *O. hammanskraalensis* shows striking similarities to *O. buriadica*, as graphically illustrated in text-figs 7.4.2- 7.4.5, and perhaps with the discovery of less obscure specimens of *O. hammanskraalensis* these taxa may prove to be conspecific.

A lobed wing is one of the most important diagnostic characters of the genus *Ottokaria*, so the absence of clearly defined lobes in *O. buriadica* and *O. hammanskraalensis* was a cause for concern - there was little separating these taxa from inclusion within *Scutum*. However, if we take pedicel and receptacle morphology into account, *O. buriadica* is definitely more closely affiliated to other members of *Ottokaria*, than to *Scutum*. This is clearly illustrated in text-figs

7.4.2 to 7.4.5, where data from the three South African species of *Ottokaria* show a high degree of clustering compared to the data points of *Scutum leslii*.

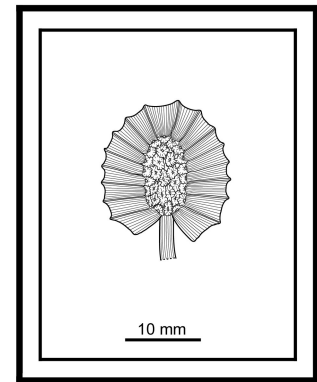
*Ottokaria* is a widespread glossopterid fructification, which has been reported from India (Zeiller, 1902; Seward & Sahni, 1920; Pant & Nautiyal, 1966, 1984), South America (White, 1908; Menéndez, 1962a; Dolianiti, 1971; Guerra -Sommer & Cazzulo-Klepzig, 2000), Australia (McLoughlin, 1990a; 1995), Southern Africa (Plumstead, 1956b; Lacey, 1959; Lacey and Huard-Moine, 1966; Smithies, 1978; Anderson & Anderson, 1985) and Madagascar (Singh & Shah, 1966). It is generally regarded as typical of Lower Permian sediments, although there have been some unusual reports of this genus from the Upper Permian (Banerjee, 1978; White, 1978; McLoughlin, 1990a).

Pant & Nautiyal (1984) gave a comprehensive account of *Ottokaria* specimens collected from the locality where the holotype specimen of Zeiller's (1902) *O. bengalensis* was found, in Giridih, India. They erected a new species, *O. zeilleri* to accommodate these new specimens. Unlike *O. bengalensis*, some of these specimens appear to have had a more fan-shaped receptacle, with somewhat reflexed basal lobes. Pant & Nautiyal (1984) distinguished the species mainly on account of *O. zeilleri* specimens being smaller and associated with different *Glossopteris* leaves. Although some of the specimens figured by Pant & Nautiyal (1984) have a well-defined receptacle and a lobed wing, most of them bear a close resemblance to certain species of *Arberia* (see section 6.1) They have a more laminate structure, and are more fan-shaped, without clear differentiation of a receptacle, and in some cases even have the characteristic apical dichotomy and opposite lateral branches typical of *A. minasica* and *A. madagascariensis* (e.g. pl. 5, fig 35, 37; pl. 8, figs 60, 61; pl. 9, fig. 63). Rigby (1972a) noted the similarities between Pant & Nautiyal's (1965, 1966) *Ottokaria*-like fructifications and *Arberia*, and synonymised some of them with *Arberia minasica*. This course of action was vigorously disputed by Pant (1977), who considered them to be 'in no way similar'. Pant & Nautiyal (1965, 1966, 1984) may have been describing a mixture of *Ottokaria* and *Arberia minasica* fructifications.

## 7.5 *SCUTUM* Plumstead 1952 emend.

### 7.5.1 INTRODUCTION

*Scutum* and *Lanceolatus* (= *Plumsteadia*) were the first genera of ovuliferous glossopterid fructifications to be described by Plumstead in her landmark 1952 paper. It was through the examination of these fructifications from Vereeniging that Plumstead (1952, 1956a,b, 1958a) developed her theories on a bicupulate, bivalved, bisexual fructification which proved to be so controversial in the years to follow.



*Scutum leslii*

Plumstead (1952) initially recognised five species of *Scutum* from the Vereeniging locality, on the basis of fructification morphology and perceived differences in attached leaves, which she assigned to various existing species of *Glossopteris* from other parts of Gondwana. Later Plumstead (1958a) transferred some of these early species into *Hirsutum*, eventually settling on six species of *Scutum* in the Vereeniging material, viz. *S. leslium*, *S. rubidgeum*, *S. stowanum*, *S. sewardii*, *S. thomasii* and *S. damudica*. Plumstead (1958a) also created varieties of *S. rubidgeum* and *S. leslium*, but these have never gained acceptance.

Anderson & Anderson (1985) revised the genus, acknowledging its dorsiventral, unipartite structure, and retained two of Plumstead's (1952) species, *S. rubidgeum* and *S. draperium*. They also created an additional species *S. ermeloense* to accommodate new specimens from the Ermelo locality.

The findings of this investigation are that the South African *Scutum* species constitute a morphological continuum, and that the interspecific differences in attached leaf morphology as described by Plumstead (1952, 1958a), are unconvincing. As a result, the species of Plumstead (1952, 1956a, 1958a) and

Anderson & Anderson (1985) have been incorporated into a single species, *S. leslii*<sup>6</sup>.

The genus *Scutum* has a very broad circumscription, accommodating a wide range of sizes, shapes and wing morphologies. There is potential for overlap with broad-winged members of *Plumsteadia* in particular. Generally speaking, *Scutum* has a fairly small length to width ratio, compared to the commonly more elongated forms seen in members of *Plumsteadia*. The wing of *Scutum* fructifications tends to be broader with more intensely developed fluting and scalloping of the margin. *Scutum* is distinguished from *Gladiopomum* on the basis of its generally lower length to width ratio, and its wing which is uninterrupted at the apex and which has well-developed, persistent fluting.

*Scutum* has a relatively broad geographical distribution, having been found in Australia (McLoughlin, 1990b) and India (Surange & Chandra, 1974a).

### 7.5.2 FOSSIL MATERIAL

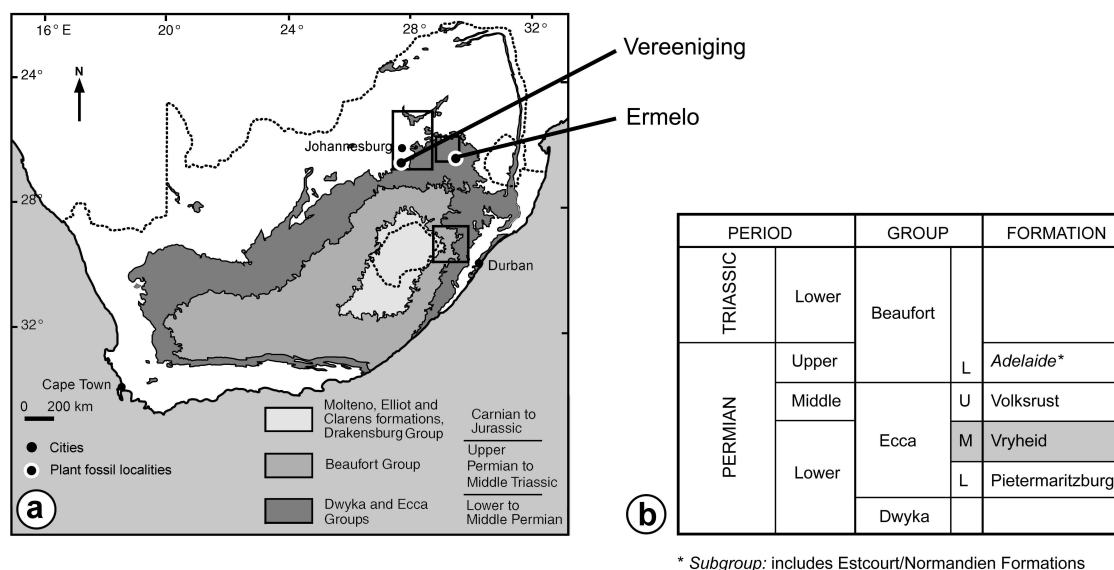
All specimens are impression fossils, and are housed at the BPI for Palaeontology, University of the Witwatersrand, Johannesburg, and the Vaal Teknorama Museum at Vereeniging (see Table A.I.9, Appendix I).

### 7.5.3 LOCALITY INFORMATION

Specimens were derived from the Leeukuil quarries at Vereeniging, and the fossil plant locality at Ermelo. Both localities are situated in the northern Karoo Basin [text-figs 2.2.2, 2.2.3 (b)]. The deposits are Vryheid Formation, middle Eccu Group and are from the Lower Permian (Artinskian) (text-fig. 7.5.1 a&b below).

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<sup>6</sup> '*Scutum leslii*' is considered here to have priority over Anderson & Anderson's (1985) *S. rubidgeum*, as it was the first of the *Scutum* species to be described in Plumstead's 1952 publication. The taxon was originally called '*S. leslium*' by Plumstead (1952), but was later modified to '*S. leslii*' (Andrews, 1970), which according to Prof. H.J. Lam (Discussion, p. 226 in Plumstead, 1956b) is the correct genitive of the Latinised name for 'Leslie'.



**Text-figure 7.5.1.** (a) Locality map indicating reported occurrences of *Scutum leslii* in South Africa; (b) lithostratigraphic table of the Permian and Lower Triassic deposits in the northern and eastern parts of the Karoo Basin, with shaded areas representing stratigraphic occurrences of *Scutum leslii* (table adapted from Keyser, 1997).

## 7.5.4 SYSTEMATIC PALAEOBOTANY

### *Type species*

*Scutum leslii* (Plumstead 1952) *nom. corr.* by subsequent designation of Andrews (1970); Vryheid Formation, middle Ecca Group; Early Permian; Vereeniging, northern Karoo Basin, South Africa.

### *Etymology*

Latin: 'scutum' - shield; referring to the shape of the fructification.

### *Emended generic diagnosis*

Solitary, pedicellate, isobilateral, dorsiventral polysperm borne proximally on midrib or petiole of otherwise unmodified glossopterid leaf. Multi-ovuliferous receptacle bifacial, with fertile surface bearing numerous seed scars facing subtending leaf; sterile surface laminate with spreading, reticulate venation. Receptacle circular, elliptical, obovate or ovate to broadly lanceolate. Receptacle flanked by prominent wing, continuous and of regular diameter,

except at point of pedicel insertion where it is sharply constricted to form a rounded or laterally truncated lobe to either side of pedicel. Wing with fine radial striations and prominent fluting perpendicular to margin of receptacle and extending from receptacle to wing margin. Margin dentate, undulating, scalloped or entire. Wing fluting corresponds to venation on sterile surface of the receptacle, and to positions of marginal seed scars which are square and form a distinctive rank along periphery of receptacle. Central seed scars tend to be oriented longitudinally to receptacle. Scars are raised cushions (in impressions), each with a central depression bearing a tubercle which represents a seed detachment scar. Seeds are ovate, flattened, typically small, (c.4 mm long, 2.5 mm wide), with a narrow to prominent wing. Pedicel slender, striated. Subtending leaf variable: elliptical, oblong to narrowly oblanceolate, with cuneate base tapering into a long, narrow petiole, or decurrent base which may be slightly expanded at base of leaf into small, inconspicuous, sagittate lobes; leaf apex moderately acute. Veins diverge from well-defined and persistent midrib at a steep angle, arching gently across lamina at an angle of 40 - 70°. Meshes elliptical to elongate polygonal near midrib, becoming linear in mid-laminal and marginal regions.

### ***Discussion***

This emended diagnosis differs from that of Anderson & Anderson (1985) in that the numerous 'ovules' with 'small circular micropyle exposed at centre of free end' on the fertile surface of the receptacle are re-interpreted as impressions of depressed seed scars, each with a central cicatrix, the mature seeds having been dispersed prior to preservation of the fructification. Anderson & Anderson (1985) described the wing as comprising a 'fused outer ring of modified ovules'. This is disputed, and the wing is considered to be a peripheral extension of the edge of the receptacle, continuous with the sterile surface. Veins extend from the edge of the receptacle into the wing where they form radial ridges or grooves between the wing flutes. On the fertile surface, the fine wing striations originate at the cicatrix of each marginal seed scar.

There is a large degree of variability in size and shape of the subtending leaves, of the South African *Scutum* species, although the venation appears to be fairly consistent. The leaf bases of the fertiligers of *S. leslii* tend to be poorly preserved, and in many cases it is not clear whether the bases of the leaves are slightly expanded or whether they are differentiated into sagittate lobes. Fructifications borne on leaves with sagittate bases do not appear to differ morphologically from those borne on leaves lacking this feature.

#### 7.5.4.1 ***Scutum leslii*** Plumstead 1952 emend. Anderson & Anderson 1985

- 1952 *Scutum leslium* Plumstead, p. 286, pl. 43, figs 1, 2; pl. 44, figs 1-4; text-figs 1a,b.
- 1952 *Scutum rubidgeum* Plumstead, p. 295, pl. 46, figs 1-4; pl. 47, figs 1-3; text-fig. 3.
- 1952 *Scutum draperium* Plumstead, p. 298; pl. 48, figs 1-4; text-fig. 4.
- 1956 *Scutum leslium* Plumstead; Plumstead, p. 6, pl. 1, fig. 1; pl. 2, figs 1, 2; pl. 3, figs 1-5; pl. 4, fig. 1; pl. 10, figs 1, 2. [1956a].
- 1956 *Scutum draperium* Plumstead; Plumstead, p. 9, pl. 8, figs 1-4. [1956a].
- 1956 *Scutum rubidgeum* Plumstead; Plumstead, p. 7, pl. 4, fig. 1; pl. 5, figs 1-3; pl. 9, figs 3, 4 [1956a].
- 1958 *Scutum stowanum* Plumstead, p. 55, pl. 7. [1958a].
- 1958 *Scutum rubidgeum* var. *vaalense* Plumstead, p. 55, pl. 8, figs 1, 1a; pl. 9, figs 1, 2. [1958a].
- 1958 *Scutum leslium* var. *cornelium* Plumstead, p. 57, pl. 10, figs 1-5a. [1958a].
- 1958 *Scutum damudica* Plumstead, p. 57, pl. 11. [1958a].
- 1958 *Scutum sewardii* Plumstead, pars. p. 59, pl. 13, fig. 2; non. figs 1, 1a. [1958a].
- 1958 *Pluma longicaulis* Plumstead, p. 68, pl. 22; pl. 23, figs 1, 2. [1958a].
- 1963 *Scutum*; Plumstead, p. 150; pl. B, fig. 2.
- 1969 *Scutum rubidgeum* Plumstead; Plumstead, pl. 12, fig. 4.
- 1969 *Scutum leslium* Plumstead; Plumstead, pl. 12, fig. 4; text-fig. 3.
- 1973 *Scutum rubidgeum* Plumstead, pl. 3, figs 3, 9.
- 1985 *Scutum rubidgeum* Plumstead; Anderson & Anderson, p. 116, pl. 67, figs 1-21; pl. 68, figs 1-13; pl. 95, fig. 5; text-figs 115.1, 115.2, 115.5, 115.6, 116.1, 116.2, 116.4.
- 1985 *Scutum draperium* Plumstead; Anderson & Anderson, p. 117; pl. 71, figs 1-6; pl. 72, figs 1-2; pl. 95, fig. 6; text-figs. 117.1, 117.2.
- 1985 *Scutum* spp.; Anderson & Anderson, pl. 74, figs 1-5.
- 1985 *Scutum ermeloense* Anderson & Anderson; p. 117; pl. 73, figs 7-12; pl. 95, fig. 7; text-figs 115.8, 117.4
- 1997 *Scutum rubidgeum* Plumstead; Anderson & Anderson, p. 15, fig. 4a,b,d.

#### **Holotype**

In her original description of the species *Scutum leslii*, Plumstead (1952) assigned two type specimens, L.I.1 & L.I.4. These syntypes were subsequently re-registered as BP/2/13732 & BP/2/13751, and are housed at the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg. Both are impression fossils of fertiligers; BP/2/13732 bears an impression of the sterile surface of the fructification, BP/2/13751 an impression

of the fertile surface. The latter specimen, BP/2/13751, is recognised here as the holotype.

### ***Etymology***

'*leslii*' - after Thomas Nicolas Leslie (1858-1942), an amateur palaeobotanist who made large collections of fossil plants at the Vereeniging locality.

### ***Type formation and locality***

Vryheid Formation (middle Ecca Group); Lower Permian (Artinskian); Vereeniging and Ermelo, northern Karoo Basin.

### ***Species diagnosis***

(Adapted from Anderson & Anderson, 1985).

Circular, elliptical, ovate, obovate to broadly lanceolate receptacle, with a L:W of 1.1-2.1; wing broad (>2.5 mm wide), with prominent and persistent striations and fluting. Seeds of the *Indocarpus* type, with a small, elliptical sclerotesta, flanked distally by an elongated, elliptical to falcate, apically pointed, striated wing. Attached in basal portion of a narrowly elliptical to oblong *Glossopteris* leaf, with a long, tapering base, moderately acute to obtusely pointed apex, and a well-defined, persistent midrib; may be petiolate, or base may expand slightly into small, inconspicuous, sagittate lobes; veins diverge from midrib at steep angle, gently arch across lamina at 24° (48°) 75°; meshes elliptical to elongate polygonal near midrib, becoming linear in mid-laminal and marginal regions.

### ***Description***

(See pls 49-58; Table A.II.5, Appendix II for data summary).

Isobilateral, dorsiventral, multi-ovuliferous glossopterid fructifications comprising a central, seed-bearing receptacle and a peripheral wing. Fructifications are



pedicellate, and are attached to the midrib of an apparently unmodified *Glossopteris* leaf. Overall dimensions of the polysperms (excluding the pedicel) are 12.9 (24.6) 38.4 mm long {n=58; SD: 6.1}, and 11 (21.9) 31.5 mm wide {n=63; SD: 4.2}.

Receptacles are highly variable in shape, ranging from circular, elliptical, ovate, obovate to broadly lanceolate (see pl. 58), and are 7.2 (17.5) 33.9 mm long {n=62; SD: 6.3} and 5.4 (11.2) 20 mm wide {n=65; SD: 3.4}, with a L:W of 1.1 (1.5) 2.1 {n=60; SD: 0.3}, and an area of 38 (159.4) 470 mm<sup>2</sup> {n=52; SD: 101.2}. Receptacle is bifacial with a sterile and a fertile surface: sterile surface bears coarsely anastomosing venation [pl. 57, figs (d)-(f)]; fertile surface bears approximately 35 (101.9) 300 {n=26; SD: 69.4}, closely spaced seed scars at a density of 8 (16.5) 35 scars per 25 mm<sup>2</sup> {n=31; SD: 5.5}. Seed scars are represented in impressions by raised, radially striated, polygonal, elliptical to circular cushions with a central depression containing a tubercle; scars 0.6 (1.1) 1.7 mm wide {n=103; SD: 0.2} and 1 (2) 3.2 mm long {n=156; SD: 0.5}. Marginal seed scars tend to be more rectangular, and are aligned into a conspicuous rank along the periphery of the receptacle.

Wing is conspicuous, with a medial width of 2.3 (5.8) 9 mm {n=66; SD: 1.4}, and is continuous along the periphery of the receptacle except at the base, where it is sharply constricted, forming a rounded or laterally truncated lobe (1.8 (4.2) 7 mm deep {n=47; SD: 1}) to either side of the pedicel. The ratio of wing width to receptacle width is 0.1 (0.6) 1.2 {n=64; SD: 0.2}. The wing bears prominent radial fluting and striations. Fluting is delimited in impressions by grooves on the fertile surface, ridges on the sterile surface (of impressions). These grooves or ridges correspond to the junctions between marginal seed scars and the exit points of veins from the receptacle into the wing on the sterile surface. Wing margin is usually poorly preserved and incomplete, but may be clearly dentate [e.g. pl. 49, fig. (b)], gently scalloped or entire. When dentate, the mid-line of each narrow, pointed 'tooth' corresponds to the groove/ridge that runs from the junction between two adjacent seeds scars to the wing margin.

Pedicel is 3.5 (9.9) 36 mm long {n=32; SD: 5.7}, with basal width of 1 (1.8) 3.3 mm {n=10; SD: 0.7}, expanding slightly to 1.2 (2.3) 4.2 mm {n=29; SD: 0.7} at

point of insertion into receptacle; long, striated, associated with a prominent abscission scar in the midrib at point of attachment to subtending leaf.

Fructifications are attached to the top of the petiole or to the midrib (basal quarter) of a narrowly elliptical to oblong *Glossopteris* leaf, 45.8 (105.3) 258 mm long {n=11; SD: 62.8} and 14.6 (26.2) 44.3 mm wide {n=14; SD: 8.8}, with a long, tapering base and moderately acute to obtusely pointed apex. Leaf base is variable, in some cases cuneate with a well-defined, 29.7 to 49.5 mm long, 2.1-5.8 mm wide petiole [e.g. pl. 49, fig. (f)], or lamina may taper at base without delimitation of a petiole, in some cases expanding slightly into small, inconspicuous, sagittate lobes [e.g. pl. 49, fig. (i)]. Midrib is 0.3 to 5 mm thick, well-defined and persistent to apex. Veins arise from midrib at a steep angle, and arch gently across the lamina to the margin, with a mid-laminal vein angle of 24° (48°) 75° {n=27; SD: 15.6}, a marginal vein angle of 56° (67.5°) 79° {n=28; SD: 7.2}, and a marginal vein density of 18 (26.4) 32 veins per 10 mm {n=11; SD: 5.1}; in some cases veins follow a straight course across distal two thirds of the lamina. Meshes elliptical to elongate polygonal near midrib, becoming linear in mid-laminal and marginal regions.

Seeds generally indistinct, but apparently with an elliptical sclerotesta 2 (3) 4.8 mm {n=17; SD: 0.8} long and 1.5 (2.4) 4.5 mm {n=17; SD: 0.8} wide, and a distally elongated, elliptical to falcate, finely striated wing, at least 6.4 (12.1) 23.5 mm long {n=41; SD: 4} and 1.9 (3.6) 5.1 mm wide {n=53; SD: 0.8}. Seed details obscured in many cases by overlying impression of the wing and receptacle, resulting in a fringe of bract-like wings protruding from the margin of the fructification [pls 54 & 55; pl. 57, figs (a), (b)].

### **Comments**

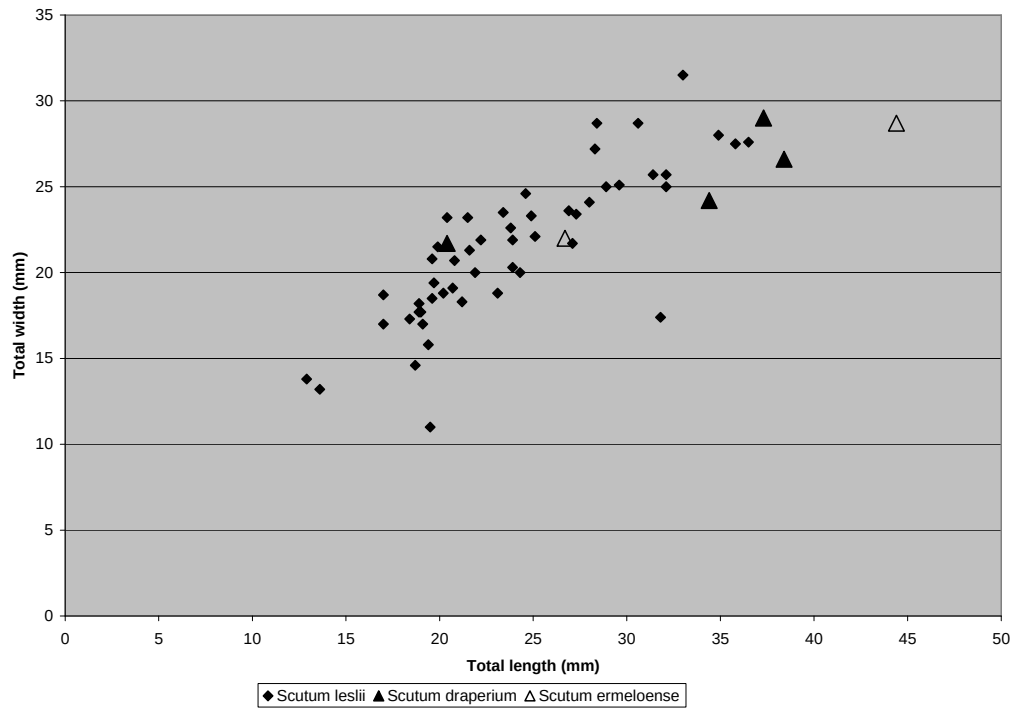
As demonstrated in pl. 58, members of this species are highly variable in both size and shape, and wing morphology. The wing margin varies from entire to scalloped to dentate, although in all cases the wing fluting is persistent and pronounced. Receptacles are highly variable in size and range in shape from

circular to elliptical, obovate to ovate to broadly lanceolate, with rounded, truncated to slightly cordate bases.

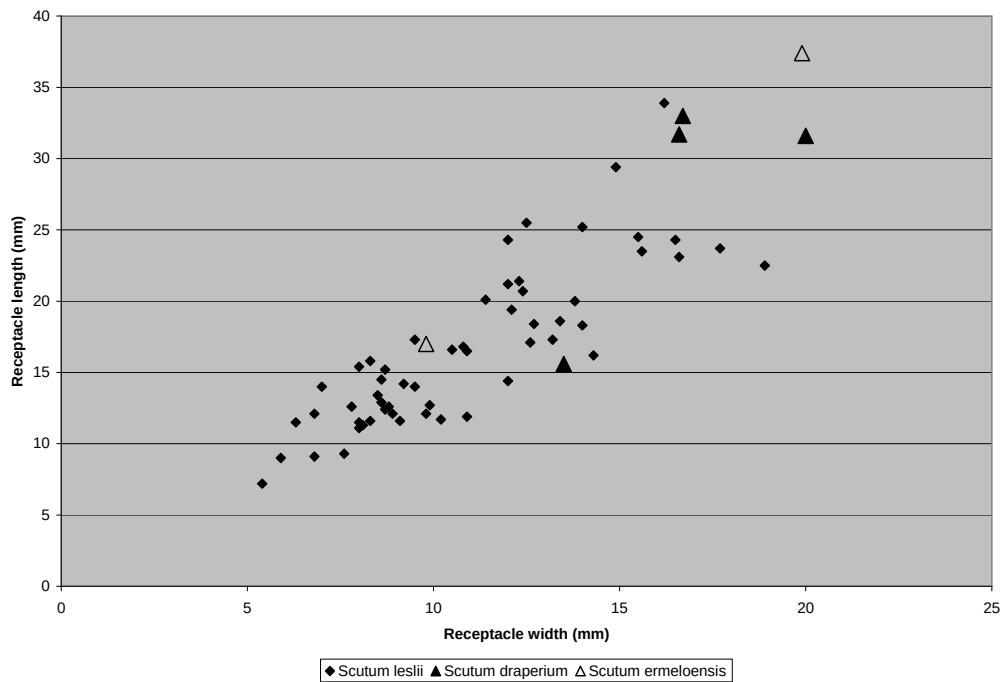
The elongate, bract-like structures interpreted here as seed wings, were difficult to observe, as they lie at a lower level in the sediment than the receptacle. In many cases it was only possible to measure the section of wing protruding beyond the edge of the fructification.

### **7.5.5 DATA ANALYSIS**

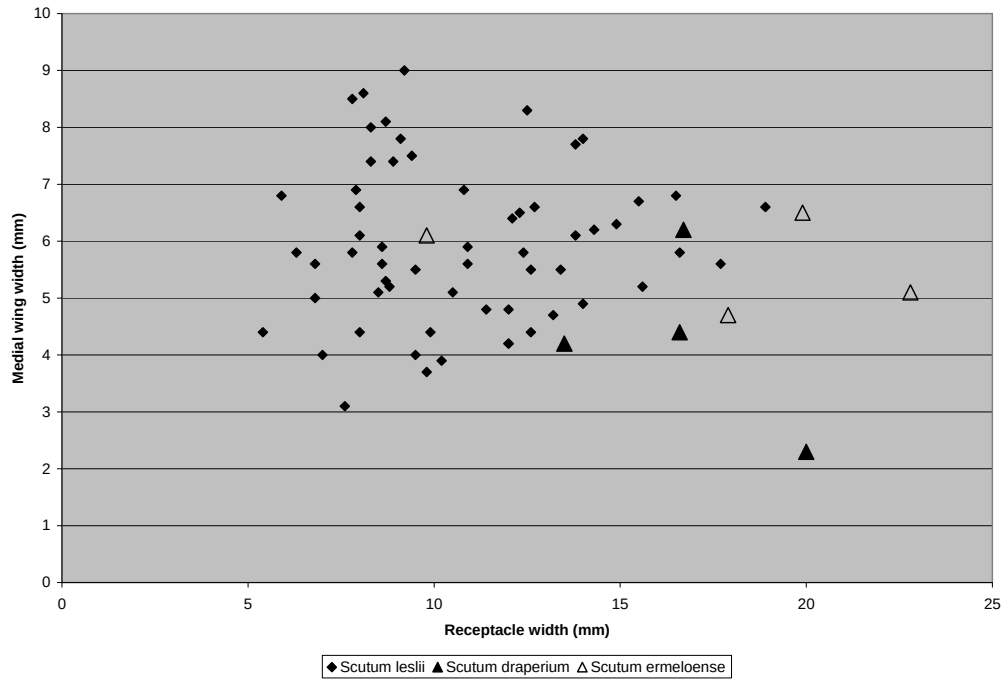
Scatter plots were constructed to assess the relationships between specimens previously assigned to *S. draperium* and *S. leslii* (Plumstead, 1952, 1956a, 1958a; Anderson & Anderson, 1985), and those specimens from Ermelo, placed in *S. ermeloensis* by Anderson & Anderson (1985). Text-figs 7.5.2-7.5.5 demonstrate that *S. leslii* specimens form a distinct group with a high degree of continuous variation as far as the dimensions of the receptacle and wing are concerned. Specimens previously attributed to *S. draperium* represented the upper size limits of the group, with a single, particularly large specimen of *S. ermeloense* being the only isolated data point on the plots. A second specimen of *S. ermeloense* fell well within the ranges occupied by *S. leslii*. Plots of wing width versus receptacle width (text-fig. 7.5.4) and receptacle area (text-fig. 7.5.5) produced an interesting result - the wing width is remarkably constant, irrespective of the overall size of the fructification or width of the receptacle.



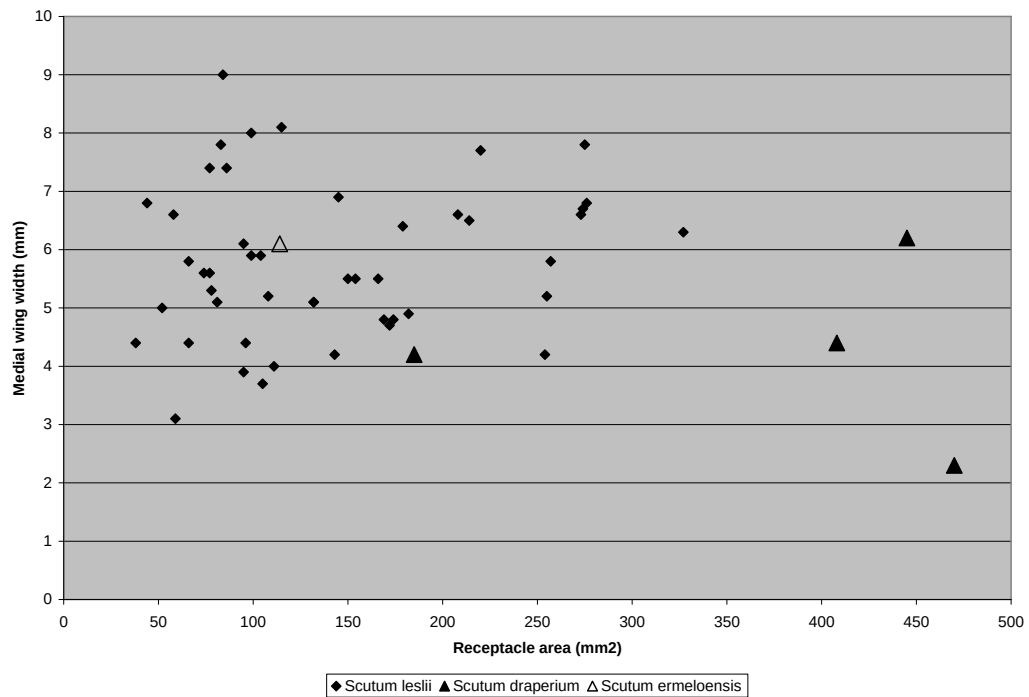
**Text-figure 7.5.2.** Scatter plot of total lengths against total widths of specimens here assigned to *S. leslii*, but distinguishing those previously assigned to *S. draperium* and *S. ermeloensis*.



**Text-figure 7.5.3.** Scatter plot of receptacle lengths against receptacle widths of specimens here assigned to *S. leslii*, but including those previously assigned to *S. draperium* and *S. ermeloensis*.



**Text-figure 7.5.4.** Scatter plot of medial wing widths versus receptacle widths of specimens here assigned to *S. leslii*, but including those previously assigned to *S. draperium* and *S. ermeloense*.



**Text-figure 7.5.5.** Scatter plot of medial wing widths versus receptacle areas of specimens here assigned to *S. leslii*, but including those previously assigned to *S. draperium* and *S. ermeloense*.

### 7.5.6 DISCUSSION

*Scutum* perhaps displays the greatest degree of morphological diversity of any member of the Dictyopteridiaceae. The variety of wing and receptacle shapes and dimensions from the single locality at Vereeniging is illustrated in pl. 58.

The high degree of morphological variability in Plumstead's (1952, 1956a, 1958) and Anderson & Anderson's (1985) species, predisposed them for synonymisation. By their own admission, the distinctions made were more distinctions of degree, in quantitative features, rather than qualitative ones, and the ranges of the quantitative features overlapped.

Anderson & Anderson (1985) noted that there was a morphological continuum between the polysperms of *S. rubidgeum* (= *S. leslii*) and *S. draperium*, but considered their attached leaves to be 'perfectly distinct'. However, apart from the sagittate base in leaves attached to *S. rubidgeum*, the descriptions of the leaves in these two taxa appear to be remarkably similar. Even the sagittate base is not a good distinguishing feature, as it is not apparent in all of the fertiligers assigned by Anderson & Anderson (1985) to *S. rubidgeum*.

The large sizes and apparently entire wing margin the specimens from Ermelo, may reflect regional variation within the species. On the other hand, we cannot be sure that the Ermelo specimens do in fact have an entire margin, as none of them have any section of wing margin that is complete and undamaged. In some cases, the margin appears to be gently scalloped rather than entire. A scalloped or dentate margin could not be demonstrated for most of the Vereeniging specimens, mainly because of poor preservation of the apparently delicate wing margin, and could therefore not be used as a diagnostic character for the species. This uncertainty contributed to the decision to synonymise *S. ermeloense* with *S. leslii*.

Anderson & Anderson (1985) distinguished *S. ermeloense* and *S. draperium* on the basis of differences in their subtending *Glossopteris* leaves. Unfortunately, the subtending leaf of the Ermelo specimens is unknown, and Anderson &

Anderson (1985) therefore made this distinction on the basis of associated leaf material alone. Text-figs 7.5.2-7.5.5 illustrate the strong similarities in size ranges between those specimens previously assigned to *S. draperium* and *S. ermeloense*. The view held here is that these specimens represent the upper size limits of a single species, *S. leslii*. This distinct clustering of the three '*S. draperium*' specimens in text-fig. 7.5.5 may be an indication that there is more to this story.

Plumstead referred the leaves attached to the different species of *Scutum* she described (1952), to existing species of *Glossopteris* from other parts of Gondwana. Her descriptions were, on the whole, very vague and emphasised the high degree of intraspecific variability that she observed. She generally attributed the leaves to the various species on the grounds of them looking very similar, without further elaboration or comparison.

The elongated, bract-like structures found attached to some specimens of *S. leslii* from Vereeniging [pls 54 & 55; pl. 57, figs (a), (b)], were considered by Plumstead (1956a, 1958a) to represent pollen-bearing organs, equivalent to the purported hair-like structures she described in *Hirsutum*. These hair-like features are striations on the wing, and there is no evidence to suggest that any of the glossopterid fructifications were bisexual (see section 3.2). Although Plumstead (1956a) claimed to have isolated clusters of pollen grains from these structures, all the Vereeniging specimens are impression fossils with little or no organic material present, and it seems unlikely that such a precise extraction of pollen was feasible.

Anderson & Anderson (1985) were unsure about the nature of the 'scale-like appendages' attached to *S. leslii*, but did not consider the possibility that they were winged seeds. Perhaps this was in light of their interpretation of the wing of the fructification as being a series of modified ovules. Here, these structures are provisionally considered to be the elongated wings of platyspermic seeds. Although detached seeds of this nature have never been found at the Vereeniging locality, isolated seeds similar to these have been found in India. Surange & Maheshwari (1970) reported several 'ovule-bearing scales' which

resembled the structures found attached to *Scutum leslii* fructifications. Surange & Chandra (1974a) described further examples of seeds with an elongated wing at the micropylar end of an ovate sclerotesta. They assigned these seeds to *Indocarpus elongatus*.

Plots of overall size and receptacle dimensions for the South African *Scutum* specimens showed a typically linear relationship between length and width, as expected (text-figs 7.5.2, 7.5.3). However, the '*S. draperium*' specimens seem to have a slightly different correlation co-efficient. They also consistently occupy the upper size ranges of *S. leslii*, although one of the specimens is well nested within the middle ranges of the taxon. Considering the broad and gradational nature of the variation in *S. leslii*, it is more likely that the specimens selected for inclusion in *S. draperium* by Plumstead (1952, 1956a, 1958a) and Anderson & Anderson (1985), were chosen because they lie at one end of the size spectrum, and when compared with moderate specimens and those at the other end of the range they appear to be dramatically different. The consistency in wing width, irrespective of receptacle size, would also contribute to a large but superficial difference in the appearance of fructifications at the two ends of the size spectrum.

The even spread of receptacle size and wing width data, unequivocally supports Anderson & Anderson's (1985) decision to merge *S. leslii* (*S. leslium*) and *S. rubidgeum*.

Unfortunately very few specimens of *Scutum* have been recovered from the Ermelo site, so any meaningful assessment of the range of fructification morphology is not possible. What is apparent from text-figs 7.5.2-7.5.5, is that there is at least some overlap with the *S. leslii* specimens from Vereeniging, and until additional specimens are found at Ermelo to provide more convincing proof that these specimens belong within their own species, they have been grouped within *S. leslii*.



The genus *Scutum* has a particularly broad diagnosis, and a wide range of specimens may potentially be accommodated within this taxon. It is therefore unlikely to be useful as a biostratigraphic indicator.

Surange & Chandra (1974a) described a beautifully preserved ovuliferous fructification from the Raniganj Stage of India (Handappa, Orissa), which they assigned to *Scutum sahnii*. The holotype differs from *S. leslii* in having a narrow wing with weakly developed, radial fluting. The wing margin is entire. It falls well within the size ranges for *S. leslii*. Surange & Chandra (1974a) described two additional new species, *Scutum elongatum*, and *S. indicum*. These taxa, with their large length to width ratios, may be better assigned to *Plumsteadia*. Chandra & Surange (1977a) also described a new genus, *Venustostrobus*, which could probably be included within *Scutum*. The rounded receptacle and prominently fluted wing are highly reminiscent of the genus.

## 7.6 GLADIOPOMUM Adendorff et al. 2002

### 7.6.1 INTRODUCTION

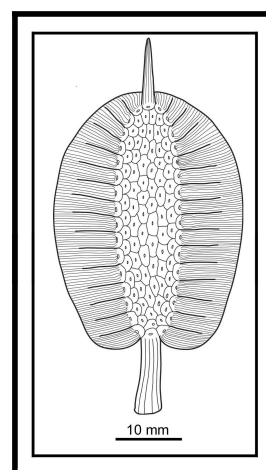
*Gladiopomum* was recently created (Adendorff et al., 2002<sup>7</sup>) to accommodate a group of Lower Permian capitate fructifications with a broad, radially striated wing and an elongated, sword-shaped receptacle bearing an apical spine. These were features that had not been recognised during their original diagnosis and description as *Hirsutum dutoitides* by Plumstead (1956a, 1958a) and later by Anderson and Anderson (1985). In fact, the description by Anderson & Anderson (1985), incorporated none of the key diagnostic characters of the genus, even though it was the type species for *Hirsutum*. As discussed in Chapter 3 (and Appendix IV), the genus *Hirsutum* has been contentious since its inception, and moving the type species *H. dutoitides* and *Hirsutum acadarensense* Anderson & Anderson 1985 to *Gladiopomum* has hopefully helped resolved the issue.

See Section 3.2 for a detailed historical account of this taxon and for explanations regarding the morphological interpretations used in the following diagnosis.

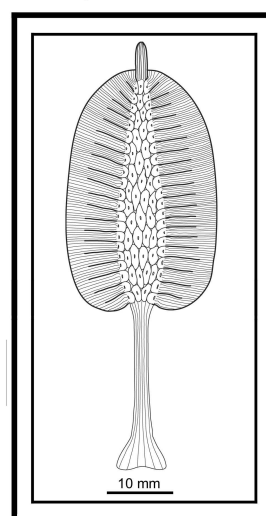
### 7.6.2 FOSSIL MATERIAL

(Adapted from Adendorff et al., 2002)

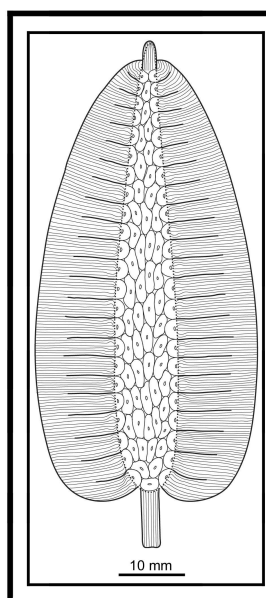
All fossils were in the form of impressions although there were some carbonaceous residues in the Rietspruit material (no cuticle was recovered). Most of the specimens from the Vereeniging locality were derived from previous collections housed in the fossil herbarium at the Bernard Price Institute,



*Gladiopomum dutoitides*



*Gladiopomum acadarensense*



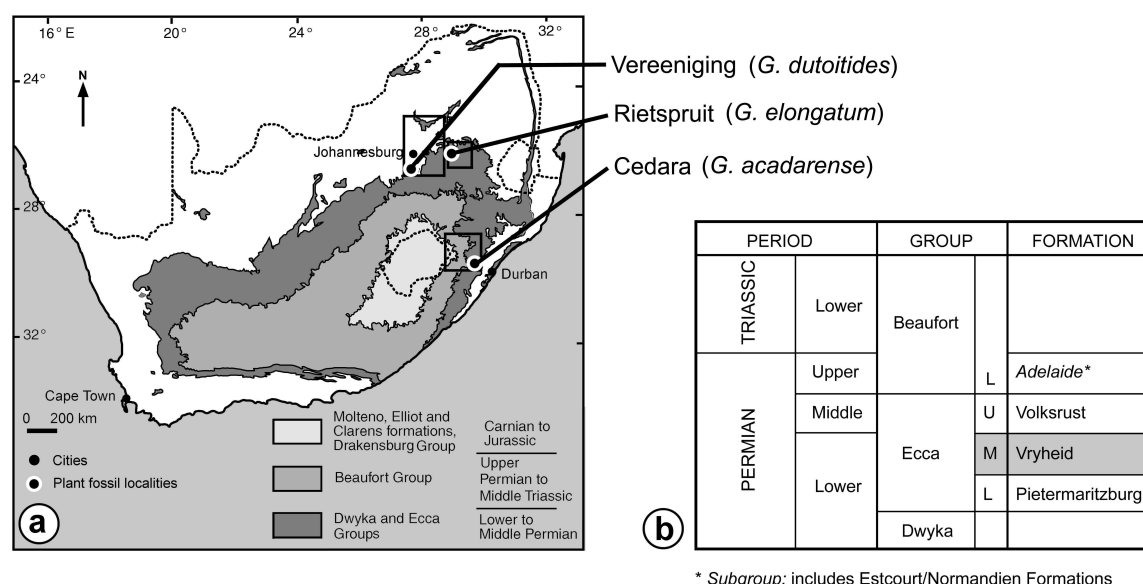
*Gladiopomum elongatum*

<sup>7</sup> The publication was based on work conducted during the course of this Ph.D. study.

University of the Witwatersrand, although one specimen was found in the Le Roux collection at the Vaal Teknorama Museum in Vereeniging. Also housed at the BPI were the specimens from Cedara and a single fructification from Hlobane collected by Drs J.M. and H.M. Anderson. A single specimen was loaned from the Council for Geosciences in Pretoria. Several specimens were collected from the Rietspruit Colliery during an excursion undertaken in 1999 by Dr Marion K. Bamford, Mrs Ray Renaut and me, all of the Bernard Price Institute (see Table A.I.10, Appendix I for catalogue numbers and repositories).

### 7.6.3 LOCALITY INFORMATION

*Gladiopomum dutoitides* has only been found at the Vereeniging and Hlobane localities. The Vereeniging specimens were collected from the Old Sandstone Quarry, the Shale Quarry and the River Quarry (text-fig. 2.2.5), as outlined by Le Roux & Anderson (1977). *Gladiopomum acadarensense* has been found at a single locality, near Cedara in the Kwa-Zulu Natal Province, and the species *G. elongatum* is based on 2 specimens from the Rietspruit coal mine (see text-figs 7.6.1; 2.2.2, 2.2.3 a&b).



**Text-figure 7.6.1** (a) Locality map indicating reported occurrences of *Gladiopomum* in South Africa; (b) lithostratigraphic table of the Permian and Lower Triassic deposits in the northern and eastern parts of the Karoo Basin, with shaded areas representing stratigraphic occurrences of *Gladiopomum* (table adapted from Keyser, 1997).

All these localities fall within the northern and eastern parts of the Karoo Basin, South Africa, in sediments of the Vryheid Formation, middle Ecca Group, of the Lower Permian (Artinskian). *Gladiopomum* has not been verified from other parts of Gondwana.

#### **7.6.4 SYSTEMATIC PALAEOBOTANY**

(Adapted from Adendorff *et al.*, 2002).

##### ***Type species***

*Gladiopomum dutoitides* (Plumstead 1952) Adendorff *et al.* 2002; Lower Permian; Karoo Basin, South Africa.

##### ***Etymology***

Latin: *gladius* – a sword, *pomum* – a fruit; referring to the elongate, commonly sharp-pointed receptacle (Adendorff *et al.*, 2002).

##### ***Generic diagnosis***

(Adapted from Adendorff *et al.*, 2002).

Isobilateral, dorsiventral, pedicellate ovuliferous fructification comprising a receptacle with broad, peripheral wing. Receptacle lanceolate, elliptical to lorate, with high length to width ratio (2:1 to 7:1); apex extended to form pronounced, acuminate extension or spine. Wing broad, slightly less than or equal to width of receptacle, with fine striae and fluting oriented perpendicular to receptacle, flute definition decreasing towards the margin. Wing margin entire, discontinuous at base, forming truncate to convex lobe on either side of pedicel insertion. Wing tapering abruptly at apex near base of apical spine. Fertile surface of receptacle bearing numerous, closely spaced seed scars. Sterile surface characterized by fan-shaped network of bifurcating and anastomosing veins, with strongly parallel

venation along central axis of the receptacle. Marginal veins on receptacle pass between the seed scars and are continuous with flutes developed on wing.

### **Comments**

(Adapted from Adendorff *et al.*, 2002).

*Gladiopomum* has the same basic architecture as other capitate, ovuliferous, glossopterid fructifications such as *Scutum*, *Plumsteadia* and *Dictyopteridium* in having a dorsiventrally flattened, isobilateral structure consisting of an ovuliferous receptacle flanked by a fluted and finely striated wing. The main features distinguishing *Gladiopomum* from other genera, are the extremely narrow, elongate receptacle with its pronounced spine-like, apical extension, and the broad, entire wing that is of similar width to the receptacle and which is discontinuous both at the base and the apex of the fructification. These features are deemed consistent and distinctive enough to warrant erection of a new genus.

Most of the specimens here assigned to *Gladiopomum* had been previously placed in *Hirsutum* by Plumstead (1958a) and Anderson & Anderson (1985). However, the taxonomic status of the latter has been controversial since its inception, as it was based on a disputed morphological interpretation of the fructifications (viz., the presence of hair-like and bract-like pollen-bearing organs on a bivalved, bisexual fruit as envisaged by Plumstead, 1956a, 1958a). Authors such as Rigby (1978) and Mukherjee *et al.* (1966) rejected the use of *Hirsutum*, but Anderson & Anderson (1985) retained the name with an emended diagnosis, and included within it the specimens described here from Vereeniging and Cedara. The main diagnostic characters of *Hirsutum* cited by Anderson & Anderson (1985) were the presence of upwardly curving wing striations, and a wing that was markedly reduced towards the stalk. However, neither of these features is evident in the type species, *H. dutoitides*, or in *H. acadarensis*. *Gladiopomum* was instituted (Adendorff *et al.*, 2002) to accommodate elongate, broad-winged, acuminate fructifications previously attributed to *H. dutoitides* and *H. acadarensis*.

*Gladiopomum* is most similar to *Scutum* in its gross architecture, and their seed scar morphology is almost identical. However, *Scutum* lacks an apical spine and, although its wing can be relatively broad, the receptacle is typically ovate and proportionately wider. The wing of *Scutum* is uninterrupted, except at the point of pedicel insertion, and the fluting is pronounced across the entire breadth of the wing.

*Gladiopomum* fructifications may also bear a superficial resemblance to some broad-winged specimens of *Dictyopteridium*, which have narrowly lanceolate receptacles. However, *Dictyopteridium* lacks an apical spine and the wing width does not usually match that of the receptacle. The seed scars of *Dictyopteridium* are usually substantially smaller and represented by minute raised tubercles on a relatively smooth receptacle surface (on impressions).

#### 7.6.4.1 ***Gladiopomum dutoitides*** (Plumstead 1952) Adendorff *et al.* 2002

(Adapted from Adendorff *et al.*, 2002).

- 1952 *Scutum dutoitides* Plumstead, pars, p. 289, pl. 45, fig. 1; text-fig. 2. non pl. 45, figs 2, 3.
- 1952 *Scutum stowanum* Plumstead, p. 298, pl. 50, figs 1-3; text-fig. 5.
- 1956 *Scutum dutoitides* Plumstead; Plumstead, pars, p. 8, pl. 6, figs 1, 2; text-fig. 2a. non pl. 7, figs 1-3; pl. 10, fig. 3; text-fig. 2b,c. [1956a].
- 1956 *Scutum stowanum* Plumstead; Plumstead, pars, p. 10, pl. 9, figs 1, 2. non. pl. 10, fig. 4. [1956a].
- 1958 *Hirsutum dutoitides* (Plumstead) Plumstead, p. 60.
- 1958 *Pluma thomsonii* Plumstead, p. 69, pl. 21, fig. 2. non. pl. 21, fig. 3.
- 1963 *Hirsutum*; Plumstead, p. 150, pl. B, fig. 1.
- 1969 *Hirsutum dutoitides* (Plumstead) Plumstead; Plumstead, pl. 12, fig. 5.
- 1973 *Hirsutum* Plumstead; Plumstead, pl. 3, fig. 12.
- 1985 *Hirsutum dutoitides* (Plumstead) Plumstead; Anderson & Anderson, p. 119, pl. 75, figs 1, 2, 7-13; pl. 95, fig. 11; text-figs 118.1, 118.5, 119.2, 119.3.
- 2002 *Gladiopomum dutoitides* (Plumstead) Adendorff *et al.*, p.4-8, figs 3-30.

#### ***Holotype***

Designated L.II.1 by Plumstead (1952; pl 45, fig. 1; text-fig. 2).

Re-registered BP/2/13945a by Anderson and Anderson (1985; pl 75, figs 1, 2); Adendorff *et al.* (2002), figs 3-4 & 24; this volume, pl. 60; pl. 68; fig. (e). The

specimen is housed in the Bernard Price Institute. The counterpart, BP/2/13945b is missing.

### ***Etymology***

After Alexander 'Logie' Du Toit (1878-1948), a prominent South African geologist.

### ***Type formation and locality***

Vryheid Formation (middle Ecca Group); Lower Permian (Artinskian); Vereeniging, northern Karoo Basin.

### ***Emended species diagnosis***

Receptacle elongate elliptical to lanceolate, with L:W ratio of about 3:1; very pronounced apical spine; broad wing (wing width:receptacle width of about 0.7:1). Attached to base of petiole of elongate oblanceolate *Glossopteris* leaf, with obtuse apex, attenuate base and strongly developed, persistent midrib. Venation straight to gently arching with few bifurcations and anastomoses, forming parallel meshes at an angle of approximately 45° to midrib.

### ***Description***

(See Adendorff *et al.*, 2002; figs 3-10; 21-24, 29, 30A; this document: pls 59, 60, 68, 69 figs (d), (e.i); Table A.II.6, Appendix II for data summary).

The fructifications are 33 (47) 58 mm long {n=6} [Hlobane specimen: 31 mm] and 15 (22) 27 mm wide {n=6} [Hlobane specimen: 18 mm]. They have a gross L:W ratio of 1.8:1 (2.2:1) 2.6:1 [Hlobane specimen: 1.7:1].

The fructifications have pedicels 11-17 mm long {n=4} [Hlobane specimen: 9 mm], and 1-4 mm wide {n=5} [Hlobane specimen: 2 mm]. The pedicel is, in

some cases, slightly expanded at the contact with the receptacle. Pedicels bear striae that continue into the receptacle on the sterile surface of the fructification.

The receptacle varies from oblong, elliptical to lanceolate with a L:W ratio of 2.2:1 (2.9:1) 3.9:1 [Hlobane specimen: 3.2]. Receptacles are 16 (30) 41 mm long {n=6} and 6 (10) 14 mm wide {n=6} [Hlobane specimen: 20 x 6 mm].

The diagnostic sterile extension or spine at the apex of the receptacle is particularly well developed in specimens BP/2/13936 and BP/2/13941 [pl. 59, figs (d), (f)]. The spine tapers slightly towards the tip, and is finely striated. It lies at a higher level than the surface of the seed scars in the impression fossils, indicating that it was flush with the sterile surface of the fructification. The spine is 6 (7) 10 mm long {n=3}, with a basal width of 2 (3) 3 mm {n=3} [Hlobane specimen: 2 mm].

Only two specimens show the sterile surface of the fructification [viz., BP/2/13937 from Vereeniging and BP/2/16037 from Hlobane; pl. 59, figs (e), (c)]. The striations persisting from the pedicel, continue mostly parallel (longitudinally) along the axis of the receptacle, but bifurcate and anastomose towards the margins to form meshes. Veins diverge and arch sharply at the receptacle margin before passing into the wing striae. These points of vein divergence into the wing correspond to the grooves between marginal seed scars on the fertile surface.

The wing is finely striated and fluted, the flutes corresponding to the sites of vein divergence from the receptacle. Both striae and flutes run perpendicular to the receptacle margin. Fluting is well developed adjacent to the receptacle, but diminishes before reaching the margin. The margin is entire, except where contracted to form broadly rounded or slightly auriculate basal lobes flanking the point of pedicel insertion into the receptacle, and at the base of the apical spine. Unfortunately, none of the specimens has a well-preserved apex, specimen BP/2/13941 giving the best indication as to the nature of the apical region of the wing [pl. 59, fig. (f)]. The wing constricts abruptly near the base of the apical spine. The wing is broadest in the medial region of the fructification, reaching widths of 5 (7) 10 mm {n=6} [Hlobane specimen: 6 mm], with basal wing widths



of 5 (5) 6 mm {n=4} [Hlobane specimen: 5 mm] and apical widths of approximately 4 mm {n=2}. The wing width: receptacle width ratio is 0.4:1 (0.7:1) 0.9:1 {n=6} [Hlobane specimen: 1].

Seed scars, borne on the fertile surface of the receptacle, are elliptical near the centre, becoming circular or sharply polygonal near the margin. On impressions, each scar is represented by a raised cushion with a relatively flat crest, and a central, low, indistinct tubercle. There are approximately 30 (72) 130 scars on the receptacle {n=5} [Hlobane specimen: 43], with a density of about 4.4 (8.5) 12.7 seed scars per 25 mm<sup>2</sup> {n=5} [Hlobane specimen: 11.6 per 25 mm<sup>2</sup>]. The dimensions of central seed scars are 2.5 x 1.5 mm {n=32} and peripheral seed scars are 1.8 x 1.5 mm {n=16} [Hlobane specimen: central scars 3 x 1.7 mm; peripheral scars 2.1 x 1.8 mm].

The holotype of *G. dutoitides* (BP/2/13945a) is attached to the base of the petiole of a *Glossopteris* leaf (pl. 60), the fertile surface of the fructification facing the leaf. The leaf is narrowly oblanceolate with a very slightly expanded basal lobe. The lamina tapers proximally into a broad petiole (7 mm wide). The leaf is entire, at least 225 mm long and 26 mm wide (L:W ratio = 8.7). The midrib is robust (5 mm wide) in the lower third of the leaf, striate and persistent, tapering to 1 mm at the apex. Veins arise from the midrib at an angle of about 37° and span the lamina with very little or no arching (mid-laminal angle: 50°). Veins bifurcate two or three times before reaching the margin, and anastomoses are rare, resulting in the formation of very regular, parallel meshes. Marginal vein density is 8 per 5 mm.

### **Comments**

All six specimens are derived from Vereeniging except for a single example from Hlobane [pl. 59; fig. (c)]. Measurements of the latter specimen are listed separately for comparative purposes, and were not included in the mean calculations. This specimen falls in the lower part of the range for most measurements but its gross shape and concordant character ratios favour its attribution to *G. dutoitides*.

Representatives of this species have a lower length:width ratio than specimens of *G. acadarens* and *G. elongatum*, and the receptacle tends to be elongate-elliptical to lanceolate, rather than the extreme lorate shapes seen in some examples of *G. acadarens*. The wing is also narrower relative to the receptacle than in the other two species. The apical spine is particularly clear and well developed in *G. dutoitides*.

The slightly laterally compressed specimen in pl. 59, fig. (c) was originally classified by Plumstead (1958a) as *Pluma thomasii*, and she interpreted the fluted wing (only exposed on the right side of the fructification) as a series of pendulous pollen sacs. All members of her genus *Pluma* appear to be taphomorphs of existing taxa of ovuliferous glossopterid fructifications.

According to Mukherjee *et al.* (1966), 26 specimens of '*Scutum dutoitides*' were found at the Murulidih Collieries in Bihar (Raniganj Formation, Upper Permian), three of them attached to *Glossopteris indica* leaves. The fructifications were broadly elliptical, with a narrow wing and no apical spine. They are clearly not referable to *Gladiopomum dutoitides*.

Banerjee (1968) reported the occurrence of *Scutum stowanum* from the Raniganj Formation of India. These fructifications do show some similarities to *Gladiopomum*: they have elongated, oval receptacles with a L:W ratio of approximately 3:1 to 4:1, and a very broad wing relative to the width of the receptacle. However, the presence of an apical spine is not mentioned (and is not discernable in the figure provided, Banerjee, 1968, pl. 1, fig. 2), and the wing fluting is very conspicuous across the entire width of the wing. The attached *Glossopteris* leaf also differs significantly from the leaf attached to the holotype of *Gladiopomum dutoitides*, in terms of its steeper venation angle, more acute apex, and lack of a pronounced midrib. In addition, the Indian fructification is attached to the midrib in the lower third of the leaf, as opposed to the more axillary attachment evident in *G. dutoitides*. Banerjee (1968) based her identification on Plumstead's (1958a, p. 55, pl. 7) account of *Scutum stowanum* in organic attachment to *Glossopteris decipiens*. However, this South African specimen appears to be a *Scutum rubidgeum* fructification that has undergone

slight lateral compression. There is no sign of an apical spine, and the wing is considerably narrower than the receptacle and has well-defined fluting traversing its entire width. The point of attachment to the leaf is on the midrib, in the lower third of the leaf, and the leaf itself is closer in appearance to Banerjee's (1968) specimens than to the leaf attached to *Gladiopomum dutoitides*.

The type specimen of *G. dutoitides* is poorly preserved, but was presumably selected by Plumstead (1952) because it is attached to a glossopterid leaf (pl. 60). Since the publication of Adendorff *et al.* (2002), following the discovery of the double-wing structure of *Bifariaia intermittens* (*Hirsutum intermittens*), a potentially enormous problem with this type specimen has come to light. It could very well be a poorly preserved example of *B. intermittens*, in which the secondary wing is fully exposed, and in which the primary wing is only visible in the apex. The apical spine is suspiciously broad and conical compared to other specimens of *Gladiopomum*. The taxonomic implications of this revelation are discussed in Appendix IV.

**7.6.4.2      *Gladiopomum acaderense*** (Anderson & Anderson 1985) Adendorff *et al.* 2002

(Adapted from Adendorff *et al.*, 2002).

1985 *Hirsutum acaderense* Anderson & Anderson, pars, p. 120, pl. 77, figs 6-11; pl. 95, fig. 9; text-figs 120.1, 120.2. [Basionym].  
2002 *Gladiopomum dutoitides* (Plumstead) Adendorff *et al.*, p.4-8, figs 3-30.

***Holotype***

BP/2/16331a; designated by Anderson & Anderson (1985, pl. 77, fig. 7); Adendorff *et al.* (2002, Figs 12 & 26); this volume, pl. 61; housed at the Bernard Price Institute.

***Etymology***

'acadarensen' - an anagram of 'Cedara', the locality of origin.

### ***Type formation and locality***

?Vryheid Formation (middle Ecca Group), Lower Permian (Artinskian); Cedara, eastern Karoo Basin.

### ***Emended species diagnosis***

Receptacle lanceolate, extremely elongate oblong, to lorate and in some cases falcate, with a high L:W ratio (up to 5:1); apical spine present, but weakly developed; wing very broad, wing width : receptacle width ratio up to 1.5:1; pedicel long and striated.

### ***Description***

(See Adendorff *et al.*, 2002; figs 11-18; this document: pls 61-66, 69 figs (a), (b), (e.ii); Table A.II.6, Appendix II for data summary).

The fructifications are 31 (49) 69 mm long {n=15} and 16 (24) 32 mm wide {n=15}, with a L:W ratio of 1.2:1 (2.1:1) 3.3:1. The pedicel is striated, commonly expanded at the point of contact with the receptacle, and it may also be slightly expanded at the base. Pedicels are 7 (18) 28 mm long {n=15}, and have a maximum width of 2 (3) 7 mm {n=16}.

The receptacle is oblong, lorate or lanceolate, with a L:W ratio of 2.6:1 (4.1:1) 5.4:1. In some cases the receptacle is slightly falcate. Receptacle dimensions are 21 (34) 50 mm {n=16} by 5 (8) 15 mm {n=23}. The apical spine is generally not well preserved. The clearest example is seen in BP/2/16329a [pl. 62, fig. (c)]. Spines are 4 (6) 9 mm long {n=3}, and have a basal width of 2 (3) 4 mm {n=4}.

Sterile surface features of the fructifications are generally unclear. Striations are indistinct on the receptacle; the venation is mostly concealed by indentations corresponding to seed scars on the fertile surface. Where evident, striations

extend from the pedicel into receptacle and remain mostly parallel to the longitudinal axis of the fructification.

The very broad wing, 7 (9) 11 mm wide {n=20}, generally attains its maximum width in the medial section of the fructification. Basal and apical wing widths are 4 (6) 9 mm {n=10} and 4 (5) 6 mm {n=5} respectively. The wing width: receptacle width ratio is 0.8:1 (1:1) 1.5:1 {n=20}. The wing is striate, with striae oriented perpendicular to the receptacle. Fluting is moderately developed adjacent to the receptacle but ill defined towards the margin. The wing is rounded or slightly auriculate where it contracts at the point of pedicel insertion, and it narrows sharply at the base of the apical spine.

There are 61 (108) 172 seed scars on the receptacle {n=8}, with a scar density of 6 (9) 12 per 25 mm<sup>2</sup>. Seed scars are elliptical near the centre of the receptacle, becoming circular or square near the margin. Scars are 1.5 (3) 4 mm long {n=73} and 1.2 (1.5) 1.9 mm {n=59} wide. Each scar is represented by a raised cushion with a shallow apical depression and a central, low, indistinct tubercle.

### **Comments**

This taxon exhibits the greatest degree of morphological variability of the three *Gladiopomum* species, although this may just be a reflection of the large number of fructifications available for examination (over 20). The outstanding features of this species are the very broad wing, the sharply pointed, acuminate tip of the receptacle, and the particularly long and robust pedicel.

There are many similarities between *G. acadarensense* and *G. dutoitides*, but wing width relative to receptacle width tends to be greater, and the receptacle is narrowly lanceolate to lorate in the former, as opposed to the lanceolate, elongated elliptical to oblong receptacle of *G. dutoitides*. The length:width ratio of the *G. acadarensense* receptacle is intermediate between *G. dutoitides* and *G. elongatum*.

Fructifications were not found attached to foliage or seeds, but numerous *Glossopteris* leaves were closely associated with the fructifications. The leaves are 115 mm long, 25 mm wide, with a long tapering base to form a 2.5 mm wide petiole; the midrib is persistent, varying from 3 to 1 mm wide; veins emerge from the midrib at around 28°, and arch gently and consistently across the lamina; meshes are long and narrow; mid-laminal venation angle is approximately 43° to the midrib; marginal vein density is 11 per 5 mm.

#### **7.6.4.3      *Gladiopomum elongatum* Adendorff *et al.* 2002**

(Adapted from Adendorff *et al.* 2002).

##### ***Holotype***

BP/2/28880b [pl. 67; pl. 69, fig. (c)], housed at the Bernard Price Institute for Palaeontological Research, Johannesburg.

##### ***Etymology***

Latin: referring to the very elongated receptacle.

##### ***Type formation and locality***

Vryheid Formation (middle Ecca Group); Lower Permian (Artinskian); Rietspruit Colliery, northern Karoo Basin, South Africa

##### ***Species diagnosis***

Receptacle elongate lanceolate to lorate, with a high L:W ratio (up to 7:1); apical spine present but not well defined; broad wing, with a wing width:receptacle width of about 1.

## **Description**

(See Adendorff *et al.*, 2002; figs (19), (20); this document: pl. 67; pl. 69 figs (c), (e.ii); Table A.II.6, Appendix II for data summary).

The holotype, BP/2/28880 a&b [pl. 67, figs (a), (b)] is not very well preserved. One side of the wing is clearly defined but the other half is damaged and obscured by sediment. The proximal margin of the receptacle (on the same side as the damaged wing) is also partially degraded. The fertile surface of the receptacle is not clear, but locally provides adequate details of the seed scar morphology and density. BP/2/28880a [pl. 67, fig. (a)] reveals an impression of the sterile surface of the fructification. Unfortunately, the preservation is very poor and the venation detail is indistinct and mostly obscured by indentations corresponding to seed scars on the fertile surface.

The fructifications are 40 to 75 mm long, 18 to 25 mm wide, with an overall L:W ratio of 2.2:1 to 3:1. The pedicel is only preserved in the holotype. It is striated and is at least 12 mm long and 4 mm wide. The lanceolate receptacle is 33-63 mm long, 9 mm wide, with a L:W ratio of 3.7:1 to 7:1. The apical spine on the holotype is incomplete but reaches 7 mm long and 2 mm wide.

The wing is entire and very broad, reaching a maximum width of 10-12 mm in the medial part of the fructification, 4-6 mm near the base and 5 mm near the apex. It bears striations and fluting perpendicular to the receptacle margin. Fluting is well-developed adjacent to the receptacle but indistinct near the margin. The wing width : receptacle width ratio is 1.1:1 to 1.3:1.

The receptacle is estimated to have borne 53-87 seed scars, with a density of 6.6 scars per 25 mm<sup>2</sup>. Scars are longitudinally elliptical near the centre of the receptacle, becoming circular, square or rectangular near the margin. Scar dimensions are 2-3.5 mm long, 1.6-2.2 mm wide. Each scar is represented by a raised cushion with a shallow, featureless, apical depression.

## Comments

No additional organs were found attached to *G. elongatum*, and no clear associations were noted with a particular leaf type. The most distinguishing features of this species are the extremely large length:width ratio of the receptacle and the gross length of the fructification. In other respects, these fructifications are very similar to *G. acadarensis*. The dimensional differences are deemed sufficient to warrant specific segregation on the basis of the available material. The apical spine on the holotype of *G. elongatum* is not complete, but appears to be less pronounced than in *G. dutoitides*.

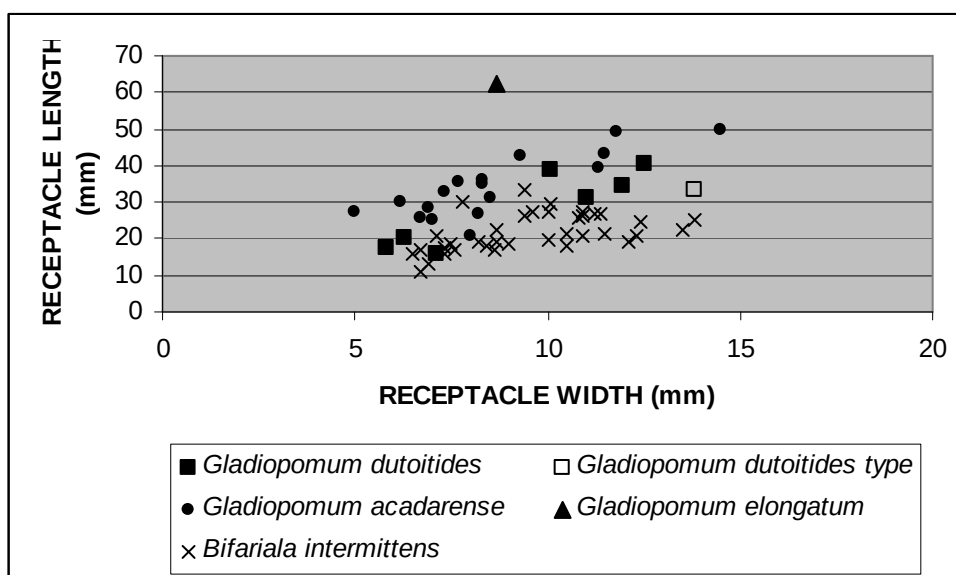
### 7.6.5 DATA ANALYSIS

The three species of *Gladiopomum* and *Bifariola intermittens* were clearly separated in a scatter plot of receptacle length versus the ratio between medial wing width and receptacle width (text-fig. 7.6.3), although there was some overlap in the ranges of the taxa. Scatter diagrams in text-figs 7.6.2 & 7.6.3 indicate that *G. dutoitides* and *G. acadarensis* form two ends of a morphological continuum. The holotype of *G. elongatum* is very different from members of the other two species. Its size measurements and ratios lie way beyond those of *G. dutoitides* and *G. acadarensis*.

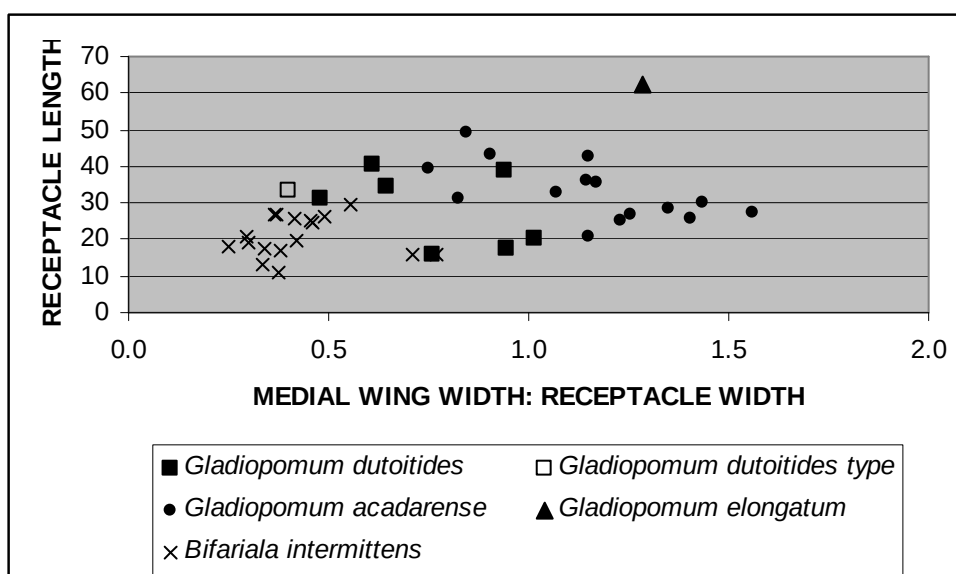
Scatter plots of receptacle lengths versus widths (text-fig. 7.6.2) and receptacle length versus the ratio of medial wing width to receptacle width (text-fig. 7.6.3) place the type specimen of *G. dutoitides* on the border between clusters for *G. dutoitides* and *Bifariola* in both cases.

Text-figs 7.6.2 & 7.6.3 indicate that specimens of *Bifariola intermittens* are consistently shorter and have a narrower medial wing than members of the *Gladiopomum* species.





**Text-fig. 7.6.2.** A scatter plot of receptacle length versus receptacle width for the three species of *Gladiopomum* and *Bifariaia intermittens*.



**Text-fig. 7.6.3.** A scatter plot of receptacle length versus the ratio of medial wing width to receptacle width, for the three species of *Gladiopomum* and *Bifariaia intermittens*.

## 7.6.6 DISCUSSION

Morphological differences between the three species of *Gladiopomum* may be relatively superficial, perhaps a consequence of growth under different environmental conditions since the two localities of origin are spatially distant. Dimensional characters have been used to differentiate the species but size is of course a variable feature, and not a particularly reliable diagnostic character

in plant studies. There is some overlap in the range of fructification dimensions between the three taxa but they are generally distinguishable on the basis of length: width ratios and wing width: receptacle width ratios that provide measures of gross shape (text-figs 7.6.2 & 7.6.3). The L:W ratio of the receptacle provided a more robust character for species differentiation than the L:W of the whole organ, as the latter includes the portions of the fructification that are prone to incomplete preservation (e.g., the apical spine, pedicel, and wings).

*Gladiopomum* fructifications are similar in appearance to *Bifaria* specimens when the latter are preserved with only the secondary, scutoid wing exposed. Both taxa have an elongated receptacle and a scutoid wing with weakly developed fluting. It is possible that the poorly preserved holotype of *Gladiopomum* is in fact a specimen of *Bifaria*, with the primary wing only preserved in the extreme apex, giving the illusion of an apical spine. There is unfortunately no means of proving or disproving this. The counterpart in Anderson & Anderson (1985; pl. 75, fig.1) is also poorly preserved, and doesn't shed any light on the matter. Scatter plots of dimensions and size ratios for *Bifaria intermittens* and the three *Gladiopomum* species did not help to clarify the situation. The type specimen of *G. dutoitides* falls within the extreme limits of the ranges for both *G. dutoitides* and *B. intermittens*, and could easily belong within either taxon.

The function of the very broad but apparently fragile wing of *Gladiopomum* fructifications is unclear. It may have had a protective role during early development, arching over the immature ovules in a manner similar to the wings of *Dictyopteridium*-type polysperms illustrated by Gould & Delevoryas (1977). If this were the case then the wings clearly unfolded upon maturation of the fructification to expose and release the seeds. Alternatively, the broad wings may have played a role in wind dispersal of the entire organ (somewhat analogous to modern *Acer* or *Gyrocarpus* fruits). Most *Gladiopomum* fructifications are preserved separately from their subtending leaves. Enhanced wind dispersal of the polysperm as a whole may have aided dissemination of any remaining attached seeds. However, no seeds were found attached to any

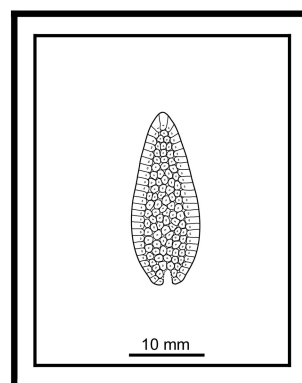
*Gladiopomum* fructifications, hence the principal function of the wing is deemed to have been protective.

The records of *Gladiopomum* from Vereeniging, Hlobane and Rietspruit are confidently assigned to the Vryheid Formation. Given that *Gladiopomum* fructifications are moderately common at three localities within the Vryheid Formation, the genus may be a useful biostratigraphic index taxon throughout the Karoo Basin. An Artinskian age is, therefore, suggested for the Cedara sediments (also hosting this genus) despite the dearth of other age-definitive taxa in this assemblage. *Gladiopomum* is apparently restricted to the Karoo Basin of South Africa. The only putative glossopterid fructification from outside the Karoo Basin that might be referable to this genus is a specimen from Upper Permian strata of the central Bowen Basin, Australia, and the specimen is apparently lost (Rigby, 1978, fig. 24). This specimen possesses a very broad, transversely striate wing and narrow receptacle (wing width: receptacle width = 1.4:1) typical of *Gladiopomum* but the distinctive extension on the receptacle apex is not clear.

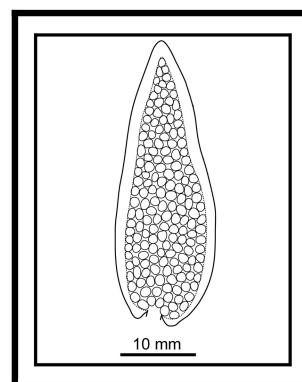
## 7.7. *PLUMSTEADIA* Rigby 1963 emend.

### 7.7.1 INTRODUCTION

Rigby's (1963) original diagnosis for *Plumsteadia* was in line with Plumstead's (1952, 1956a, 1958a) model of a bipartite fructification with a sterile 'half' and a sac-bearing fertile 'half'. He later (1971) emended his diagnosis, characterising the fructifications as unipartite, wingless, bifacial organs bearing fertile structures on one surface. However, he interpreted the tubercles on the fertile surface as sporangia. In 1978, Rigby again revised his interpretations, acknowledging the ovuliferous nature of the fructifications, and attributing the 'sac-like' features on the fertile surface to ovule attachment points.



*Plumsteadia lerouxii*



*Plumsteadia gibbosa*

In early descriptions of *Plumsteadia* the presence of a wing was overlooked or interpreted as a rank of laterally compressed ovules. In the original generic diagnosis, Rigby (1971) specified that *Plumsteadia* lacked a wing, but the holotype of the type species demonstrates the presence of a narrow wing (Rigby, 1978; fig. 4). Maheshwari (1965b) noted the presence of a narrow rim along the periphery of a specimen of *P. indica*. Anderson & Anderson (1985) depicted *Plumsteadia* as a dorsiventral fructification with a wing that was very narrow or absent. McLoughlin (1990b) provided very clear evidence that the specimens of *Plumsteadia* he examined were dorsiventral structures with a tuberculate fertile surface and a broadly pitted or weakly veined sterile surface, and they did not possess any form of sterile scale or bract. He reported the presence of a wing in all mature specimens examined, although the wing width was highly variable. McLoughlin (1990b) distinguished *Plumsteadia* from *Scutum*, *Ottokaria*, and *Dictyopteridium* on the basis of its narrow to broadly ovate or elliptical receptacle with a narrow, fluted or smooth wing of consistent width and with an entire margin.

*Plumsteadia* is one of the most common and widespread genera of ovuliferous fructifications. This may be more to do with its broad circumscription than its accurate representation of a ubiquitous taxon. In the past, *Plumsteadia* has been the recipient of many genera and species with ovate to lanceolate receptacles and narrow wings. This appears to be a common format for glossopterid fructifications, and when dealing with form taxa attached to similar leaves, one has little choice but to group them within these broadly defined genera.

Anderson & Anderson (1985) and McLoughlin (1990b) synonymised the following fructifications with *Plumsteadia*: *Fetura* (Benecke, 1976), *Scopus* (Benecke, 1976) and *Plumsteadistrobus* (Chandra & Surange, 1977b), decisions supported here. McLoughlin (1990b) also synonymised *Lanceolatus* (Plumstead, 1952), *Cistella* (Plumstead, 1958a) and *Gonophylloides* (Maheshwari, 1968). In this document, *Cistella* has been retained as a distinct genus, and Maheshwari's (1968) name *Gonophylloides* has been adopted. *Fetura* has been transferred to *Dictyopteridium natalensis*.

Since *Lanceolatus* is the oldest of the synonyms listed here, one might expect the name to receive priority over *Plumsteadia*. However, as numerous authors have commented in the past (e.g. Rigby, 1978; McLoughlin, 1990b), the name is not nomenclaturally valid. The word is a formal descriptor, and as outlined in Article 20.2 of the International Code for Botanical Nomenclature (Greuter, *et al.*, 1994), 'the name of a genus may not coincide with a technical term currently used in morphology'. In Ex. 4. of Article 20, *Lanceolatus* is even cited as an example of the inappropriate use of a technical term as a generic title: 'The intended generic name(s) "*Lanceolatus*" (Plumstead, 1952) ... coincide with technical terms and are therefore not validly published'. The illegality of the name was pointed out in the discussions at the end of Plumstead's (1952) original paper describing the genus. Prof. W.J. Jongmans expressed his objections on p.325, stating that as an adjective, *Lanceolatus* was not a valid generic title.

Plumstead (1956a; 1958a) persevered with the name, as did Anderson & Anderson who re-instated the genus in 1985, distinguishing it from *Plumsteadia* on the basis of differences in associated leaves and pollen-bearing organs. The pollen-bearing organs they attributed to *Plumsteadia* were the ovuliferous organs attributed here to *Dictyopteridium flabellatum*. In accordance with their palaeodeme-based taxonomic approach, Anderson & Anderson (1985) synonymised *D. flabellatum* with *P. natalensis*. This view is not supported here, and *D. flabellatum* has been retained as a separate species of ovuliferous fructification, as described by McLoughlin (1990a). The distinction between *Plumsteadia* and *Dictyopteridium*, however, is not always clearly defined. The genus originally described by Lacey *et al.* (1975) as *Plumsteadia natalensis*, which was then referred to *Fetura natalensis* by Benecke (1976) and then returned to *Plumsteadia* by Anderson & Anderson (1985), is here included within *Dictyopteridium*. This decision was made after observing the spectrum of seed scar morphologies present in this group of fructifications, which ranged from poorly defined, widely spaced, low seed cushions with well-developed central tubercles, to widely spaced tubercles with an absence of seed cushions. This latter morphology is diagnostic of *Dictyopteridium*.

### 7.7.2 FOSSIL MATERIAL

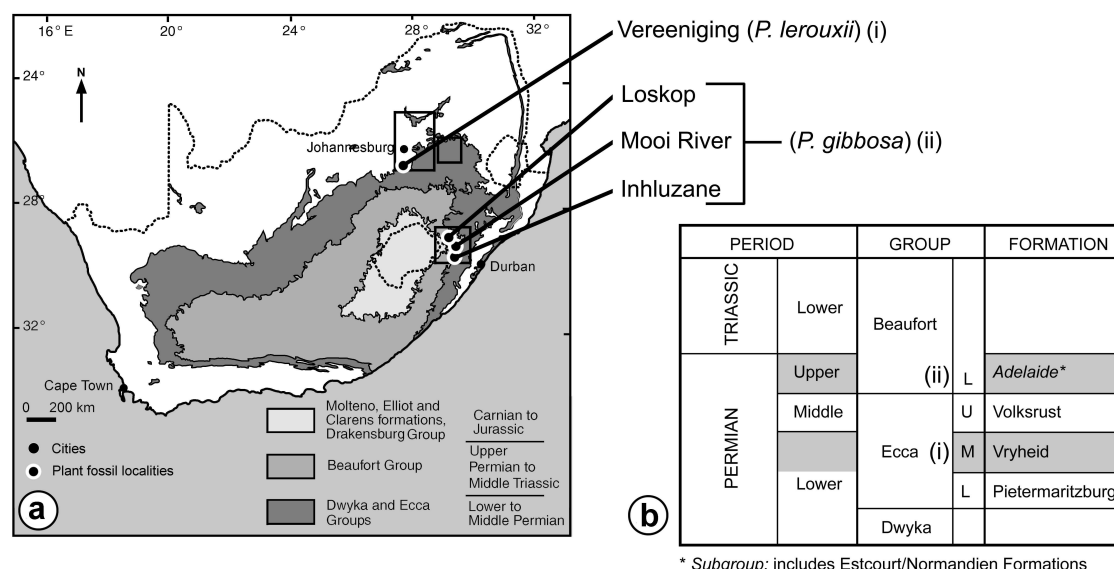
All fossils of *Plumsteadia lerouxii* were in the form of impressions. The specimens are housed in the BPI and in the Le Roux collection at the Vaal Teknorama Museum in Vereeniging (see Table A.I.11, Appendix I). Specimens of *Plumsteadia gibbosa* are compression and impression fossils. They are housed in the Natal Museum in Pietermaritzburg and the Bernard Price Institute, University of the Witwatersrand, Johannesburg.

### 7.7.3 LOCALITY INFORMATION

Specimens of *P. lerouxii* were collected from the Old Sandstone Quarry on the farm Leeukuil at Vereeniging (Le Roux and Anderson, 1977); Vryheid Formation, Lower Permian (see text-figs 2.2.1, 2.2.2 and 2.2.4; text-fig. 7.7.1 below).

*P. gibbosa* specimens were found at the Mooi River, Inhluzane and Loskop localities, all in the Kwa-Zulu Natal Midlands; Estcourt Formation, Upper Permian (see text-figs 2.2.1, 2.2.3; text-fig. 7.7.1 below) .

These localities all fall within the Karoo Supergroup, Karoo Basin, South Africa (text-fig. 7.7.1).



**Text-figure 7.7.1.** (a) Locality map indicating reported occurrences of *Plumsteadia* in South Africa; (b) lithostratigraphic table of the Permian and Lower Triassic deposits in the northern and eastern parts of the Karoo Basin, with shaded areas representing stratigraphic occurrences of *Plumsteadia* (table adapted from Keyser, 1997).

## 7.7.4 SYSTEMATIC PALAEOBOTANY

### Type species

*Plumsteadia microsacca* Rigby 1963, by original designation; Baralaba Coal Measures, Blackwater Group; Upper Permian (Upper Stage 5 palynozone); Baralaba, southeastern Bowen Basin, Queensland, Australia.

### Etymology

Named after Edna Pauline Plumstead (1903-1989), the famous South African palaeobotanist, particularly well known for her work on the first ovuliferous fructifications found attached to *Glossopteris* leaves.

### ***Emended generic diagnosis***

Isobilateral, dorsiventral, ovuliferous organ attached to midrib or petiole of a subtending *Glossopteris* leaf. Fructification comprises a central receptacle with a peripheral wing; may be sessile or petiolate. Fructification is attached with fertile surface facing subtending leaf. Receptacle is elliptical, oblong to lanceolate, with rounded to pointed apex and rounded to weakly cordate base. Receptacle is bifacial, with a fertile surface bearing closely spaced seed scars and a sterile surface with reticulate venation. Seed scars circular to elliptical, raised cushions (in impressions) with a central tubercle (cicatrix), and may be more regular at edges of receptacle, forming a rank of more rectangular scars along periphery. Wing is absent or narrow to broad and continuous except at petiole insertion where it is contracted. Wing has entire or rarely denticulate margin, bears striations and fluting perpendicular to margin of receptacle and arches towards the fertile surface. Venation on sterile surface is reticulate, fan-shaped, extends into and across wing at junctures between seed scars, delimiting contiguous wing flutes.

### ***Discussion***

The diagnosis of *Plumsteadia* has been emended here to include a clear characterisation of the wing and the seed scars, and the orientation of the fructification relative to its subtending leaf. The diagnosis is very general, and accommodates a broad spectrum of relatively unspecialised polysperms.



#### **7.7.4.1      *Plumsteadia lerouxii* (Plumstead 1952) comb. nov., emend.**

1952 *Lanceolatus lerouxides* Plumstead, p. 301; pl. 51, figs 2-6; pl. 52, figs 1-5.

1956 *Lanceolatus lerouxides* Plumstead; Plumstead, p. 16; pl. 12, figs 1, 2; pl. 13, figs 1-4; pl. 14, figs 1-4.

1963 *Lanceolatus*; Plumstead, p. 150; pl. B, fig. 3.

1969 *Lanceolatus lerouxides* Plumstead; Plumstead, pl. 12, figs 6, 7.

1976 *Lerouxoid fertiliger*; Schopf, p. 43, pl. 2, fig. 3.

1985 *Lanceolatus lerouxides* Plumstead; Anderson & Anderson, p. 122, pl. 87, figs 1-9; pl. 95, fig. 13; text-figs 122.1, 122.2.

1997 *Lanceolatus lerouxides*; Anderson & Anderson, p. 15, fig. 2a,b.

#### ***Holotype***

BP/2/14179 (Bernard Price Institute of Palaeontology); Vryheid Formation; Artinskian; Leeukuil Quarries, Vereeniging, Karoo Basin, South Africa.

#### ***Etymology***

'*lerouxii*' - after Stephanus Francois le Roux (1915-1976), a passionate amateur palaeobotanist, who collected most of the specimens from Vereeniging that are now housed at the Vaal Teknorama Museum at Vereeniging, and at the BPI for Palaeontology at the University of the Witwatersrand. He was responsible for finding and identifying the first specimens of ovuliferous glossopterid fructifications in organic attachment to leaves of *Glossopteris* (Anderson & Anderson, 1985).

#### ***Type formation and locality***

Vryheid Formation (middle Ecca Group); Lower Permian (Artinskian); Vereeniging, northern Karoo Basin.

#### ***Emended species diagnosis***

Narrowly lanceolate fructification with high length to width ratio (>3.5; av. 5) and low ratio of wing width to receptacle width (<0.5; av. 0.2). Apex acute, base rounded, truncate or slightly cordate. Seed scars small, closely spaced, with well-defined cushions. Wing narrow and entire with striations and ill-defined

fluting. Fructification borne on short pedicel or sessile; attached to midrib in lower third of elliptical, oblong to elongate-obovate *Glossopteris* leaf with long, tapering, cuneate base and rounded to obtusely pointed apex; veins follow straight path to margin, nearly perpendicular to well-defined, persistent midrib; meshes coarse, polygonal adjacent to midrib, becoming narrower and more elongated towards margin.

### **Description**

(See plates 70-73, pl. 78, figs (c)-(f); Table A.II.7, Appendix II).

Isobilateral, dorsiventral ovuliferous fructification consisting of an elongated, lanceolate receptacle with a narrow peripheral wing. Overall length is 17.4 (28.5) 42.3 mm {n=33; SD:6.2}, with a width of 4.2 (8) 11.1 mm {n=35; SD:1.8}.

Receptacle is lanceolate with a rounded to truncate or even slightly sagittate base and a sharply acute to acuminate apex. Receptacle is 26.9 (32.1) 42.3 mm long {n=6; SD: 5.5} and 4.0 (6.7) 10.5 mm wide {n=12; SD: 1.9}, with a L:W of 3.5 (5.0) 6.7 {n=6; SD: 1.3} and an area of 73 (152.5) 334 mm<sup>2</sup> {n=24; SD: 68.9}. Sterile surface indistinct, often bearing secondary imprints of seed scars. Fertile surface bears 80 (229.3) 387 seed scars {n=7; SD: 100} at a density of 23 (30.6) 40 scars per 25 mm<sup>2</sup> {n=9; SD:6.7}. Scars are circular to elliptical, closely spaced, raised cushions (in impressions), 0.8 (1.3) 2.4 mm long {n=48; SD:0.8}, 0.6 (1) 1.8 mm wide {n=47; SD:0.2}.

Wing is commonly concealed (possibly in-rolled), but when visible, is very narrow, with a width of 0.6 (1.3) 2.4 mm {n=11; SD:0.5} and a wing width: receptacle width of 0.1 (0.2) 0.5 {n=10; SD:0.1}. Wing bears faint striations and fluting perpendicular to the receptacle edge; margin is entire.

Fructifications are sessile, or borne on a short pedicel up to 3.8 mm long {n=4}, with a basal width of 1.2 (1.4) 1.7 mm {n=3}, expanding to 2.2 (2.5) 2.8 mm {n=3} at insertion.

Polysperm always found attached to the midrib (in the proximal 1/3) of an elliptical, oblong to elongate-obovate *Glossopteris* leaf with a long, tapering, cuneate base and a rounded to obtusely pointed apex. Leaf is 95 (132.3) 205.4 mm long {n=4; SD: 50.3}, 14.5 (26.7) 37.1 mm wide {n=20; SD:6.6}, with a 8.6 (9) 9.4 mm long {n=2}, 3.2 (3.4) 3.7 mm wide {n=3} petiole. Midrib is well-defined and persistent, 2.1 (0.6) 4.2 mm wide {n=15; SD:0.6} at base, tapering to 0.5 at apex; it is significantly more robust below the point of polysperm attachment, which is 12.7 (43.8) 80.6 mm {n=22; SD:15.6} from the leaf base. Veins follow a fairly straight path from the midrib to the margin, with a mid-laminal vein angle of 66° (79.2°) 89° {n=25; SD:6}, and a marginal vein angle of 72° (81.7°) 89° {n=21; SD:4.8}. Veins bifurcate and anastomose to form coarse, polygonal meshes adjacent to the midrib, becoming narrower and more elongated towards the margin; marginal vein density is 18 (21.8) 26 veins per 10 mm {n=16; SD:3}.

No specimens with attached seeds have been found.

### **Comments**

This is a slightly obscure taxon, which has been shuffled between various genera over the years, as discussed above. The most striking feature of this otherwise unremarkable fructification is the fact that it has only ever been found in attachment to its rather distinctive subtending leaf. All specimens that have been found are poorly preserved, indistinct impression fossils, and this has contributed significantly to the controversy surrounding the taxonomic status of the species. In several cases, only the secondary imprint left by the fructification in the subtending leaf is exposed [e.g. pl. 72, fig. (e); pl. 73, fig. (c)].

This species has a very high L:W of the receptacle, with the only comparable ratios seen in *Dictyopteridium* and *Gladiopomum*. The very low wing width: receptacle width falls within similar ranges to those of *P. gibbosa*, *Dictyopteridium* and *Gonophylloides*.

Some specimens of *P. lerouxii* appear to have a slightly cordate base, but this is apparently an artefact of preservation caused by extension of the robust tissues of the connective region a short way into the base of the receptacle [e.g. the type specimen, pl. 70, figs (e) and (f), pl. 70, fig. (b)]. The basal 'lobes' are adnate to the short pedicel/connective tissues along their entire length. In most cases the base is truncate. Specimen BP/2/14191 has an unusual, slightly hastate base, which may be created by small basal wing lobes, rather than being a reflection on the shape of the receptacle. The small, densely packed seed scars are most clearly visible in the holotype [pl. 70, fig. (e)], and specimens in pl. 71, figs (a) and (b).

In most cases, the wing is at least partially obscured in specimens of this taxon, perhaps due to its propensity for folding over the fertile surface. The presence of a wing is, however, indisputable, as evidenced by the holotype [pl. 70, figs (b) and (e)] and specimens in pl. 70, figs (c) and (d) (note the fluting of the wing), pl. 71, fig. (c) and its counterpart in pl. 72, fig. (c).

#### **7.7.4.2      *Plumsteadia gibbosa* (Benecke 1976) Anderson & Anderson 1985** emend.

1976 *Scopus gibbosus* Benecke, p. 104-105, figs 42-45, 55-81, 85, 89, 91, 92, 93, 94.  
 1976 *Scopus confertus* Benecke, p. 105, figs 46-54.  
 1976 *Scopus didiscus* Benecke, p. 106, figs 69, 81-84, 93, 94.  
 1976 *Scopus obscurus* Benecke, p. 107, figs 86, 87, 90, 93, 94.  
 1979 Fructification; van Dijk *et al.*, p. 114; pl. 46, fig. 31.  
 1985 *Plumsteadia gibbosa* (Benecke 1976) Anderson & Anderson, p. 125, pl. 93, figs 5, 6; pl. 94, figs 1-10; pl. 95, fig. 17; text-figs 125.1, 125.2, 125.3. non. pl. 93, figs 8, 9; pl. 94, figs 11-14; text-fig. 125.4.  
 1997 *Plumsteadia gibbosa*; Anderson & Anderson, p. 17, fig. 8a,b.

#### ***Holotype***

N-Lk 316a&b, designated by Benecke (1976; figs 42, 43); Paratypes  
 N-L 318, N-Lk 370, N-Lk 315a also assigned by Benecke (1976; figs 56, 71, 72, 73). All impression fossils housed in the Bernard Price Institute for  
 Palaeontological Research, University of the Witwatersrand, Johannesburg.

## ***Etymology***

Latin: *gibbosus* - bulgy, referring to the chunky nature of the seed scars on the receptacle (Benecke, 1976).

## ***Type formation and locality***

Loskop locality; Estcourt Formation; Upper Permian; eastern Karoo Basin.

## ***Emended species diagnosis***

Receptacle ovate to lanceolate with length to width ratio of 2-3.5; seed scars prominent and bulbous; ratio of wing width to receptacle width very low ( $<0.4$ ; av. 0.2). Wing is narrow with small basal lobes. Subtending leaf has cuneate base with steeply angled ( $20^{\circ}$ - $40^{\circ}$ ), gently arching venation with elongated polygonal to parallel meshes.

## ***Description***

(See pls 74-77, pl. 78, figs (a), (b); Table A.II.7, Appendix II for data summary).

Isobilateral, dorsiventral, multi-ovuliferous fructification with an overall length of 18.7 (26.4) 36.3 mm { $n=9$ ; SD:6.4} and width of 8.7 (10.7) 12.8 mm { $n=7$ ; SD:1.5}. Fructification comprises a bifacial receptacle, with sterile and fertile surface, flanked by a narrow wing.

Receptacle is ovate to narrowly lanceolate, with an acute apex and a truncate to rounded base; may be slightly asymmetrical (falcate). Receptacle is 16.4 (24.3) 35.4 mm long { $n=10$ ; SD:6.2} and 5.8 (8.3) 10 mm wide { $n=13$ ; SD:1.3} with an area of 95 (166) 295 mm<sup>2</sup> { $n=9$ ; SD:70.8} and a length to width ratio of 2 (2.9) 3.5 { $n=10$ ; SD:0.6}. Sterile surface is indistinct, in most cases obscured by secondary imprints of attached seeds or seed scars. Fertile surface bears 62 (105.5) 149 seed scars { $n=2$ } at a density of 15 (17.9) 21 scars per 25 mm<sup>2</sup> { $n=7$ ; SD:2.4}. Scars are elliptical, smooth, rounded cushions, in some cases with a central tubercle; they are 0.9 (1.4) 1.9 mm long { $n=47$ ; SD:0.2} and 0.6

(1) 1.4 mm wide {n=40; SD:0.2}. Marginal seed scars do not differ morphologically from medial scars.

Wing is narrow and entire with moderate to pronounced, persistent striations and fluting oriented perpendicular to the receptacle margin. Medial wing width is 0.8 (1.7) 2.6 mm {n=10; SD:0.6}, apical width is slightly greater at 0.9 (1.8) 3.6 mm {n=5; SD:1.1} and basal width is 1.5 (1.5) 1.6 mm {n=3}. Ratio of receptacle width to wing width is 0.1 (0.2) 0.4 {n=10; SD:0.1}. Small basal wing lobes are present in the holotype [pl. 74, figs (a), (b), (c) & (f)], giving the false impression of a cordate base.

Pedicel is longitudinally striated, 3.4 (5.7) 8 mm long {n=4; SD:2.1} and 1.3 (1.9) 2.3 mm wide at base {n=3; SD:0.5}, expanding slightly to 2 (2.9) 4 mm {n=5; SD:0.8} at insertion.

Numerous seeds were preserved in attachment to some of the fructifications, although obscured in many cases. Seeds are circular to elliptical, slightly pointed at one end (micropylar?), possibly with a very narrow wing. They are 1.4 (1.7) 2 mm long {n=10; SD:0.2} and 1.1 (1.3) 1.5 mm wide {n=10; SD:0.1}.

In several cases, specimens found attached to the petiole of a cuneate leaf base. Petiole broad (3.3 mm {n=2}), tapering to form a prominent midrib with a width of 1.9 to 1.3 mm {n=3} in proximal lamina; veins diverge from midrib at a steep angle, following a fairly straight to gently curving path to the margin, with a mid-laminal vein angle of 17° (21°) 24° {n=9; SD:2.9}, a marginal vein angle of 26° (33.5°) 43° {n=10; SD: 5.7}, and a marginal density of 5 (8.3) 10 veins per 10 mm {n=3}. Meshes are fairly broad, polygonal to parallel.

(Descriptions and measurements based on specimens from Loskop locality).

### **Comments**

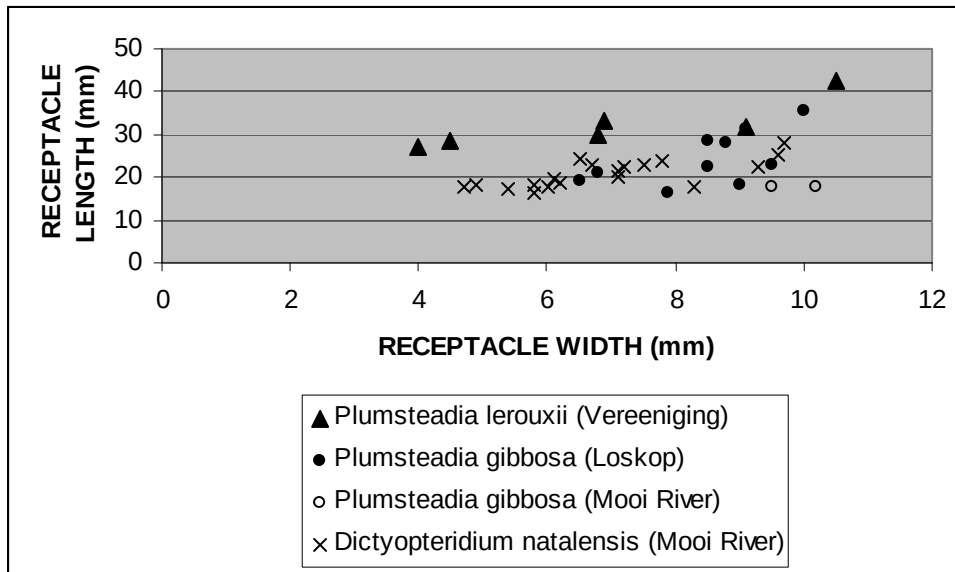
Anderson & Anderson (1985) did not provide a detailed diagnosis when they transferred Benecke's (1976) *Scopus gibbosus* to *Plumsteadia gibbosa*, simply

stating that these fructifications lacked a 'marginal rank of specialized ovules'. In a sense, this does reflect on the primary distinguishing feature of *P. gibbosa*, which is the chunky, bulbous nature of its seed scars. This results in a marginal row of seed scars that is not smoothly contiguous as seen in other fructifications such as *Dictyopteridium natalensis*. However, the seed scar - wing relationship is the same in *P. gibbosa*, as in all the other members of the Dictyopteridiaceae, and an important emendation of the specific diagnosis was the recognition of this arrangement, and acknowledgement of the presence of a well-developed (though in some cases fairly narrow) wing in all the specimens observed. Some specimens had wings which were partially obscured through folding or were poorly preserved, but there was always evidence to indicate the presence of such a structure. The wing is particularly well represented in specimens figured in pl. 74, figs (d) & (e), pl. 75, fig (b), pl. 76, figs (a)-(l).

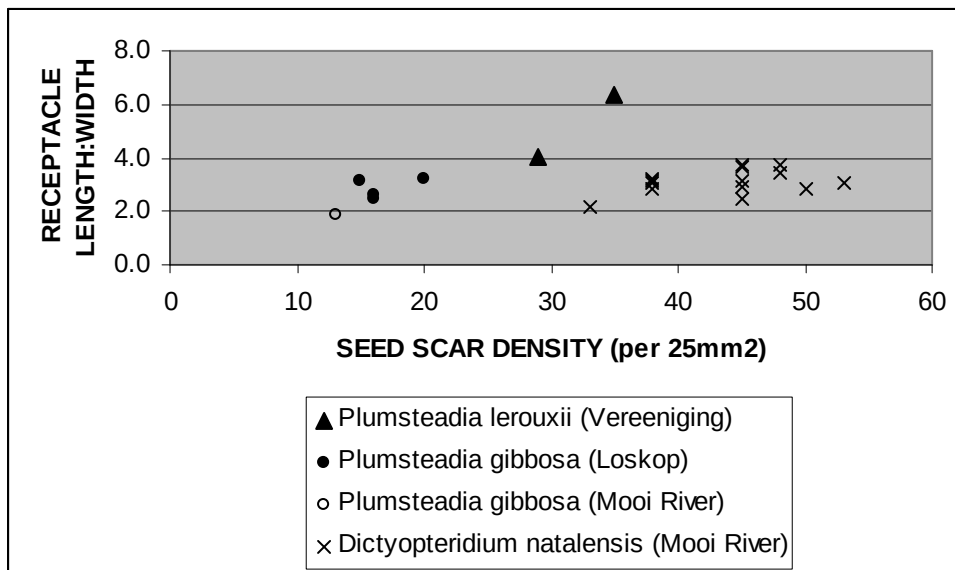
Anderson & Anderson (1985) listed the occurrence of 100 specimens of an 'Ottokariaceae fruit' from Inhluzane. Here they have been placed into *Plumsteadia gibbosa*, although they are poorly preserved and have not been included in the database of measurements for the taxon [see pl. 77, figs (f) and (g)]. The scatter-plot of total lengths and widths of these specimens alongside specimens of *P. gibbosa* from Loskop (the type locality) and Mooi River, support a strong affiliation (text-fig. 7.7.5).

The numerous attached seeds seen in several specimens, created large secondary imprints at the site of each seed scar, possibly exaggerating the size and bulbous nature of the scars. The bulbous nature of the scars and particularly the presence of attached seeds, created strong secondary imprints on the sterile surface in many of the fructifications [e.g. pl. 74, figs (a)-(f), pl. 75, figs (d) and (e), pl. 76, figs (k) and (l)].

### 7.7.5 DATA ANALYSIS

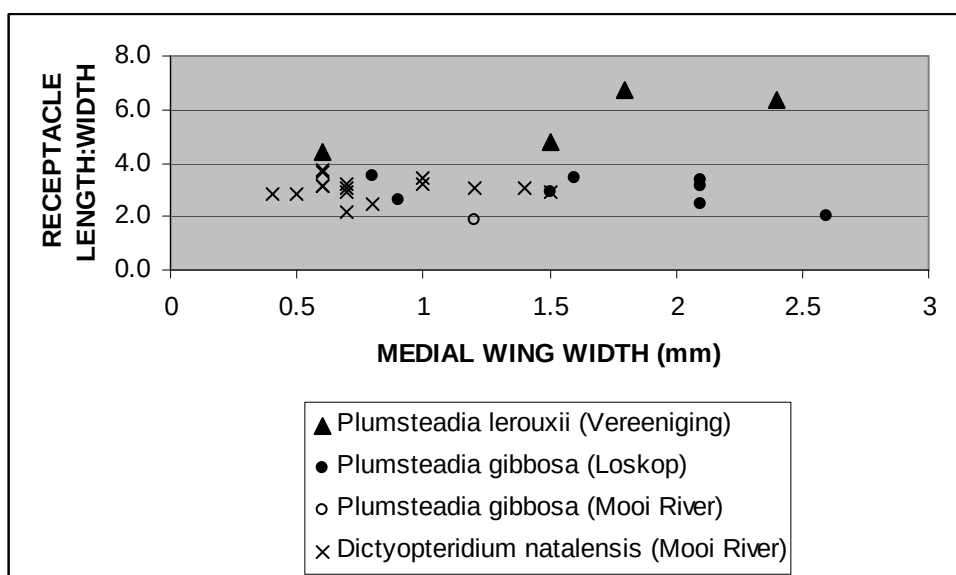


**Text-figure 7.7.2.** Scatter plot of receptacle lengths versus widths for *Plumsteadia lerouxii*, *Plumsteadia gibbosa* (from Loskop and Mooi River localities), and for comparative purposes, *Dictyopteridium natalensis*.



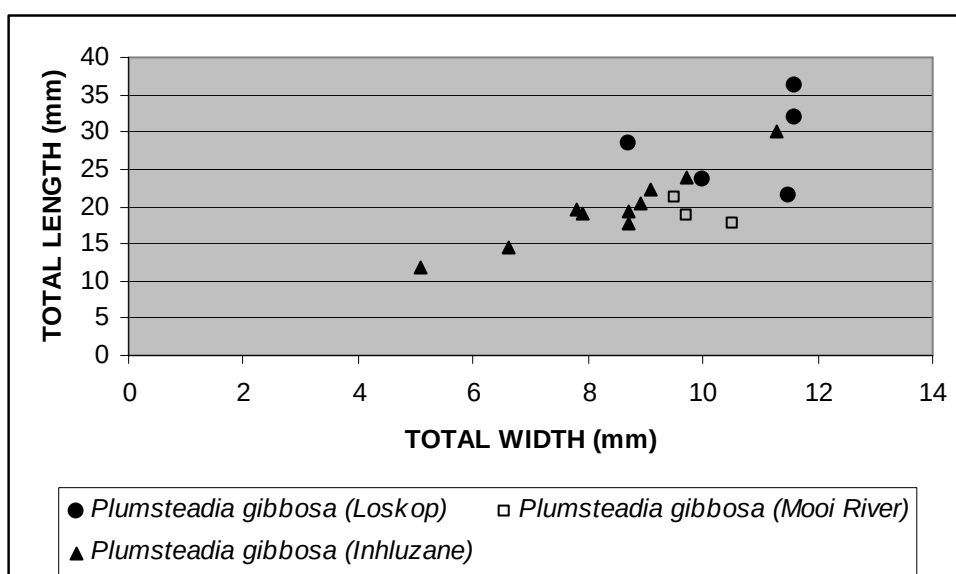
**Text-figure 7.7.3.** Scatter plot of seed scar densities versus ratios of receptacle lengths to widths, of *Plumsteadia lerouxii*, *Plumsteadia gibbosa* (from Loskop and Mooi River localities) and for comparative purposes, *Dictyopteridium natalensis*.





**Text-figure 7.7.4.** Scatter plot of medial wing widths versus receptacle length to width ratios of *Plumsteadia lerouxii*, *Plumsteadia gibbosa* (from Loskop and Mooi River localities), and for comparative purposes, *Dictyopteridium natalensis*.

In text-fig. 7.7.2, *P. gibbosa* and *Dictyopteridium natalensis* have closely overlapping ranges of receptacle lengths and widths, although *D. natalensis* tends to be slightly narrower. *Plumsteadia gibbosa* from Mooi River falls within similar size ranges to those specimens from Loskop, but tend to be slightly broader and shorter, and as evidenced in text-fig. 7.7.3, have lower seed scar densities.



**Text-figure 7.7.5.** A comparison of total length and width measurements for specimens of *Plumsteadia gibbosa* from three South African localities.

In text-fig. 7.7.3 *P. lerouxii*, *P. gibbosa* and *D. natalensis* can be clearly separated on the basis of seed scar density. *Plumsteadia gibbosa* has the lowest densities, *P. lerouxii* is intermediate, and *D. natalensis* has the highest seed scar densities.

Text-fig. 7.7.4 illustrates how *P. lerouxii* has the highest length:width ratios, and has a broad range of medial wing widths, that coincide with those of *P. gibbosa*. *Plumsteadia lerouxii* exhibits a very similar range of receptacle widths to *P. gibbosa*, although a small number of specimens are very narrow in comparison. *Plumsteadia lerouxii* is consistently longer than *P. gibbosa*. Although there is considerable overlap in the ranges of wing widths, the wings of *P. gibbosa* and *P. lerouxii* tend to be broader than in *D. natalensis*.

In text-fig. 7.7.5., *P. gibbosa* from Inhluzane shows the greatest range of sizes, and also includes the smallest specimens recorded for the taxon. The linear relationship between the length and width measurements is apparent in this plot, indicating a consistency in shape, irrespective of overall size of the fructification. The largest specimens of *P. gibbosa* are from the Loskop locality, and these appear to have a higher L:W than specimens from the other two localities.

#### 7.7.6 DISCUSSION

The scatter plots in section 7.7.5 differentiate *P. gibbosa* quite clearly from *P. lerouxii*.

Apart from their very different seed scar morphologies, *P. gibbosa* and *Dictyopteridium natalensis* are morphologically very similar. The fact that many of the specimens of *P. gibbosa* found at the type locality (Loskop) bore *in situ* seeds which appeared to exaggerate the bulbous nature of the seed scars, led the author to consider the option that these taxa may be taphomorphs, differing only in the presence or absence of attached seeds. The similarities in length to width ratios and sizes is clearly demonstrated in text-figs 7.7.2-7.7.4. However, medial wing widths tend to be narrower in *D. natalensis* (text-fig. 7.7.4), and

seed scar densities much higher (text-fig. 7.7.3). It is also highly unlikely that developmental stages would be restricted to particular localities - *D. natalensis* has not been found at Loskop, and only a few specimens of *P. gibbosa* have been found at the Mooi River locality. An additional difference relates to the morphology of the subtending leaves. The attached leaves of both genera have long, tapering bases, but the midrib in the subtending leaves of *D. natalensis* is not as prominent as in those attached to *P. gibbosa*, the marginal vein density is higher and the midlaminal vein angle is less acute.

If we consider the wide range of morphologies accommodated within the genus *Scutum*, there is probably a none-too-clear division between the two taxa, particularly when it comes to broad-winged specimens of *Plumsteadia*. Generally, *Scutum* tends to be more ovate, with a smaller L:W, and has a broad, prominent wing with well-defined fluting. *Plumsteadia* fructifications tend to have a greater L:W, and are more oblong to lanceolate, with a narrower wing. The distinction between *Dictyopteridium* and *Plumsteadia* is also not always clearly defined. As highlighted here by the similarities between *P. gibbosa* and *D. natalensis*, the only reliable difference between these taxa lies in their seed scar morphology. *Dictyopteridium* typically has a relatively smooth receptacle surface, with only very shallow delimitation of the seed scars, but with pronounced tubercles or cicatrices. The fructifications also tend to be lanceolate in shape.

Strong secondary imprints have contributed to structural misconceptions regarding both species of *Plumsteadia* described here. The prominent, protruding seed scars apparent in impressions of the fertile surface of *P. gibbosa* (which would have been deep hollows on the surface of the original plant organ) in most cases resulted in the formation of well-defined secondary imprints on the impression of the sterile surface. This phenomenon has contributed greatly to theories of radial symmetry in this group of fertile structures. In the case of *P. lerouxii*, secondary impressions of the fructification in the subtending leaf led Plumstead (1952) to hypothesise that the fructifications were borne within the leaf tissue. Other authors interpreted the smooth secondary imprints on the leaf as evidence of the fructification having a

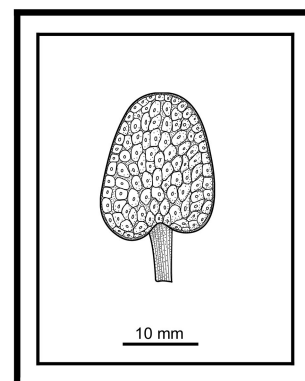
furled structure, with the seed scars completely obscured. Careful observations of the impression fossils have confirmed that these fructifications have the same basic structure as other members of the Dictyopteridiaceae, the elongated receptacle with seed scars on the surface facing the leaf, the opposing surface being veined and sterile. The presence of a narrow but distinct wing was also confirmed.

'*Lanceolatus*'-type fructifications have been reported from India (Chatterjee & Sen, 1963) and South America (Menéndez, 1962b). These fructifications are both indistinct, poorly preserved structures in sessile attachment to the midrib of a *Glossopteris* leaf. In neither case does the *Glossopteris* leaf resemble those from South Africa bearing *Plumsteadia lerouxii*. Menéndez (1962b) described a small, elongate-ovate fructification, apparently with an in-rolled wing. The fructification, although poorly preserved, exhibited the presence of seed scars/ovules and possibly wing fluting. The specimen may well be an immature fructification, especially considering its small size. Chatterjee & Sen's (1963) fructification was of a similar size to the South American specimen, and had clearer evidence of seed scars or ovules on its surface. Both these fructifications fall within the broad circumscription of *Plumsteadia*, but allocation to a species is probably not appropriate on the basis of individual specimens. *Plumsteadia* has been reported from both Lower and Upper Permian strata in India (e.g. Maheshwari, 1965b, 1968; Mukherjee *et al.*, 1966; Chandra & Surange, 1977b; Srivastava, 1978), Antarctica (Kyle, 1974), South America (Menéndez, 1962b; Archangelsky & Bonetti, 1963), Australia (White, 1963; Rigby, 1971, 1978; McLoughlin, 1990b) and South Africa (Lacey *et al.*, 1975; Benecke, 1976; Anderson & Anderson, 1985). The very broad temporal and spatial distribution may well be a reflection on the polyphyletic nature of the taxon. The diagnosis for this genus is probably too broad, and may provide refuge for a wide range of phylogenetically diverse, but morphologically convergent taxa.

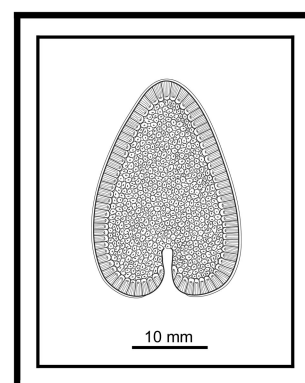
## 7.8 *GONOPHYLLOIDES* Maheshwari 1968 emend.

### 7.8.1 INTRODUCTION

Plumstead (1958a) instituted the genus *Cistella* for ovuliferous fructifications from the Vereeniging quarries which she described as resembling 'little heart-shaped caskets' ('*cistella*' is Latin for casket). She distinguished them from *Lanceolatus* (here referred to *Plumsteadia*) on the basis of their being 'free' as opposed to embedded within the leaf tissue. As discussed in section 7.7.1, her views on the morphology of *Lanceolatus* were based on a misinterpretation of the preservation of the material, and these fructifications were borne on their subtending *Glossopteris* leaves in the same manner as other members of the Dictyopteridiaceae.



*Gonophylloides waltonii*



*Gonophylloides strictum*

Wesley (1963), Maheshwari (1968) and Rigby (1969) noted that the name *Cistella* was preoccupied by both a fungus (Nannfeldt, 1932) and an orchid (Blume, 1825) and was therefore not a legitimate name for the taxon according to the International Code for Botanical Nomenclature (ICBN).

There have been various responses in the literature to this nomenclatural dilemma. Maheshwari (1968) proposed that *Cistella* be given a new name, *Gonophylloides*. Rigby (1969; 1978) transferred all species of *Cistella* to the 'melting pot' genus *Plumsteadia*, a decision supported by Plumstead (1969). Chandra & Surange (1977b) assigned the new generic designation '*Plumsteadiostrobos*' to *Cistella indica* Maheshwari 1965 = *Plumsteadia indica* (Maheshwari) Rigby 1968 = *Gonophylloides indicum* (H.K. Maheshwari) J.K. Maheshwari 1968. They did not give a valid reason for creating a new genus instead of emending either *Plumsteadia* or *Gonophylloides*, only stating that both these names were based on misinterpretations of the fossil material.

According to the ICBN, a name cannot be rejected on the basis of inappropriateness.

Benecke (1976) maintained that the group of specimens from Vereeniging was distinct enough to warrant segregation within a unique genus, apart from *Plumsteadia*, and she retained use of the name *Cistella* for these fructifications. Smithies (1978) described a single specimen from the Hammanskraal locality in South Africa that was strikingly similar to *Cistella stricta* in both fructification and leaf morphology. She chose to use Maheshwari's (1968) emended name for *Cistella*, referring the specimen to *Gonophylloides strictum*. Anderson & Anderson (1985) transferred the Vereeniging specimens to Plumstead's (1952) genus *Lanceolatus*, which has been hotly contested on many occasions for being an unmodified technical term, and therefore in contravention of Article 20 of the ICBN (Tokyo Code; Greuter *et al.*, 1994).

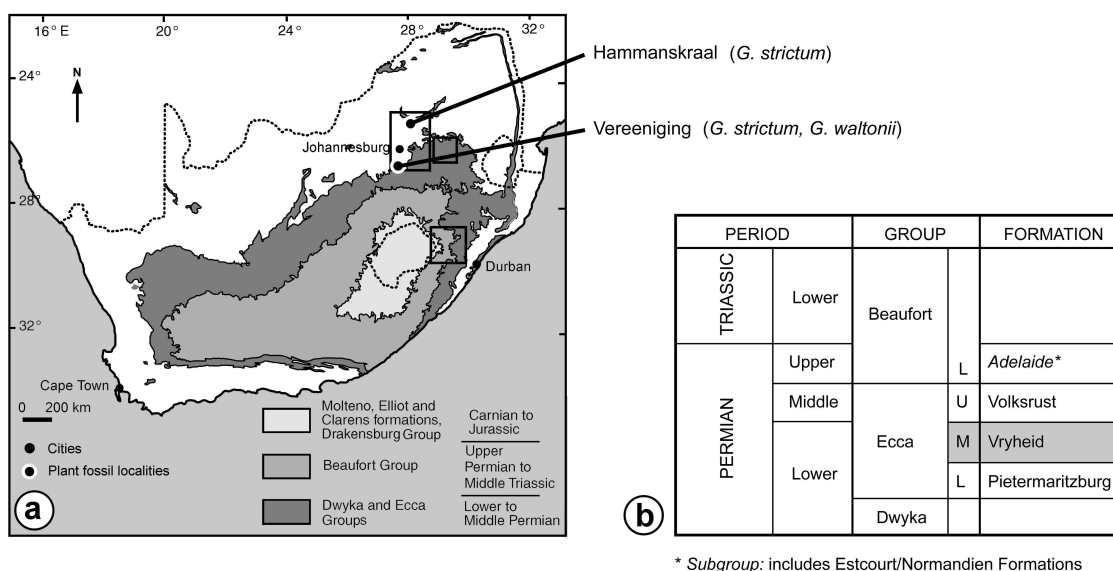
According to Article 11.3 of the ICBN (Tokyo Code, Greuter *et al.*, 1994), in a case such as this, with a history of multiple synonymisations, the correct designation is the earliest legitimate name of the same rank. Here the taxon is regarded as separate from *Plumsteadia* and '*Lanceolatus*' on the basis of its distinctive, cordate base and relatively low length to width ratio, respectively. The earliest legitimate generic designation is therefore Maheshwari's (1968) *Gonophylloides*.

### **7.8.2 FOSSIL MATERIAL**

All specimens are impression fossils in a soft claystone typical of the Vereeniging locality. A total of 15 specimens of *G. strictum*, and 4 specimens of *G. waltonii* were examined. Specimens are housed in the Vaal Teknorama Museum in Vereeniging and the Bernard Price Institute for Palaeontology, University of the Witwatersrand, Johannesburg (see Table A.I.12, Appendix I).

### 7.8.3 LOCALITY INFORMATION

Specimens originated from the Vereeniging and Hammanskraal localities (see Text-figs 2.2.2, 2.2.3a, 2.2.5 & 7.8.1; Section 2.2.2.14 for additional locality information). According to Le Roux and Anderson (1977), all Vereeniging specimens originated from the Shale Quarry. The deposits at Vereeniging are part of the Vryheid Formation, northern Karoo Basin. A single specimen has been reported from the Hammanskraal quarries, Bushveld Basin, Vryheid Formation equivalent (Smithies, 1978). Both localities are Lower Permian (Artinskian).



\* Subgroup: includes Estcourt/Normandien Formations

**Text-figure 7.8.1.** (a) Locality map indicating reported occurrences of *Gonophylloides* in South Africa; (b) lithostratigraphic table of the Permian and Lower Triassic deposits in the northern and eastern parts of the Karoo Basin, with shaded areas representing stratigraphic occurrences of *Gonophylloides* (table adapted from Keyser, 1997).

### 7.8.4 SYSTEMATIC PALAEOBOTANY

#### *Type species*

*Gonophylloides strictum* (Plumstead 1958) Maheshwari 1968 emend.

## ***Etymology***

*Gonophylloides* - according to Maheshwari (1968): 'by virtue of its apparent resemblance to one of the gonophylls', with reference to Melville's (1960) 'gonophyll theory' of angiosperm evolution from the glossopterids.

## ***Emended generic diagnosis***

Bilateral, dorsiventral, ovuliferous fructification with a veined sterile surface and a fertile surface bearing numerous, densely packed seed scars. Ovate, to broadly lanceolate receptacle with a cordate to auriculate base, and a L:W ratio of approximately 1.5:1; very narrow, indistinct wing and/or groove along periphery of receptacle.

## ***Discussion***

The primary distinguishing features of the genus are the pronounced cordate to auriculate base, and the very narrow wing. In other respects there is a fair degree of overlap with *Plumsteadia*, and is it understandable why these fructifications have been synonymised in the past (Rigby, 1969, 1978).

The circumscription for *Plumsteadia* is very broad, and the genus probably represents a phylogenetically diverse group of superficially similar fructifications with ovate, elliptical to broadly lanceolate receptacles with a narrow to fairly broad peripheral wing and well-defined, contiguous seed scars comprising a cushion (in impressions) with a central tubercle.

Here, Plumstead's (1952) genus *Lanceolatus* has been transferred to *Plumsteadia*, although it may belong within its own genus. The generally poor preservation of specimens of the type species (*P. lerouxii*) from Vereeniging, and the lack of distinctive characters, made the erection of a unique genus difficult to justify. *Gonophylloides* differs from *P. lerouxii* in having a smaller L:W and a more pronouncedly cordate base. *Plumsteadia lerouxii* has a more lanceolate shape, with a long, narrow, pointed apex, whereas in *Gonophylloides*



it is bluntly and obtusely rounded. Some specimens of *P. lerouxii* appear to have a slightly cordate base, but this is apparently an artefact of preservation. The subtending leaf of *P. lerouxii* is very different to that of *Gonophylloides strictum*.

**7.8.4.1      *Gonophylloides strictum*** (Plumstead 1958) Maheshwari 1968 emend.

1958 *Cistella stricta* Plumstead; p. 65-66, pl. 18, 19, 20 [1958a] [Basionym].  
1968 *Gonophylloides strictum* (Plumstead 1958) Maheshwari; p. 238.  
1969 *Plumsteadia stricta* (Plumstead 1958) Rigby; p. 93.  
1969 *Plumsteadia stricta* (Plumstead 1958) Rigby; Plumstead; pl. 12, fig. 8.  
1978 *Gonophylloides stricta* (Plumstead 1958) Maheshwari; Smithies, p. 90, fig. 16.  
1985 *Lanceolatus strictus* (Plumstead 1958) Anderson & Anderson; p. 123, pl. 89, figs 1-11, pl. 90, figs 1-6, pl. 95, fig 14; text-figs 123.1-3.

***Holotype***

Part and counterpart of a fertiliger, BP/2/14233, housed at the Bernard Price Institute, University of the Witwatersrand, Johannesburg; Plumstead (1958a), pl. 18, figs 1 & 1a; Anderson & Anderson (1985), pl. 89, figs 3, 4.

***Etymology***

Latin: *strictum* - after *Glossopteris stricta*, the name assigned by Plumstead (1958a) to the subtending leaf of this taxon.

***Type formation and locality***

Vryheid Formation (middle Ecca Group); Lower Permian (Artinskian); Vereeniging, northern Karoo Basin.

***Emended species diagnosis***

Receptacle ovate to broadly lanceolate with pronounced, rounded, basal auricles. Seed scars small and numerous. Sterile surface bears fine-meshed venation that radiates from point of attachment to subtending leaf. Fructification sessile, borne in lower third of long, narrowly elliptical *Glossopteris* leaf with fine, gently arching to straight venation with mid-laminal angle of approximately 60°,

and elongate polygonal to parallel meshes. Usually preserved in attachment to subtending leaf.

### **Description**

(See pls 79-80, pl. 81, figs (a)-(d), pl. 82, figs (b)-(d); Table A.II.8, Appendix II for data summary).

Dorsiventral, bilateral, capitate fructifications, 14.3 (24) 34 mm {n=10; SD:6} long, and 11.3 (16.5) 27.8 mm {n=16.5; SD:4.6} wide, with a gross L:W ratio of 1.2 (1.5) 2.5 {n=10; SD:0.4}. The elliptical, ovate, elongate ovate to broadly lanceolate receptacle has a moderately cordate to sagittate base, and a rounded to moderately acute apex. The receptacle is 13.1 (22.8) 32.4 mm {n=9; SD:6.2} long, and 9.7 (15.3) 25.4 mm {n=13; SD:4.6} wide, with a L:W ratio of 1.2 (1.6) 2.8 {n=8; SD:0.5} and an area of 137 (314) 726 mm<sup>2</sup> {n=11; SD:165.2}. Basal lobes range from moderate rounded extensions to prominent auricles, 2 (4.8) 7.4 mm {n=9; SD:2.2} deep, on either side of the point of attachment to the subtending leaf. The receptacle is flanked by a very narrow, indistinct wing with radial striations and fluting, and with a medial width of 0.7 (1.1) 1.4 mm {n=4; SD:0.3}. There is a narrow, 0.6 (0.8) 0.9 mm {n=12; SD: 0.1} wide, slightly irregular groove in the matrix along the periphery of the receptacle in some specimens. Seed scars are elliptical to circular, raised cushions with a central depression. The marginal scars are more rectangular, forming a regular rank along the periphery of the receptacle corresponding to the positions of wing flutes. The peripheral scars are 0.7 (0.9) 1.1 mm wide {n=11; SD:0.1} and the central scars are 0.6 (1) 1.7 mm long {n=29; SD:0.3}, and 0.5 (0.8) 1.1 mm wide {n=25; SD:0.1}. Seed scar density is 24 (44) 66 scars per 25 mm<sup>2</sup> {n=5; SD:16.3}, with an estimated total number of 79 (378.2) 955 {n=5; SD:344} scars. The sterile surface bears fine veins that bifurcate and anastomose to form narrow meshes that radiate out across the receptacle from the point of attachment to the subtending leaf. The fructifications are sessile, borne on the midrib of a long, narrowly elliptical *Glossopteris* leaf with a cuneate base. The midrib bears prominent striations, and is broad, 3.3 (4.8) 5.9 mm {n=6; SD:1.4}, and robust in the base of the leaf, tapering towards the apex. The fructification is

borne in the basal third to quarter of the subtending leaf. Leaf venation is fine, with a marginal vein density of 18 (25.2) 34 veins per 5 mm {n=5; SD:7}. Veins arch gently from the midrib, following a fairly straight path across the mid-laminal and marginal parts of the lamina, at an angle of 53° (59.9°) 64° {n=7; SD: 3.6} (mid-laminal) to 63° (71.7°) 80° {n=9; SD:6.6} (marginal) to the midrib. Veins anastomose and bifurcate regularly to form elongate polygonal meshes immediately adjacent to the midrib, becoming linear/parallel in the mid-laminal to marginal parts of the lamina.

### **Comments**

Nearly all the examples of this fructification were found attached to a *Glossopteris* leaf. Attachment was sessile in all cases. Fig. (f) is an unusual example of an isolated fructification.

There was a slightly irregular, but distinct groove, or step around impressions of some of the fructifications. This is particularly well-illustrated in pl. 79, figs (a), (b), (d) and (g). The narrow wing is difficult to see in most specimens. It is clearest on the lower left side of the fructification in pl. 79, fig. (d) [drawing of this specimen on pl. 82, fig.(c)].

Perhaps the most striking feature of this taxon, aside from its tiny, densely packed seed scars, is the deeply lobed base. This is particularly evident in the specimens illustrated in pl. 79, fig. (c) and (d) and pl. 80, figs (a) and (b). The reconstruction of *G. strictum* was based on specimen BP/2/14225 [pl. 79, fig. (d), pl. 82, fig. (c)].

Data from the single Hammanskraal specimen reported by Smithies (1978; pl. 81, fig. (d) this document) were not included in the description as the original specimen was not available for examination. However, measurements made from the photograph provided by Smithies (1978) do fall within the upper ranges of the examples from Vereeniging (see text-figs 7.8.2-3 for a graphical representation). The dimensions of the fructification, as well as the broadly

ovate shape, cordate base and features of the subtending leaf, are all consistent with the diagnosis for *G. strictum*.

#### **7.8.4.2      *Gonophylloides waltonii* (Plumstead 1958) Maheshwari 1968 emend.**

1958 *Cistella waltonii* Plumstead; p. 67, pl. 21, figs 1, 1a [1958a] [Basionym].

1968 *Gonophylloides waltonii* (Plumstead) Maheshwari; p. 238.

1969 *Plumsteadia waltonii* (Plumstead) Rigby; p. 93.

1985 *Lanceolatus waltonii* (Plumstead) Anderson & Anderson; p. 123, pl. 89, figs 12-17, pl. 95, fig. 15; text-fig. 123.5.

#### ***Holotype***

Part and counterpart, BP/2/14239a&b; housed at the Bernard Price Institute, University of the Witwatersrand, Johannesburg; pl. 21, figs 1&1a, Plumstead (1958a); pl. 89, figs 12, 13, pl. 95, fig 15, Anderson & Anderson (1985); pl. 81, figs (e) and (f), pl. 82, fig. (a), this document.

#### ***Type formation and locality***

Vryheid Formation (middle Ecca Group); Lower Permian (Artinskian); Vereeniging, northern Karoo Basin.

#### ***Emended species diagnosis***

Pedicellate, ovate fructification, with moderately cordate base; seed scars large and prominent, sterile surface bears strong secondary imprints of seed scars, venation indistinct.

#### ***Description***

(See pl. 81, figs (e)-(i), pl. 82, fig. (a); Table A.II.8, Appendix II).

Bilateral, dorsiventral, pedicellate ovuliferous fructification, 19.4 (19.7) 20 mm long {n=2}, 13.1 (14.8) 15.9 mm wide {n=3}, with a L:W ratio of 1.3 (1.4) 1.5 {n=2}. Pedicel 2.2 (8.3) 11.1 mm long {n=4}, 2.1 (3) 4.1 mm wide {n=4} at

insertion, tapering to 1.8 (2.1) 2.6 mm {n=3} at the base. Receptacle ovate, with rounded apex and moderately cordate base; 17.4 (17.7) 18 mm long, {n=2} 10.6 (13.9) 15.9 mm wide {n=3} with a L:W of 1.2 (1.4) 1.6 {n=2}, and an area of 150 (185) 220 mm<sup>2</sup> {n=2}. Basal lobes rounded, 1 (1.5) 2 mm deep {n=2}. Seed scars relatively large and prominent cushions with a deep central depression. Central seed scars 1.4 (2) 2.7 mm long {n=16}, 0.9 (1.2) 1.5 wide {n=14}, elliptical and tending to be longitudinally oriented; marginal seed scars 1 (1.3) 1.5 mm long {n=18}, more rectangular in shape than central scars, forming a regular rank along periphery of receptacle. Seed scar density is 9 (16.8) 26 scars per 25 mm<sup>2</sup> {n=4}, and total number of scars is estimated at 79 (117.5) 156 {n=2}. Receptacle is flanked by a very narrow, indistinct wing with a medial width of 1.3 (1.4) 1.4 mm {n=2}, and in some cases there is a peripheral groove along the edge of the receptacle. Sterile surface bears rough elliptical markings corresponding to seed scars on fertile surface; venation ill-defined. Only isolated specimens have been found.

### **Comments**

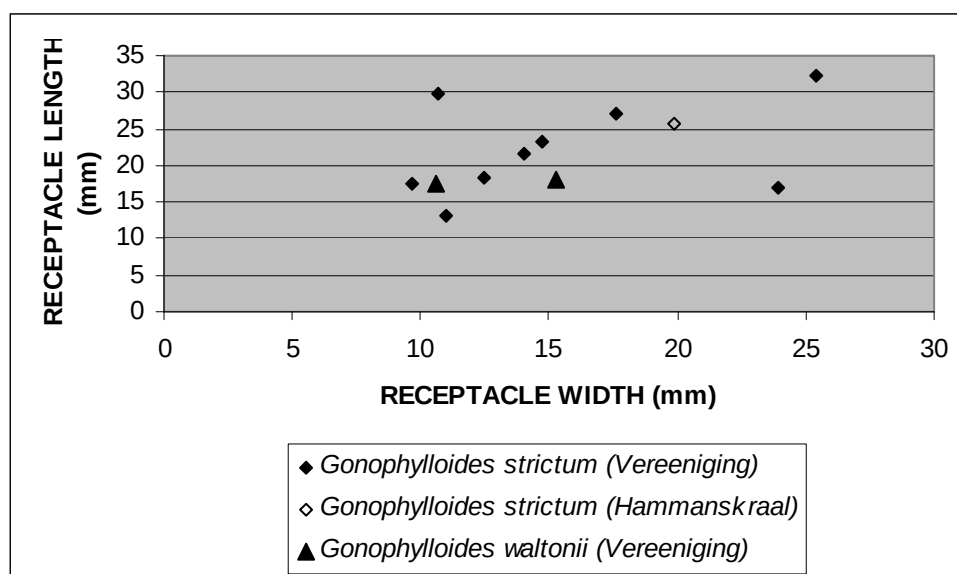
Some specimens, notably the holotype [pl. 81, fig. (e) and (f)], have prominent secondary imprints of the seed scars on the sterile surface of the fructification, in most cases completely obscuring detail of the venation. Although indistinct, venation is visible in specimen VM/03/3205/81 [pl. 81, fig. (i)].

As in *G. strictum*, there is a narrow groove running along the periphery of the receptacle, which is most clearly evident in the holotype [pl. 81, figs (e) and (f)]. There appears to be a narrow, poorly defined peripheral wing in specimens BP/2/14238 and VM/03/3205/81 [pl. 81, figs (g)-(i)]. VM/03/3205/81 is a somewhat enigmatic specimen, which may represent an unusual example of *G. strictum*. The size and shape of the specimen conforms to *G. waltonii*, but the absence of large, prominent seed scars or secondary imprints thereof, is more in line with a specimen of *G. strictum*.

The primary distinguishing features of this species are the large seed scars, short, squat shape and moderately lobed base. All specimens found have been isolated structures.

### 7.8.5 DATA ANALYSIS

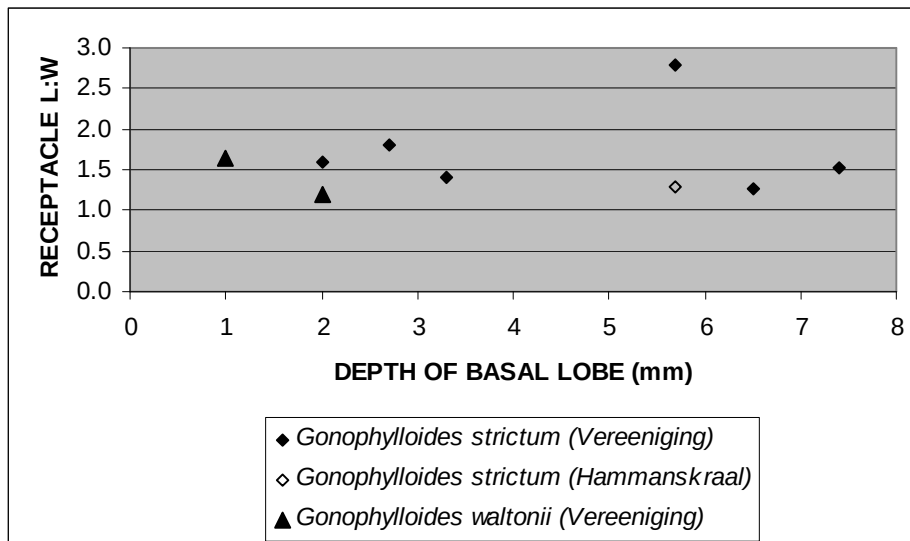
Various plots of quantitative features of *G. strictum* and *G. waltonii* were generated (text-figs 7.8.2-5). These plots indicate that *G. waltonii* falls within the lower dimensional ranges of *G. strictum*, and although it is clearly on the fringes, this species should rather be distinguished on the basis of its qualitative differences.



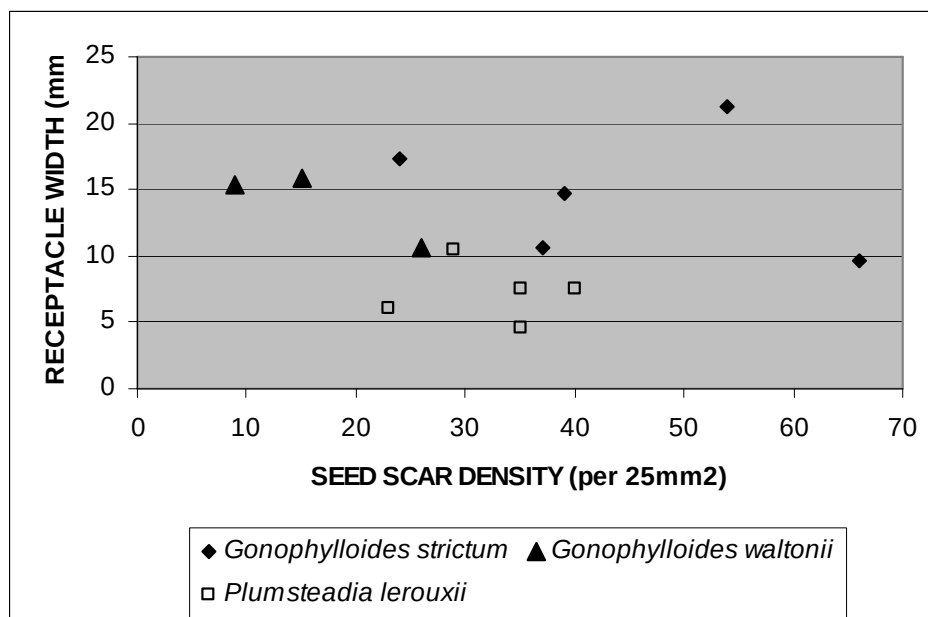
**Text-figure 7.8.2.** Scatter plot of receptacle lengths and widths of *Gonophylloides strictum* and *G. waltonii*.

Length to width ratios of the specimens depicted in text-fig. 7.8.2. are fairly constant for both taxa, apart from a single specimen of *G. strictum* that is particularly long and narrow. There is a tendency towards a linear relationship between length and width for *G. strictum*, although some data points deviate significantly, with the broadest specimen also being one of the shortest. *Gonophylloides waltonii* falls within the lower size ranges of *G. strictum*, and tends to be more ovate in shape.

Basal lobe depth, although variable, appears to be unrelated to the proportions of the receptacle. In text-fig. 7.8.3 *G. waltonii* barely overlaps the lower range of basal lobe depth for *G. strictum*.



**Text-figure 7.8.3.** Scatter plot of the receptacle length to width ratios and the depth of the basal lobes, for *Gonophylloides strictum* and *G. waltonii*.

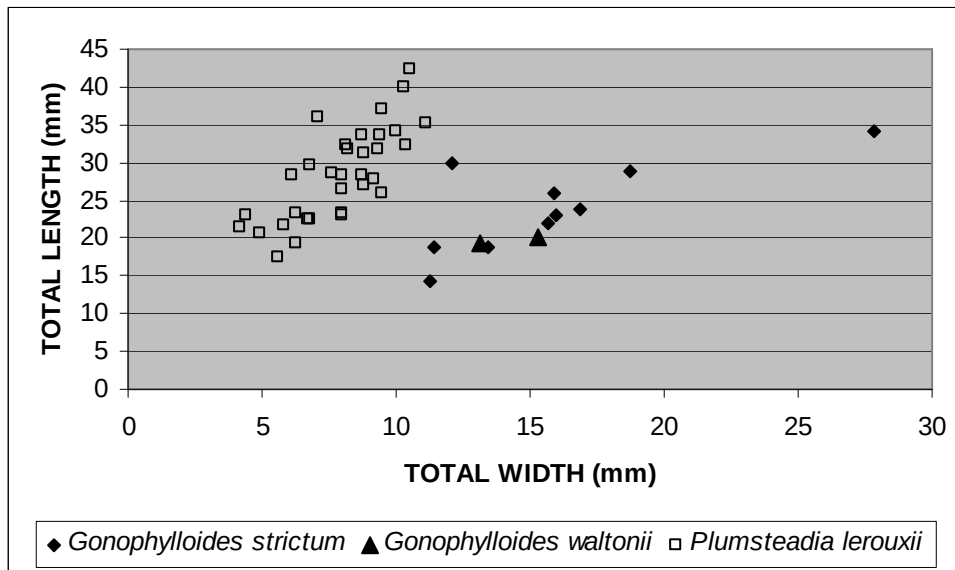


**Text-figure 7.8.4.** Scatter plot of receptacle widths versus seed scar densities of *Gonophylloides strictum*, *G. waltonii* and *Plumsteadia lerouxii*.

In text-fig. 7.8.4, *G. waltonii* and *G. strictum* have similar receptacle widths, but seed scar densities are lower in *G. waltonii*. *Plumsteadia lerouxii* has similar seed scar densities to *G. strictum*, but has narrower receptacles.

Text-fig. 7.8.5 dramatically illustrates the separation of data points of the two *Gonophylloides* species from *Plumsteadia lerouxii*, which tends to be narrower and longer, and shows a strong linear relationship between length and width.

The specimen of *G. strictum* from Hammanskraal falls within the upper limits of the dimensional ranges for the Vereeniging specimens.



**Text-figure 7.8.5.** Scatter plot of total length and widths of *Gonophylloides strictum*, *G. waltonii* and *Plumsteadia lerouxii*.

## 7.8.6 DISCUSSION

These two species have been moved back and forth between genera since Plumstead (1958a) first described them, perhaps because they are fairly generalised capitate fructifications lacking a distinctive wing morphology.

The similarities between *Lanceolatus* and *Gonophylloides* have been discussed already. The gross morphological differences in both the shape and proportions of the fructifications, and the large differences between the subtending leaves of the two taxa were deemed sufficient in the context of glossopterid ovuliferous fructification taxonomy, to retain these fructifications in separate genera.

The slightly irregular, but pronounced groove around the receptacle of some of the fructifications of both *G. strictum* and *G. waltonii* is puzzling. It could be



caused by the presence of a rudimentary flange or secondary wing such as that seen in *Bifaria*, but there is no direct evidence for such a feature.

White (1963) described *Cistella bowenensis* and *Cistella ampla* from the Upper Permian of the Bowen Basin in Australia. These fructifications lack a cordate base, and are probably both better attributed to species of *Plumsteadia*. Rigby (1978) described a group of circular to broadly ovate fructifications with a narrow wing, well-defined seed-scars and a prominently cordate base, which he named *Plumsteadia semnes*. These fructifications, from the Early Permian Blair Athol Coal Measures may be referable to *Gonophylloides*.

Maheshwari (1965b) described *Cistella indica* from India, which he later (1968) transferred to *Gonophylloides indicum*. As mentioned earlier, Chandra & Surange (1977) moved *G. indicum* to *Plumsteadistrobus ellipticus*. Both these taxa could probably be synonymised with *Plumsteadia indica*, as suggested by Rigby (1969) for *Cistella indica*.

A specimen which may well belong in *Gonophylloides*, was figured by Lambrecht *et al.* (1972) as *Plumsteadia waltonii*. The fructification was found in the Law Glacier area of the Transantarctic Mountains in Antarctica, in sediments the authors considered equivalent to the uppermost parts of the Ecca Series of South Africa. Although poorly preserved, the fructification appears to be ovate with a cordate base. There may be a small section of wing with radial striations and fluting preserved on the left side of the fructification.

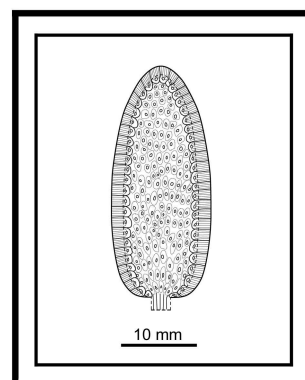
## 7.9 *DICTYOPTERIDIUM* Feistmantel emend. McLoughlin 1990

### 7.9.1 INTRODUCTION

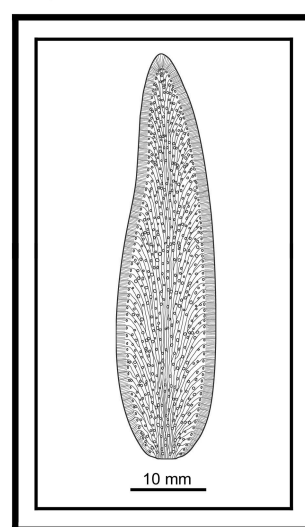
*Dictyopteridium sporiferum*, originally described from the Raniganj Formation in India by Feistmantel (1881), was the very first glossopterid fructification to be figured in the literature. Feistmantel (1881; pl.23A, fig. 4) initially described it as a flat, fern-like leaflet with sori. Zeiller (1902; pl. 4, fig. 8) re-interpreted the organ as a fleshy rhizome with the tubercles representing marks left by rootlets. Although subsequent workers recognised that it was probably a glossopterid fertile structure, it was only in 1976 that Chandra and Surange unequivocally demonstrated organic attachment of members of this genus to the *Glossopteris* leaf.

The genus has been variously emended over the years, e.g. Surange & Chandra (1973a), Banerjee (1973) and Benecke (1976). The most recent and comprehensive review and revision of the fructification was presented by McLoughlin (1990a), and his morphological and taxonomic interpretations are followed here. The numerous emendations of *Dictyopteridium* have stemmed largely from a history of disagreement amongst authors about the basic morphology of the fructifications.

Some authors have consistently regarded *Dictyopteridium* to be a radially symmetrical, cone-like organ with a protective sterile bract (Surange & Chandra, 1973a, 1974a, 1975). Others (e.g. Maheshwari, 1965b; Benecke, 1976; Anderson & Anderson, 1985; McLoughlin, 1990a) considered it to be a dorsiventrally flattened structure, on the basis of there being net venation on one of the surfaces of the fructification. Surange and Chandra (1973a) originally refuted the existence of anastomosing venation in any specimen of *Dictyopteridium*. They criticised Feistmantel's (1881) original description of the



*Dictyopteridium natalensis*



*Dictyopteridium flabellatum*

specimens he assigned to *D. sporiferum*, contesting his observation that some of the fructifications showed evidence of fine net venation, and claiming that the only one of his specimens that did have venation was a small *Glossopteris* leaf. In fact, the specimen they referred to is clearly an impression of the sterile surface of a *Dictyopteridium* fructification, complete with a peripheral wing (see Surange & Chandra, 1973; pl.1, fig. 7). They also dismissed Maheshwari's (1965b) account of *Dictyopteridium* with faint venation between the scars, summarily attributing the phenomenon to 'wrinkles' on the surface of the specimen. Maheshwari (1965b) even described how he extracted two layers of cuticle from his specimen of *Dictyopteridium*, one of which bore distinct venation patterns. Still Surange & Chandra (1973a) adhered to their argument that the fructification was a radially symmetrical strobiloid structure bearing seeds across the entire surface of the fructification, stating how unlikely it would be 'that a fructification would have such unusual structure, seeds on one face and net venation on the other'. In their 1974a paper, Surange & Chandra finally acknowledged the presence of venation on one surface of the polysperm, but have since tenaciously interpreted this as evidence for the presence of a sterile bract covering one side of a cylindrical or conical receptacle.

Although Banerjee (1973) acknowledged the dorsiventral nature of the fructifications, she regarded both surfaces of the receptacle to be seed-bearing, and also endorsed the presence of a sterile bract. Benecke (1976), whilst acknowledging the dorsiventral, bilateral and bifacial nature of the receptacle, adopted Plumstead's (1952, 1956a,b, 1958a) ideology of a bipartite structure with a sterile and a fertile 'half'.

Rigby (1972b, 1978) initially considered *Dictyopteridium* to be a radially symmetrical strobilus lacking a wing, and instituted *Isodictyopteridium* for linear to lanceolate, dorsiventral, tuberculate fructifications with a continuous marginal wing. He based his diagnosis on an Australian specimen of *Dictyopteridium* originally described by Walkom (1922). Holmes (1974) characterised both *Dictyopteridium* and *Isodictyopteridium* as laminate, sporangiate organs of *Glossopteris*, and did not clearly state how he distinguished between the taxa. He described a new species, *I. costatum*, which had a fluted wing with a

scalloped margin, and a very pronounced medio-longitudinal aggregation of veins, which had seed scars characteristic of *Dictyopteridium*. Holmes (1974) described a specimen of *D. sporiferum* which had pits on the part and tubercles on the counterpart. As discussed by McLoughlin (1990a), this provided further evidence for bilateral rather than radial symmetry of the organ. The presence of secondary imprints (as described in Chapter 3) has apparently contributed significantly to views of radial symmetry in the glossopterid fructifications.

Surange & Chandra (1974a) dismissed Rigby's (1972b) insistence on the presence of a wing in *Isodictyopteridium*, suggesting it did not 'look like a structural feature', and was 'untenable'. They suggested that 'a little lateral compression of marginal seeds can enhance a wing-like impression', and recommended that *Isodictyopteridium* and *Dictyopteridium* be synonymised. Surange & Chandra (1974a) apparently overlooked Rigby's (1972b) observation that veins on the sterile surface of the fructification continued into the wing, and the fact that no seeds were present on the specimen. The lectotype of *D. sporiferum*, refigured by Surange and Chandra (1973, pl.1, fig.1), clearly possesses a narrow fluted wing, and others show even more distinct wings (pl.1; figs.5, 8).

Banerjee (1973) acknowledged the presence of a fluted wing in her revised diagnosis of the genus, although she referred to the structure as a 'marginal flap' rather than a wing. Specimens figured by Benecke (1976) and McLoughlin (1990a) exhibit well-defined wings with the fluting and striations seen in all the winged members of the Dictyopteridiaceae. The absence of attached seeds or ovules in the majority of specimens, and the continuous nature of the peripheral flange, precludes the hypothesis that the wing represents laterally compressed seeds/modified ovules, as suggested by Surange & Chandra (1974a) and other authors (Anderson & Anderson, 1985).

Benecke (1976) and McLoughlin (1990a) shared Surange & Chandra's (1974a) view that *Isodictyopteridium* and *Dictyopteridium* should be synonymised, but on the grounds that members of both taxa had peripheral wings and were dorsiventral structures with a sterile and a fertile surface. A strong medio-

longitudinal aggregation of veins has been observed in members assigned to both taxa.

Currently, the most widely accepted view of the fructifications is that they are bilaterally symmetrical, dorsiventrally flattened organs lacking a subtending sterile bract, but with a peripheral wing and a bifacial receptacle with a seed-bearing, fertile surface and a sterile, veined surface (McLoughlin, 1990a).

Although several authors have suggested that *Dictyopteridium* may be a sporangiate organ (White, 1963; Banerjee, 1973; Holmes, 1974; Anderson & Anderson, 1985), there can be little doubt of its ovuliferous nature since the discovery of specimens bearing attached seeds (Surange & Chandra, 1973a, 1975).

The first report of *Dictyopteridium*-like fructifications in South Africa was made by Lacey *et al.* (1975), who placed these fertile structures from Mooi River in *Plumsteadia natalensis*. They acknowledged the close similarities between the Mooi River specimens and Feistmantel's (1881) *Dictyopteridium*, but excluded them from the taxon on the understanding that *Dictyopteridium* was a radially symmetrical fructification. Benecke (1976) transferred *Plumsteadia natalensis* of Lacey *et al.* (1975) to a new genus '*Fetura*', and described some new specimens from Loskop within *Dictyopteridium flabellatum*. She also placed two lanceolate specimens with unusual seed scar morphology from Mooi River within *D. sporiferum*. Benecke (1976) considered the possibility that *Dictyopteridium flabellatum* represented the pollen-bearing organ of *D. sporiferum*.

Anderson & Anderson (1985) later synonymised the South African species of *Dictyopteridium* with *Plumsteadia*, and interpreted members of *D. flabellatum* as the radially symmetrical, pollen-bearing structures of *Plumsteadia gibbosa*. This was in accordance with their palaeodeme approach to taxonomy, where pollen-bearing and ovuliferous structures and associated leaves were grouped within the same genus. They did, however, acknowledge the controversy surrounding these structures, and considered the possibility they may eventually be shown to be ovuliferous structures.

Anderson & Anderson (1985) reconstructed *D. flabellatum* as a radially symmetrical structure, with the medio-longitudinal aggregation of veins representing a central axis. They omitted the wing and tubercles from their reconstruction, and interpreted the prominent, raised venation as tightly packed, linear, microsporangia attached radially to the central axis. They acknowledged that the wing-like margin present in some specimens was more suggestive of dorsiventral symmetry.

Here *Dictyopteridium* is considered to be an ovuliferous structure, with a design very similar to that of other ovuliferous glossopterid organs of the Dictyopteridiaceae, and is distinguished from *Plumsteadia* primarily on differences in seed scar morphology. It is likely that the permineralized fructifications described by Gould & Delevoryas (1977), are examples of *Dictyopteridium*, demonstrating the smooth, flattened receptacle with a small depression at each site of seed attachment. Benecke's (1976) *D. flabellatum* is accepted, and *Plumsteadia natalensis* of Lacey *et al.* (1975) and Anderson & Anderson (1985) has been transferred to *Dictyopteridium*.

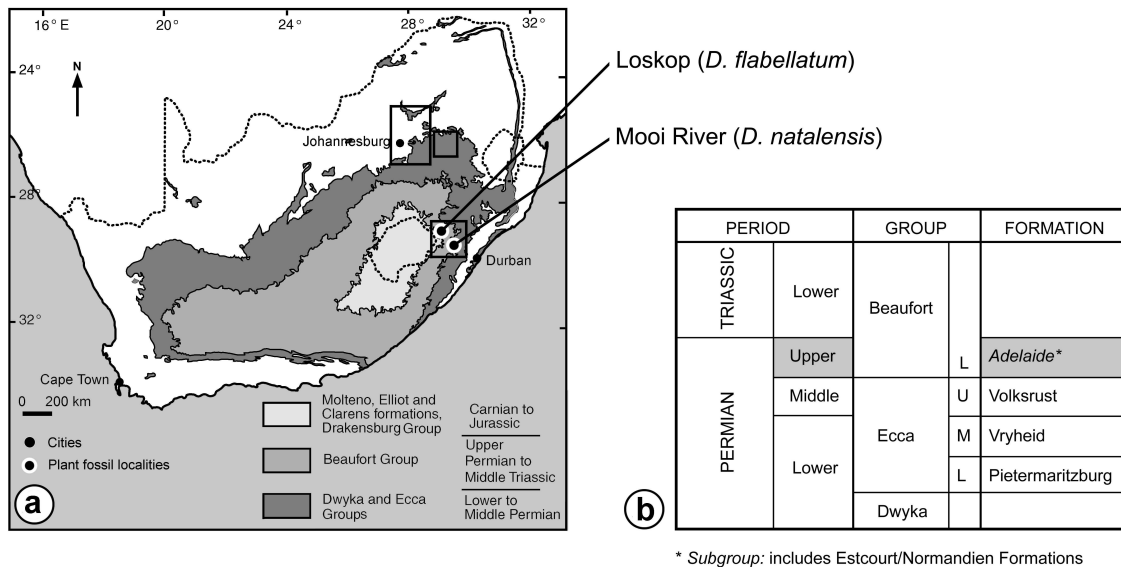
### 7.9.2 FOSSIL MATERIAL

Specimens are all impression fossils (in some cases with carbonaceous residues), from Loskop (*Dictyopteridium flabellatum*) and Mooi River (cf. *Dictyopteridium sporiferum*, *Dictyopteridium natalensis*).

[See Table A.I.13, Appendix I for specimen numbers].

### 7.9.3 LOCALITY INFORMATION

All specimens of *D. flabellatum* originated from the Loskop locality, and those of *D. natalensis* from the Mooi River locality, in the Kwa-Zulu Natal Province. Both sites are in the eastern Karoo Basin; the deposits belong to the Estcourt Formation, lower Beaufort Group, and are Late Permian in age (see text-figs 2.2.2, 2.2.4 & 7.9.1a&b).



**Text-figure 7.9.1.** (a) Locality map indicating reported occurrences of *Dictyopteridium* in South Africa; (b) lithostratigraphic table of the Permian and Lower Triassic deposits in the northern and eastern parts of the Karoo Basin, with shaded areas representing stratigraphic occurrences of *Dictyopteridium* (table adapted from Keyser, 1997).

## 7.9.4 SYSTEMATIC PALAEOBOTANY

### *Type species*

*Dictyopteridium sporiferum* Feistmantel ex Zeiller 1902 emend. McLoughlin 1990.

### *Type specimen of D. sporiferum*

Lectotype G.S.I. 5210 (Geological Survey of India, Calcutta), Feistmantel (pl.23A, fig. 4; 1881); refigured by Surange & Chandra (1973; pl. 1, fig. 6); Raniganj Formation (Upper Permian).

### *Etymology*

Greek: *dictyo* - net; *pteris* - fern; Feistmantel (1881) considered the specimens of *D. sporiferum* he described to be fertile fern fronds, and presumably 'net' refers to the anastomosing venation pattern apparent in some specimens.

## **Generic Diagnosis**

Reproduced from McLoughlin (1990a):

'Isobilateral, dorsiventral, pedicellate, ovuliferous fructifications, linear-lanceolate, apex acute, base truncate-rounded, consisting of inner fertile receptacle surrounded by peripheral sterile wing. Ovules or attachment points (pits) irregularly arranged over fertile surface of compressed receptacle (mould of fertile surface being tuberculate). Reverse surface with anastomosing venation with or without midrib, rarely faint bulges (depressions on mould) corresponding to ovule attachment points on fertile surface. Venation less clear on fertile surface; continuous from receptacle on to wing. Wing margin entire except for insertion of short, broad pedicel.'

## **Discussion**

The most important diagnostic characters of the genus, as outlined by McLoughlin (1990a) are the elongated shape and the simple, tuberculate nature of the seed scars, represented only by cicatrices on a relatively smooth receptacle surface lacking any well-defined seed cushions. The presence of a most commonly entire, peripheral wing is acknowledged.

**7.9.4.1**      **c.f. *Dictyopteridium sporiferum*** Feistmantel ex Zeiller 1902 emend.  
McLoughlin 1990

1976 *Dictyopteridium sporiferum* Feistmantel; Benecke, p. 99-100, figs 4-6.

1985 *Plumsteadia natalensis* Lacey, van Dijk and Gordon-Gray; Anderson & Anderson, pars, pl. 92, fig. 13. non pl. 92, figs 1-12; pl. 95, fig. 16; text-figs 124.1, 124.3.

## **Formation and locality of origin**

Estcourt Formation; Upper Permian; Mooi River locality, eastern Karoo Basin, South Africa.



## **Description**

(See pl. 83, figs (a)-(c); pl. 89, figs (a), (b); Table A.II.9, Appendix II for data summary).

Isobilateral, dorsiventral, ovuliferous fructification, 43.2 mm long and 12.4 mm wide, with a L:W of 3.5. Isolated polysperm sessile, or possibly with very short pedicel 2.1 mm wide at insertion.

Receptacle elongate-lanceolate to linear with long, tapering, pointed apex and truncate base; 42 mm long, 9 mm wide, with a L:W of 4.7 and an area of 270 mm<sup>2</sup>. Receptacle surface smooth, with randomly placed, elliptical to circular tubercles (0.9 x 0.7 mm; n=7), each sharply delimited by a narrow groove in receptacle surface. Tubercles number 464, at a density of 43 per 25 mm<sup>2</sup>.

Peripheral wing narrow, entire with faint, ill-defined fluting and striations; medial width 1.8 mm, wing width: receptacle width 0.2.

## **Comments**

Lacey *et al.* (1975) noted that some of the specimens of *Plumsteadia natalensis* they examined from the Mooi River locality, were 'not easily separated from *Dictyopteridium sporiferum* Feistmantel, as revised by Surange & Chandra (1973a)', and they only distinguished between the taxa on the basis of *D. sporiferum* being radially symmetrical. Benecke (1976; p. 111, figs 4-6) figured two specimens from the same locality, and had less compunction about attributing them to *D. sporiferum*. Later, Anderson & Anderson (1985) transferred one of these specimens (BP/2/13056; pl. 92, fig. 13) to *Plumsteadia natalensis* (*P. natalensis* has been referred here to *Dictyopteridium*).

Although BP/2/13056 (pl. 83, figs (a), (b), this document) has much in common with *D. natalensis*, and could conceivably represent one end of a morphological spectrum within this species, the smooth wing, lacking the pronounced fluting seen in most well-preserved specimens of *D. natalensis*, and the particularly

elongated, narrowly lanceolate shape with acute apex, probably warrants placement of this fructification within a separate taxon. Together with the particularly smooth receptacle surface and simple tubercles devoid of any seed scar cushion definition, these features are highly reminiscent of the examples of *D. sporiferum* refigured by Surange & Chandra (1973a; pl. 1, fig. 6) from Feistmantel's (1881) original description of the species.

It is also conceivable that BP/2/13056 is a specimen of *D. flabellatum*, in which the distinctive pattern of flabellate grooves and ridges has not been preserved. There is evidence of faint venation along the right side of the receptacle which is reminiscent of that seen in *D. flabellatum*. *Dictyopteridium flabellatum* has only ever been found at the Loskop locality, and BP/2/13056 could therefore represent a regional variant of this species. Scatter diagrams of the receptacle dimensions for *D. natalensis*, *D. flabellatum* and BP/2/13056 in text-figs 7.9.2-4 below, place the latter specimen well within the size and dimensional ratios observed for *D. flabellatum*, although its seed scar density lay more within the ranges of *D. natalensis*.

Since only one complete and one partial specimen of this type of fructification have been found after many years of extensive sampling of the Estcourt Formation, a definitive stance on the taxonomic position of these fructifications has not been taken.

**7.9.4.2      *Dictyopteridium natalensis*** (Lacey, van Dijk & Gordon-Gray 1975)  
comb. nov., emend.

- 1975 *Plumsteadia natalensis* Lacey, van Dijk & Gordon-Gray; p. 396, figs NM1260, NM1243a, NM1243b, NM1265, NM1274a, NM1274b, NM1257.  
1976 *Fetura natalensis* (Lacey, van Dijk & Gordon-Gray) Benecke; p. 102-104, figs 25-41.  
1978 *Plumsteadia natalensis* Lacey, p. 186.  
1979 *Plumsteadia natalensis* Lacey, van Dijk and Gordon-Gray; van Dijk, Gordon-Gray, Reid and Lacey, p. 114, pl. 46, figs 26-30.  
1985 *Plumsteadia natalensis* Lacey, van Dijk & Gordon-Gray; Anderson & Anderson, pars, p. 124; pl. 92, figs 1-12; pl. 95, fig. 16; text-figs 124.1, 124.3; non pl. 92, fig. 13.

### ***Holotype***

NM1260, lodged at the Natal Museum, Pietermaritzburg, KwaZulu-Natal Province.

### ***Type formation and locality***

Estcourt Formation; Upper Permian; Mooi River locality, eastern Karoo Basin, South Africa.

### ***Emended species diagnosis***

Isobilateral, bifacial fructification, either sessile or with short pedicel, attached to midrib in long, narrow cuneate base of a *Glossopteris* leaf with steeply inclined venation following a straight path to margin. Meshes larger and more elliptical to polygonal near midrib, becoming narrower and more parallel towards margin. Receptacle ovate-lanceolate with rounded to truncate or slightly cordate base, pointed to obtusely rounded apex, and surrounded by a narrow peripheral wing. Wing margin entire or rarely dentate, bearing prominent fluting and fine striations perpendicular to margin of receptacle. Surface of receptacle smooth or with low, ill-defined, non-contiguous seed scars, each bearing a pronounced elliptical to circular tubercle clearly delimited by a narrow peripheral groove in the receptacle surface. Marginal seed scars particularly prominent, corresponding to positions of wing flutes. Sterile surface of fructification with reticulate venation that passes into wing, corresponding to flute junctions. Venation may be aggregated in medio-longitudinal region, particularly in basal two-thirds of fructification.

### ***Description***

(See pl. 83, figs (d)-(r); pls 84-86; pl. 89, figs (c), (d); Appendix II, Table A.II.9 for data summary).

Isobilateral, dorsiventral, ovuliferous fructification comprising an elongated, pedicellate receptacle with a narrow, peripheral wing, and with an overall length of 17.4 (21.6) 29.7 {n= 26; SD:3.3}, a width of 5.5 (8.1) 12.4 {n=34; SD:1.6} and a length:width ratio of 2.1 (2.7) 3.4 {n=26; SD:0.3}.

Receptacle is elliptical, oblong to lanceolate with a rounded to bluntly pointed apex and a rounded, truncate or slightly cordate base; there is a tendency to be asymmetrical [falcate; e.g. pl. 84, figs (c), (d)]. Receptacle is 16.4 (20.8) 28.2 mm long {n=19; SD:3.3}, 4.7 (6.9) 9.7 mm wide {n=29; SD:1.4} with a L:W of 2.1 (3.1) 3.7 {n=19; SD:0.4} and an area of 70 (112.2) 180.7 {n=16; SD:31.6}. It is a bifacial structure, with a sterile and a fertile surface.

Sterile surface is veined, with a strong medio-longitudinal density of parallel veins, and a fairly open mesh pattern (only 1 or 2 meshes from longitudinal bundle to wing); veins recurve at receptacle edge, running between marginal scars and traversing the wing, where they delimit consecutive wing flutes.

Fertile surface is smooth, bearing 132 (190.8) 320 {n=12; SD:} widely and irregularly spaced, circular tubercles at a density of 32 (44.4) 63 tubercles per 25 mm<sup>2</sup> {n=27; SD:7}. Tubercles, which represent seed attachment points, are 0.5 (0.1) 1.4 mm long {n=204; SD: 0.2} and 0.4 (0.7) 1 mm wide {n=155; SD: 0.1}, and may be situated on low, indistinct cushions (in impressions). Cushions may be more distinct towards margin of receptacle, and become more rectangular in shape.

Receptacle is surrounded by a narrow wing that arches away from the fertile surface of the receptacle (in impressions). Wing is continuous along the periphery except at pedicel insertion, and has a wing width: receptacle width of 0.1 (0.1) 0.2 {n=27; SD:0.03}. Wing margin is entire, or more rarely undulating to dentate (e.g. pl. 85, figs (d), (e)), and bears fine striations and persistent fluting perpendicular to the receptacle margin or slightly inclined towards apex. Wing is broadest in the medial or sub-apical region with a width of 0.4 (0.8) 1.5 {n=31; SD:0.3}, tapering towards base and apex. Wing is in many cases folded over surface of receptacle and at least partially obscured by sediment.

Pedicle is short, striated and slightly expanded at insertion, with a length of 1.2 (2.0) 2.5 mm {n=4; SD: 0.5} and a proximal width of 1.4 to 3.5 mm {n=6}.

A few fructifications were found attached to their subtending leaves [e.g. pl. 83, figs (m), (n); pl. 86, figs (a)-(g)], but only the long, narrow, cuneate leaf bases were preserved. Fructifications attached to the weakly defined, 1.9 to 0.5 mm wide {n=6} midrib, near the base of the lamina. Veins depart from midrib at a steep angle, and follow a fairly straight path to the margin, with a mid-laminal vein angle of 38° (47°) 58° {n=12; SD: 6} and a marginal density of 22 (24.3) 26 veins per 10 mm {n=4; SD: 1.7}. Meshes are larger, elliptical to polygonal immediately adjacent to midrib, becoming finer and parallel in mid-laminal and marginal sectors.

No attached seeds have been found.

### **Comments**

Seed scar morphology is one of the diagnostic features of this taxon. The well-defined, raised tubercles, which represent seed detachment points (cicatrices), are widely spaced, and are not associated with prominent, raised cushions as in *Plumsteadia gibbosa* and other members of the Dictyopteridiaceae. There are low, flat, ill-defined cushions in some of the specimens, particularly in the marginal rank of scars, but the overall appearance of the receptacle surface is smoother than in other genera such as *Plumsteadia*.

The species diagnosis was emended to re-enforce Benecke's (1976) acknowledgement of the wing as a 'true' wing, and not just an artefact of preservation as stated in Lacey *et al.* (1975). The veined nature of the sterile surface of the fructification also needed mention, as well as characterisation of the 'raised bodies or sacs' as seed scars each with a central cicatrix. Lacey *et al.* (1975) made erroneous reference to the abaxial and adaxial surfaces of the fructification and its subtending leaf, basing these observations on the assumption that the impressions represented positive casts of the original plant surfaces. The wing margin of this taxon appears to be entire in most cases,

although the steep angle of inclination of the wing relative to the receptacle surface means that the margin is frequently not well represented. A few specimens displayed a distinctly dentate margin, as mentioned by Lacey *et al.* (1975). Unlike *D. sporiferum*, the wing bears prominent fluting, and the receptacle lacks the fan-shaped pattern of grooves and ridges that correspond to the venation of *D. flabellatum*. *Dictyopteridium natalensis* also tends to be more elongate ovate, as opposed to the linear-lanceolate receptacles seen in *D. flabellatum* and *D. sporiferum*.

The medio-longitudinal concentration of veins apparent particularly on the sterile surface of the receptacle in many specimens [e.g. pl.84, fig. (c)] is not in all cases a secondary imprint of the subtending leaf midrib, as it is present in fructifications preserved at angle to the long axis of the leaf, as well as those lying parallel to the midrib.

#### **7.9.4.3      *Dictyopteridium flabellatum* Benecke 1976 emend.**

1976 *Dictyopteridium flabellatum* Benecke, p. 100-102, figs 7-24, 88.

1985 *Plumsteadia gibbosa* (Benecke 1976) Anderson & Anderson, p. 125, pl. 93, figs 8, 9; pl. 94, figs 11-14; text-fig. 125.4. non pl. 93, figs 5, 6; pl. 94, figs 1-10; pl. 95, fig. 17; text-figs 125.1, 125.2, 125.3.

#### ***Holotype***

N-Lk 424 (PM 005a) and N-Lk 360 (PB 005b) - listed by Benecke (1976; figs 9,10); N-Lk 424 re-accessioned as BP/2/12533, counterpart not found.

Specimen lodged at the BPI fossil herbarium, University of the Witwatersrand, Johannesburg.

#### ***Paratypes***

N-Lk (PB 008) - Benecke (1976; figs 13, 14), re-accessioned as BP/2/12972 (#2); counterpart N-Lk 411a (PB 012) - Benecke (1976; figs 23, 24), re-accessioned as BP/2/12529a (#2); N-Lk 406a&b (PB 011a&b) - Benecke (1976; figs 19, 20, 21); re-accessioned as BP/2/12525a&b (#1). All specimens are

lodged at the BPI fossil herbarium, University of the Witwatersrand, Johannesburg.

### ***Type formation and locality***

Loskop locality, Kwa-Zulu Natal Province, South Africa; Estcourt Formation; Upper Permian; eastern Karoo Basin.

### ***Emended species diagnosis***

Solitary, multiovuliferous, isobilateral, dorsiventral fructification; narrowly oblong-lanceolate with acute, pointed apex and truncate to rounded base. Peripheral wing entire, continuous except at base, bearing faint striations perpendicular to margin of receptacle; receptacle bears prominent, flabellate pattern of venation on both surfaces, with veins manifesting as ridges on sterile surface, grooves on fertile surface, with intervening areolae particularly prominent along edge of receptacle; medio-longitudinal concentration of veins present; veins anastomose and bifurcate, arching at steep angle to margin of receptacle, before traversing wing. Randomly scattered seed scars round to elliptical, raised tubercles on impressions of fertile surface, often secondary imprints (pits) on sterile surface.

### ***Description***

(See pls 87, 88; pl. 89, figs (e)-(g); Table A.II.9, Appendix II for data summary).

Isobilateral, dorsiventral ovuliferous fructification, 21 (42) 54.2 mm long {n=9; SD:10.1} and 8 (10.6) 12.5 mm wide {n=9; SD: 1.4}, comprising a pedicellate receptacle with a narrow peripheral wing.

Receptacle is narrowly lanceolate, with an acute, pointed apex and a truncate or slightly rounded base. Receptacle is 20.8 (39.3) 51.7 mm long {n=9; SD: 9.2}, 5.7 (8.7) 12.6 {n=18; SD: 1.9} mm wide, with a L:W of 3.3 (4.8) 6.7 {n=9; SD: 1.1}, and an area of 90.3 (266.4) 413 mm<sup>2</sup> {n=8; SD:118.5}.

Sterile surface bears prominent, flabellate pattern of venation, which manifests in impressions as fine, raised ridges that radiate from the base and arch towards the margin. Veins bifurcate regularly and anastomose in receptacle centre. A prominent median cluster of veins is evident in some specimens. Veins arch sharply at receptacle margin and produce prominent ridges in impressions before traversing wing perpendicular to receptacle margin.

Fertile surface smooth in some specimens, but most have prominent ridging in impressions corresponding to the depressed interveinal areas or areolae in impressions of the sterile surface. Approximately 53 (350.6) 1289 {n=11; SD: 433.4} seed scars are borne on the fertile surface, at a density of 42 (61.7) 78 scars per 25 mm<sup>2</sup> {n=7; SD: 12.3}. Randomly placed seed scars represented by a shallow depression with a prominent central tubercle 'cicatrix', and are 0.4 (0.8) 1.2 mm long {n=59; SD: 0.2}, 0.4 (0.5) 0.8 mm wide {n=32; SD: 0.1}.

Wing entire, narrow, with wing width: receptacle width of 0.1 (0.3) 0.5 {n=12; SD: 0.1}; arches strongly away from the fertile surface (towards the slab) and towards the sterile surface (away from the slab) in impressions. Medial wing width is 1 (1.9) 3.3 mm {n=13; SD: 0.8}, tapering slightly to 0.9 (1.3) 1.9 {n=5; SD: 0.4} towards apex. Wing is finely striated perpendicular to receptacle margin; some specimens lack fluting but most possess strong transverse grooves/ridges near the receptacle margin.

Pedicel is short and longitudinally striated, with an observed length of 2.5 mm {n=1} and width of 2.7 (2.6) 2.7 mm {n=2; SD: 0.1} at insertion; fructifications may be sessile.

No attached leaves or seeds have been found.

### **Comments**

This species is unusual in its overall appearance, and superficially it does not closely resemble other members of the Dictyopteridiaceae. However, on closer inspection, these fructifications have all the features common to other members



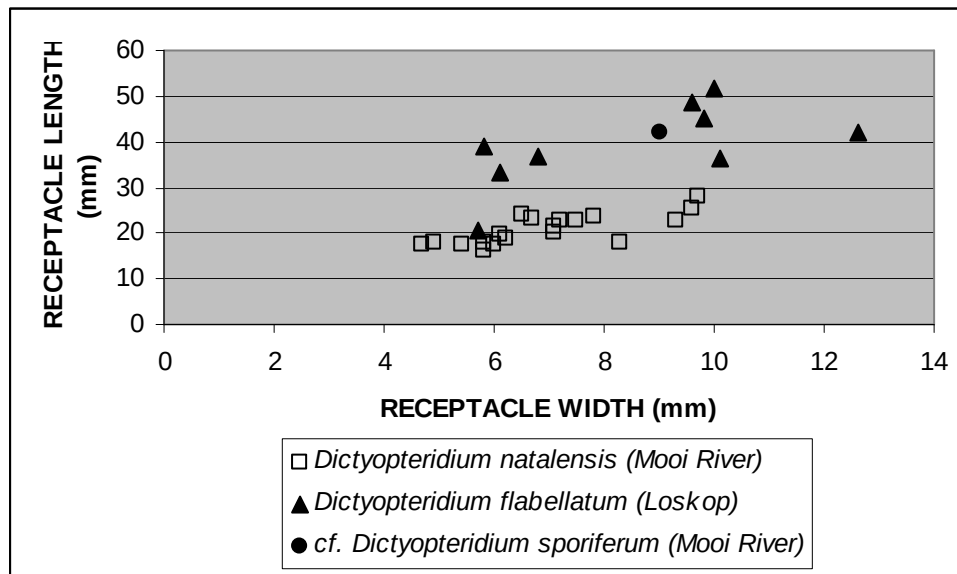
of the family. The strikingly prominent venation pattern that dominates the topography of both surfaces of the receptacle detracts from the presence of small, round tubercles, identical to those seen in other species of *Dictyopteridium*, on the surface of the receptacle, between the deeply defined veins. In the original plant, the tubercles would have been pits nestled in recesses between raised ridges created by the venation.

The most distinctive features of the species are its high length to width ratio, the absence of seed cushions associated with the tubercles on the receptacle surface, and its unusual venation pattern, which is prominent on both surfaces of the receptacle. The clarity of the venation on both the sterile and fertile surfaces may imply that these fructifications were thin and papery or leathery, rather than fleshy. The inclination of the wing is consistently away from the plane of the fertile surface of the fructification in the impressions, which means that it arched over the seed-bearing surface in the original plant organ [e.g. pl. 87, fig. (h); pl. 88, fig. (f)].

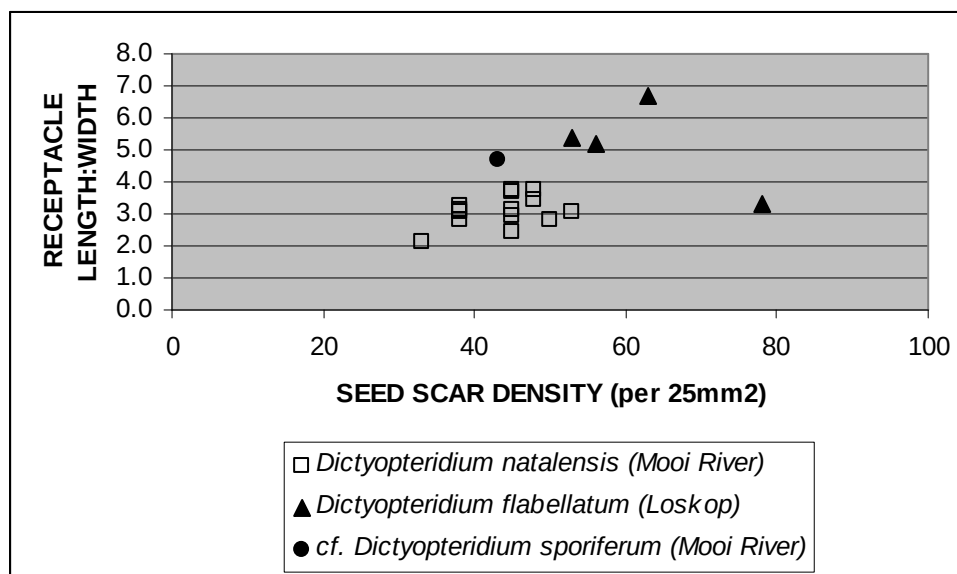
As with other species described by Benecke (1976), she interpreted these fructifications as bilaterally symmetrical organs with a sterile ‘half’ or scale. Following a careful examination of all the fructifications in the BPI, there was no evidence to suggest the presence of such a structure, although the holotype [BP/2/12533; pl. 88, fig. (f)] has a folded wing which has been exposed at a lower level in the sediment than the receptacle surface. This could have contributed to Benecke’s (1976) convictions regarding the presence of a sterile scale.

Specimens of *D. flabellatum* were, in several cases, preserved as an opposing pair, apparently with a common point of attachment to the leaf/stem of the parent plant, although the attachment site itself was not visible [see pl. 88, fig. (i)]. Examples of *Dictyopteridium* occurring in clusters or with overlapping bases have also been recorded by Holmes (1974) and McLoughlin (1990).

## 7.9.5 DATA ANALYSIS



**Text-figure 7.9.2.** Scatter plot of receptacle widths and lengths of the three South African *Dictyopteridium* spp.

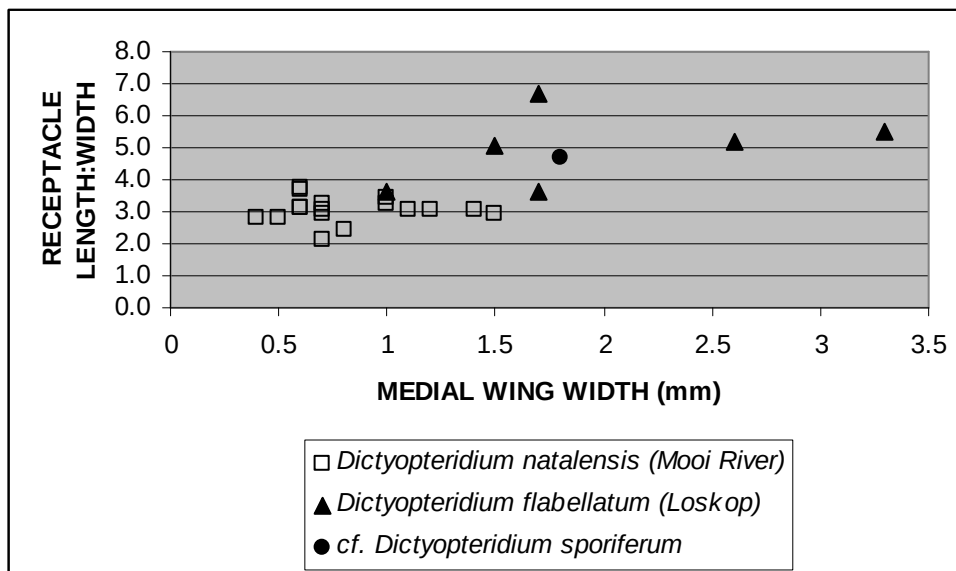


**Text-figure 7.9.3.** Scatter plot of receptacle length to width ratios versus medial wing width for the three South African *Dictyopteridium* spp.

In text-fig. 7.9.3, *D. flabellatum* and *D. natalensis* show very distinct clusters of datum points with little overlap of wing widths and receptacle lengths. The length to width ratios of their receptacles are also distinct, as illustrated in text-fig. 7.9.2.

A single specimen of *D. flabellatum* shares similar ranges to *D. natalensis* in text-figs 7.9.2 & 7.9.3. The single specimen comparable to *D. sporiferum* falls

comfortably within the ranges exhibited by *D. flabellatum*, although having a lower seed scar density. The close similarities between *D. flabellatum* and BP/2/13056 support the theory that this specimen may be a product of localised variation within this species.



**Text-figure 7.9.4.** Scatter plot of receptacle length to width ratios seed scar densities for the three South African *Dictyopteridium* spp.

## 7.9.6 DISCUSSION

The distinction between *Plumsteadia* and *Dictyopteridium* is, at times, a tenuous one. McLoughlin (1990b) distinguished between these two genera primarily on the basis of seed scar morphology. He considered *Dictyopteridium* to have 'more numerous, smaller, generally circular tubercles on a very narrow-elliptical, lanceolate or linear receptacle'. This is in contrast to *Plumsteadia* and all other members of the Dictyopteridiaceae, which have seed scars with prominent, in most cases contiguous or closely spaced cushions each bearing a single tubercle. These cushions are raised structures in impression fossils, but represent what would have been hollows in the original plant surface. Specimens of *Plumsteadia gibbosa*, with their prominent, bulbous seed scars clearly illustrate this difference in seed-scar morphology.

The seed scar morphology in *D. natalensis* was more variable than that seen in *D. flabellatum*. Although the receptacle surface in specimens assigned to *D. natalensis* is generally very smooth in overall appearance, and in no cases

bears the prominent seed scar cushions seen in members of *Plumsteadia*, the tubercles are in some cases associated with slight doughnut-shaped swellings which vary in intensity from specimen to specimen.

*Dictyopteridium* has been recorded from in Upper Permian sediments in India (Surange & Chandra, 1973a), Argentina (Archangelsky, 1992), South Africa (Benecke, 1976) and Australia (Rigby, 1978), and is considered to be a useful biostratigraphic indicator for this time period (see Discussion, section 9.3.2, p. 354).

White (1963) figured several glossopterid fructifications from the Upper Bowen Series of Queensland, Australia, including a specimen she assigned to *Dictyopteridium sporiferum*. This fructification is comparable to *D. flabellatum*, as the steeply angled venation is very prominent on the fertile surface of the receptacle. However, it lacks the distinctive areolae along the margin of the receptacle.

Holmes' (1974) genus *Isodictyopteridium* is here regarded as synonymous with *Dictyopteridium*. His *I. costatum* appears to be a species of *Dictyopteridium* with a particularly pronounced medio-longitudinal aggregation of veins. As in *D. flabellatum*, the wing fluting in *I. costatum* is particularly prominent but the fructifications lack the steeply inclined, marginal areolae of the former species.

Maheshwari (1965b) figured specimens he assigned to *D. sporiferum* which are highly reminiscent of Holmes' (1974) '*I. costatum*' specimens, also with a prominent medio-longitudinal vein aggregation. These specimens also have much in common with *D. flabellatum*, the venation inclined at a steep angle and prominent in impressions of both fertile and sterile surfaces of the receptacle. There are indications from the figures provided by Maheshwari (1965b; pl. 1, figs 2-5) that there may be well-defined areolae along the periphery of the receptacle margins, but this could not be confirmed from the poor reproduction of the paper available to me.

Banerjee (1984) also figured a specimen (pl. 2, fig. 12) which is very similar to the South African species *D. flabellatum*. She noted how the venation of the megasporophyll was visible on the impression of the fertile surface. The characteristic, steeply inclined areolae resulting from the extreme prominence of the veins are clearly visible along the margin of the receptacle. It would be biostratigraphically intriguing to find this species of *Dictyopteridium* in far-off India, as it has only been found at a single locality in South Africa.

There were no South African specimens of *Dictyopteridium* that revealed the presence of a sterile bract as proposed by Surange & Chandra (1973a). However, several fructifications gave the initial impression of having a dual structure of some nature. Following careful inspection all such examples were found to either have a wing that had been infolded during preservation [e.g. holotype specimen of *D. flabellatum*, pl. 87, fig. (h)], or to have a portion of the embossed leaf impression lying beneath the impression of the fructification [e.g. pl. 83, figs. (m), (n), pl. 85, figs (a), (c)]. None of the Australian specimens has confirmed the presence of a separate bract-like feature either (McLoughlin, 1990a). It is conceivable that the *Dictyopteridium* material from India represents a taxon with a radically different body plan, but there is no clear evidence of this apart from reports of multiple pairs of cuticles being extracted from a single specimen (see section 3.1.2.3). It should be possible, in light of the current study, to determine from careful dissections of compression or impression fossils whether the purported protective scale of *Dictyopteridium* is a misinterpretation and an artefact, or an existing structure. All cases in which fructifications have been reported to have a protective scale, appear to have been based on incorrect interpretations of impression fossils, as discussed earlier in Chapter 3.1.

## CHAPTER 8 LIDGETTONIACEAE Banerjee 1984

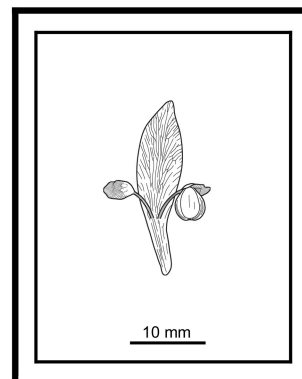
### 8.1 LIDGETTONIA Thomas 1958 emend.

#### 8.1.1 INTRODUCTION

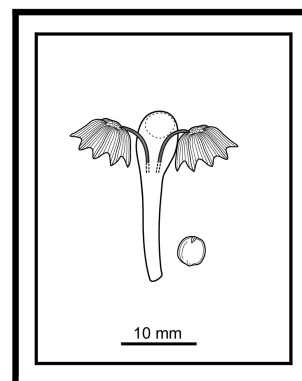
Thomas (1958) described the first compound, cupulate glossopterid fructification to be reported in the literature, from the Upper Permian of South Africa. He named the new genus *Lidgettonia*, after the type locality. The original generic diagnosis by Thomas (1958) encompassed associated seeds and vegetative *Glossopteris* leaves as well as the scale leaf bearing multiple cupules.

Lacey *et al.* (1975) later described a diverse range of ovuliferous fructifications from the Estcourt Formation of Natal, South Africa, and revised the diagnosis for *Lidgettonia africana* on the basis of a large collection of well-preserved specimens, omitting associative evidence from the diagnosis. They also described two new genera of the Lidgettoniaceae from the same area, viz. *Mooia* and *Rusangea*.

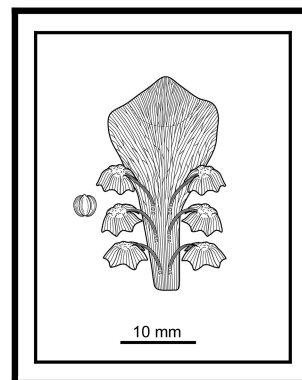
Anderson & Anderson (1985) revised the genus again and included associated vegetative *Glossopteris* leaves, pollen-bearing organs and seeds within the circumscription of each species. Anderson & Anderson (1985) synonymised *Mooia* and *Rusangea* with *Lidgettonia*, and erected three new species of *Lidgettonia* from other South African localities. These new species appear to have been created mainly to accommodate differences in the associated organs. Their approach was in line with their palaeodeme concept of taxonomic organisation, but has perhaps led to some confusion at a time when the system of form genera is most commonly used. In this revision, purely associative relationships amongst affiliated glossopterid organs are considered too tentative to form the basis of taxonomic decisions, and the genus



*Lidgettonia elegans*



*Lidgettonia lidgettonioides*



*Lidgettonia africana*

*Lidgettonia* is only applied to scale leaves with attached capitula and capitula which have become detached from their parent scale leaves. The associated pollen-bearing organ *Eretmonia* is recognised as a distinct form genus. The South African species of *Lidgettonia* have been reduced to three on the basis of scale leaf and capitulum morphology, viz. *Lidgettonia africana*, *L. lidgettonioides* and *L. elegans*.

### 8.1.2 FOSSIL MATERIAL

Specimens from Lawley are housed at the Bernard Price Institute (University of the Witwatersrand, Johannesburg), and National Botanical Institute (Pretoria); all other specimens are housed at the Bernard Price Institute or the Natal Museum (Pietermaritzburg) (see Table A.I.14, Appendix I). Most of the *Lidgettonia* fossils are impressions, although there are a few compressions e.g. from the Lidgetton locality.

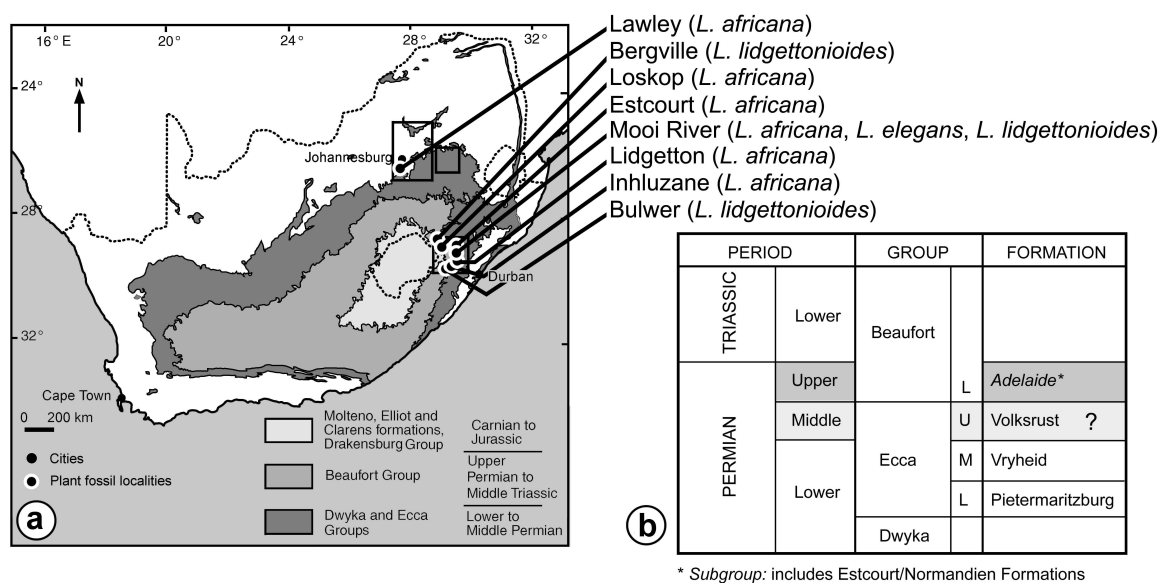
### 8.1.3 LOCALITY INFORMATION

*Lidgettonia* is a widespread genus found predominantly in sediments of the Estcourt Formation, Lower Beaufort Group (Upper Permian) of Kwa-Zulu Natal, in the eastern Karoo basin (see text-figs 2.2.2, 2.2.4 and 8.1.1a&b). *Lidgettonia africana* has also been found at Lawley, in sediments of uncertain age which are currently thought to belong to the Volksrust Formation (Middle Permian) (Anderson & Anderson, 1985).

*L. lidgettonioides* - Bergville (Anderson & Anderson, 1985),  
Mooi River (Lacey *et al.*, 1975),  
Bulwer (Anderson & Anderson, 1985).

*L. africana* - Lawley (Rayner & Coventry, 1985; Anderson & Anderson, 1985),  
Loskop (Anderson & Anderson, 1985),  
Estcourt (Lacey *et al.*, 1975),  
Mooi River (Lacey *et al.*, 1975),  
Lidgetton (Thomas, 1958),  
Inhluzane (Anderson & Anderson, 1985).

*L. elegans* - Mooi River (Lacey *et al.*, 1975).



**Text-figure 8.1.1** (a) Locality map indicating reported occurrences of *Lidgettonia* in South Africa; (b) lithostratigraphic table of the Permian and Lower Triassic deposits in the northern and eastern parts of the Karoo Basin, with shaded areas representing stratigraphic occurrences of *Lidgettonia* (table adapted from Keyser, 1997).

#### 8.1.4 SYSTEMATIC PALAEOBOTANY

##### *Type species*

*Lidgettonia africana* Thomas 1958; Estcourt Formation (Upper Permian); Lidgetton, Kwa-Zulu Natal, South Africa.

##### *Etymology*

'*Lidgettonia*' - after the type locality, near the small town of Lidgetton.

##### *Emended generic diagnosis*

Compound, ovuliferous fructifications with 1 to 7 pairs of small (2-15 mm diameter) seed-bearing capitula borne on slender pedicels attached in opposite to sub-opposite ranks to a reduced fertile leaf (scale leaf). Capitula dorsiventral, isobilateral structures comprising a small, bifacial receptacle with a fertile and sterile surface, flanked by a relatively broad, peripheral wing; capitula spatulate, palmate to campanulate, the wing reflexed to varying degrees towards fertile surface of receptacle. Receptacle circular, transversely elliptical to obovate,



bearing 2 to 13 elliptical seed scars/ seed attachment points on fertile surface; sterile surface veined. Seed scars indistinct, raised cushions (in impressions) with a central depression; a single seed scar present at base of each wing segment, and across surface of receptacle. Wing contracted at base of receptacle, at point of lateral insertion of pedicel. Wing with 3 to 9 shallowly to deeply divided, faintly striated, acute to obtusely pointed teeth; each tooth with a pronounced striation along its midline, arising from the junction between adjacent marginal seed scars on the receptacle. Seeds small (3-4 mm long) and elliptical, with conspicuous to very narrow lateral wings; micropylar and chalazal ends truncate or slightly recessed. Scale leaf glossopterid, variable in shape and size (<50 mm long); venation divergent, bifurcating with anastomoses, forming long, narrow meshes.

## **Discussion**

Previous diagnoses of the genus have not recognised the bifacial nature of the capitula, or the existence of a distinct (though reduced) receptacle and wing such as those seen in members of the Dictyopteridiaceae. They have also failed to encompass the morphology and positioning of the seed scars, and how this in turn, relates to the morphology of the wing. The emended diagnosis does not take associated organs into account.

### **8.1.4.1      *Lidgettonia africana* Thomas 1958 emend. Anderson & Anderson 1985**

- 1958 *Lidgettonia africana* Thomas, p. 181, pl. 22, figs 2, 3; pl. 23, fig. 4; text-fig. 2.
- 1969 *Lidgettonia* Thomas; Plumstead, p. 50; pl. 17, fig. 3.
- 1974 *Lidgettonia africana* Thomas; Lacey, van Dijk and Gordon-Gray, p. 154, fig1: NM 1001, NM 1051, NM 1596, p. 155.
- 1975 *Lidgettonia africana* Thomas; Lacey, van Dijk and Gordon-Gray, pp. 385, 386, 387, 388; figs NM1596a, NM1001, NM1051b, NM1035a, NM1040a,b, NM1098b, NM1002, NM1066.
- 1976 *Lidgettonia africana* Thomas; Schopf, p. 45; pl. 3, figs 1-5; text-figs 8a-d.
- 1978 *Lidgettonia africana* Thomas; Lacey, p. 186.
- 1979 *Lidgettonia africana* Thomas; van Dijk, Gordon-Gray, Reid & Lacey, p. 114, pl. 46, figs. 20, 21 & 22, p. 119.
- 1981 *Lidgettonia africana* Thomas; van Dijk, pp. 43-61; figs 11-13.
- 1983 *Lidgettonia africana* Thomas; Melville, p. 287; fig. 3f. [1983b].
- 1984 *Lidgettonia*; Banerjee, pp. 30, 35; text-fig. 2.
- 1985 *Lidgettonia africana* Thomas; Anderson and Anderson, p. 134, pl. 113, figs 1-7; text-figs 133.1. 134.1.
- 1985 *Lidgettonia mooiriverensis* Anderson & Anderson; p. 134; pl. 115, figs 1-7; text-figs 133.3, 134.6.

1985 *Lidgettonia inhluzanensis* Anderson & Anderson; p. 135, pl. 119, figs 1-6; pl. 122, figs 1-3; text-figs 133.5, 135.1.  
1997 *Lidgettonia africana* Thomas; Anderson and Anderson, p. 17, fig. 10b.

### ***Holotype***

An impression fossil, NHMV34633, housed at the Natural History Museum, London.

### ***Type formation and locality***

Estcourt Formation, Beaufort Group; Upper Permian; Lidgetton, Kwa-Zulu Natal, South Africa.

### ***Species diagnosis***

(Adapted from Anderson & Anderson, 1985).

Two to eight capitula borne in pairs on an obovate to rhombic scale leaf with mucronate apex; capitula palmate to campanulate, with 6-13 seed scars; wing moderately scalloped (<1.6 mm deep), producing an obtuse to acutely pointed tooth at the junction between each wing segment. Seeds small (1.6-3.7 mm long), transversely elliptical with broad lateral wings (0.6 – 1 mm); micropylar and chalazal ends truncate or slightly recessed.

### ***Description***

(See pls 90-95; pl. 100, figs (a)-(c); Table A.II.10, Appendix II for data summary).

Compound, ovuliferous fructification comprising two to eight pairs of palmate to campanulate capitula, each borne on a slender pedicel (2->7 mm long, 0.2-1 mm wide), and attached in opposite to sub-opposite ranks to the mid-section of a reduced, glossopterid scale leaf. Capitula are dorsiventral, isobilateral structures with a small, central receptacle flanked by a relatively broad peripheral wing that is reflexed towards the fertile surface, forming a cup-

shaped structure. Dorsiventrally compressed specimens are 3-7.5 mm {n=50} in diameter. The elliptical to obovate receptacle has a diameter of 1.6-3 mm, and bears 6-13, sub-circular to elliptical seed scars on the fertile surface. The scars are indistinct, raised cushions (in impressions) with a central depression, and are approximately 0.4-1 mm long. The sterile surface is veined. The finely striated wing reaches a maximum wing width of 1.1-3 mm, and is scalloped to varying degrees. Scallops are 0.4 to 1.6 mm deep, and result in a toothed wing margin. Each of the 6-11 {n=50} obtuse to acutely pointed tooth bears a medial striation running from the junction between adjacent peripheral seed scars on the receptacle, to the wing margin. Distance between adjacent teeth is 1.2-3 mm. Wing is contracted at base of receptacle, at pedicel insertion.

Scale leaf is obovate, to rhombic, 22-40 mm long {n=50} and 6 to 17 mm {n=50} wide. Apex is mucronate with a bluntly to acutely pointed tip, and base is long and tapering, with a basal width of 0.7-3 mm {n=50}. Capitula are attached roughly at point of lamina expansion. Venation is divergent, bifurcating and anastomosing to form narrow elongated meshes. Midrib is absent, although there may be a weak medial aggregation of veins. Veins arch acutely from the midline, with a mid-laminal vein angle of 11.5°-49°, and a marginal vein angle 28°-53°. Marginal vein density is 12 to 14 veins per 5 mm.

Attached seeds transversely elliptical, (1.6-3.7) x (2-3.6) mm, with a L:W of 0.8 - 0.9. Sclerotesta is ovate, 1 to 2.5 mm long and 0.8 to 1.2 mm wide, flanked by conspicuous, 0.6-1 mm wide lateral wings.

### **Comments**

The diagnosis has been revised to exclude all associated organs.

Several *Lidgettonia* specimens have been found at the Lawley locality near Johannesburg. They were first described by Rayner and Coventry (1985) as *L. africana*, but Anderson & Anderson (1985) placed them in a new species, *L. lawleyensis*, mainly to accommodate differences in the associated pollen-bearing structures. Although their capitula tend to be smaller, the Lawley

specimens fall within the circumscription of *L. africana*, and have been synonymised with this taxon. See pl. 93 and pl. 94, figs (a)–(j) for examples of *L. africana* from Lawley.

Anderson & Anderson (1985) also placed *Lidgettonia* specimens from Inhluzane and Mooi River in separate species, viz. *L. inhluzanensis* and *L. mooiriverensis*. Their decision appears to have been based mainly on differences in the seeds, *Eretmonia* fructifications and *Glossopteris* leaves associated with the fructifications at each of the localities. However, since associative evidence is not regarded here to be an adequate pretext for taxonomic distinctions, and since all these *Lidgettonia* specimens fall within the ranges established for *L. africana*, these species have been synonymised.

*L. africana* is similar to *L. lidgettonioides*, but the capitula are smaller, and the wing lobes are less deeply incised in the former. The capitula of *L. africana* also tend to be less reflexed than those of *L. lidgettonioides* and the scale leaf of *L. lidgettonioides* is distinctively elongate-obovate with a narrow petiole, as opposed to the broader, more rhombic forms which predominate in *L. africana*.

**8.1.4.2      *Lidgettonia lidgettonioides*** (Lacey *et al.* 1975) Anderson & Anderson  
1985 emend.

1974 new seed-bearing cupular fructification; Lacey *et al.*, p. 155, figs NM1471, NM1476.

1975 *Mooia lidgettonioides* Lacey, van Dijk and Gordon-Gray, pp. 389–392, figs NM1476b, 1479a,b, NM1471a, NM1533, NM1539, NM1576b, NM1579, NM1474.

1983 *Mooia lidgettonioides* Lacey *et al.*; Melville, fig. 3e. [1983b].

1984 *Mooia*; Banerjee, p. 35, text-fig. 5.

1985 *Lidgettonia lidgettonioides* Lacey *et al.*; Anderson & Anderson, p. 136; pl. 125, figs 1–9; pl. 128, figs 1, 2; pl. 129, figs 1–3, 5; text-figs 133.10, 133.12, 136.1, 136.3.

***Holotype***

An impression fossil, NM1539, housed at the Natal Museum, Pietermaritzburg.

### ***Type formation and locality***

Estcourt Formation; Upper Permian; Mooi River National Road, eastern Karoo Basin, Natal, South Africa.

### ***Emended species diagnosis***

Two to four capitula attached to a small, narrow, club-shaped scale leaf. Apex of scale leaf rounded, with distinct region of localised thickening in distal portion of lamina. Capitula large (8-13 mm diameter) and deeply campanulate. Wing with prominent scallops, and well-defined, acutely pointed teeth. Seeds broadly elliptical (4-4.3 mm long) with very narrow lateral wings (<0.4 mm).

### ***Description***

Compound, ovuliferous fructification with two to four capitula borne on slender (5.2-10 mm long, 0.3 to 0.8 wide), laterally inserted pedicels, and attached in opposite ranks to a club-shaped glossopterid scale leaf. Capitula are aligned approximately with the broadest part of the scale leaf. Capitula dorsiventral, isobilateral structures with a fertile and sterile surface. They are large and deeply campanulate, with a diameter of 8.6 to 12.7 mm. Fertile surface of the small, indistinct receptacle bears 5-7 elliptical seed scars (1.5 x 1.2 mm), represented by raised cushions, each with a central depression (in impressions); sterile surface is veined. Receptacle is flanked by a broad, finely striated wing with deeply incised (1.4-2 mm) scallops corresponding to the positions of the marginal seed scars. Wing teeth are prominent, with obtuse to acuminate tips that are 3.9-5.4 mm apart. A prominent striation marks the midline of each tooth, corresponding to the junctions between adjacent peripheral seed scars on the receptacle. Wing is contracted at the base of the capitulum, forming a deep sinus at the point of pedicel insertion.

Scale leaf is 10 to 23 mm long, 4.5-7 mm wide, with a bluntly rounded apex and a long, narrow (1.1-2 mm wide) base. There is a distinctive, rhombic region that appears to represent thickened tissue in the distal portion of the lamina. The

capitula are attached at the base of the expanded portion of the lamina. Venation is ill-defined, but appears to be divergent, with bifurcations and anastomoses forming elongated, narrow meshes.

Attached seeds are broadly elliptical, 4-4.3 mm long, 3.3-3.7 mm wide, with a very narrow lateral wing (<0.4 mm). The micropylar and chalazal ends are relatively rounded, possibly with a short pointed tip or a narrow cleft at the micropyle.

### **Comments**

Anderson & Anderson's (1985) diagnosis is revised to exclude associated organs, thereby broadening the application of the species. Although this taxon is superficially similar to *L. africana*, the scale leaf morphology is distinctly different with its club-shape and thickened apical region, and the capitula are much larger and more markedly campanulate. The wing scallops are also deeper and the teeth have sharply acute apices. Although Anderson & Anderson (1985) reconstructed the seeds of *L. lidgettonioides* with broad lateral wings such as those seen in *L. africana*, the lateral wings are in fact much narrower in the former taxon.

#### **8.1.4.3      *Lidgettonia elegans* (Lacey et al. 1975) Anderson & Anderson 1985 emend.**

1974 *Rusangea elegans* Lacey, van Dijk and Gordon-Gray; p. 154.  
1975 *Rusangea elegans* Lacey, van Dijk and Gordon-Gray, p. 392-394; figs NM1362a&b, NM1363a, NM1361a&b, NM1384a&b.  
1983 *Rusangea elegans* Lacey, van Dijk and Gordon-Gray; Melville, fig. 3d. [1983b].  
1984 *Rusangea*; Banerjee, p. 35, text-fig. 6.  
1985 *Lidgettonia elegans* Lacey, van Dijk and Gordon-Gray; Anderson & Anderson, p. 136, pl. 131, figs 1-5; text-figs 133.14, 136.9.

### **Holotype**

NM1361a,b (Natal Museum, Pietermaritzburg).

### ***Etymology***

'*elegans*' - refers to the slender, elegant appearance of the fructification, with its particularly reduced capitula (Lacey *et al.*, 1975).

### ***Type formation and locality***

Estcourt Formation; Upper Permian; Mooi River National Road, eastern Karoo Basin, Natal, South Africa.

### ***Emended species diagnosis***

One to three pairs, small (2.4-3.4 mm long), spatulate to spoon-shaped capitula attached to an elliptical to obovate scale leaf. Receptacle ill-defined, with 2 or 3 seed scars on fertile surface. Wing striated, margin entire or weakly scalloped with 3 or 4 obtuse, poorly differentiated teeth; wing reaches maximum breadth distally, tapering away at base of receptacle. Attached seeds small (3-4 mm diameter), sub-circular, with conspicuous lateral wings and truncate micropylar and chalazal ends.

### ***Description***

Compound, ovuliferous fructification with one (or rarely up to 3 three) pairs of, small (2.4-3.4 mm long), spatulate, pedicellate capitula, borne on an elliptical to obovate scale leaf. Pedicels slender (0.3-0.5 mm wide) and relatively short (1.4-6.8 mm); inserted laterally at base of receptacle. Capitula are bifacial structures with a small and poorly defined receptacle and finely striated wing. Fertile surface of receptacle is slightly concave; bears only two or three elliptical seed scars, 0.8-1 mm long {n=16} and 0.6-0.8 mm wide {n=16}. Wing is slightly reflexed away from the seed-bearing surface, and reaches a maximum width distally (0.7-2.5 mm), tapering away towards base of receptacle. Wing margin is entire or weakly scalloped with 3 or 4 obtuse, poorly differentiated teeth.

Scale leaf is 15.8 (25) 29.2 mm {n=16} long, 4.3 (6) 8 mm {n=16} wide; obovate to elliptical with long tapering base (0.9 (1.5) 2 mm wide {n=16}) and rounded to acutely pointed apex. Midrib absent, but weakly developed medio-longitudinal aggregation of veins is present; veins arch gently from medial region, with a mid-laminal vein angle of 20°-32°, and dichotomise and anastomose to form a coarse reticulum of long narrow meshes, reaching the margin at an angle of 37°-42°, and with a density of 12 to 14 veins per 5 mm. Capitula are attached roughly at the point of lamina expansion.

Attached seeds are roughly circular, 3.3-4 mm long, 3.7-4.3 mm wide, with conspicuous lateral wings (0.9-1.3 mm wide); micropylar end is broad and truncated, hylar end slightly pointed.

### **Comments**

Emendations include the characterisation of wing and receptacle beyond the 'scale-like projections' of Lacey *et al.* (1975), and the 'ovuliferous scales' of Anderson & Anderson (1985). Neither authors described the capitula in any detail, or acknowledged the existence of a wing and a receptacle with two or three seed scars.

The single pair of reduced, spatulate rather than campanulate capitula of *L. elegans* makes this taxon easy to distinguish from *L. africana* and *L. lidgettonioides*.

The spatulate shape of the capitula of *L. elegans* is directly attributable to the reduced number of ovules present: if there are only two or three ovules, the wing can have a maximum of three scallops (one per ovule), and 4 teeth.

The scale leaf of *L. elegans* displays less variability than in the other two species, always being obovate to elliptical.

The morphology of the seeds apparently in attachment to specimens of *L. elegans* is puzzling. In both the holotype [NM/1361; pl. 98, figs (a)-(d)] and



another specimen [BP/2/8222; pl. 99, figs (m), (n)], seeds which are apparently attached to the capitula have wings which taper towards the hylar end of the seed, becoming broader towards the micropyle. In the holotype, the sclerotesta is also unexpectedly tapered towards the site of attachment. It is possible these seeds became rotated during preservation, but this seems unlikely considering the convincing nature of their apparent organic attachment to the capitulum. Virtually all other seeds that have been described in attachment to glossopterid fructifications have been broader at the chalazal end, tapering towards the micropyle. However, Taylor & Taylor (1992a) described some permineralized ovuliferous glossopterid fructifications from Antarctica that had attached seeds which were narrow at the chalazal end and broad at the micropylar end.

#### 8.1.5 DISCUSSION

Members of the Lidgettoniaceae are well represented in the Upper Permian of South Africa (Lacey *et al.*, 1975; Anderson & Anderson, 1985) and India (Surange & Chandra, 1974a, 1975) with only a few examples having been found in Australia (White, 1978; Holmes, 1974, 1990). The genus is apparently unknown from other parts of Gondwana.

The South African members of *Lidgettonia* are particularly abundant and morphologically diverse. Lacey *et al.* (1975) collected numerous specimens from the famous Mooi River locality and other Upper Permian eastern Natal sites, and demonstrated the variability in form exhibited by these fructifications and their sporangiate counterparts of the genus *Eretmonia*. Anderson & Anderson (1985) synonymised all the South African members of the Lidgettoniaceae within the genus *Lidgettonia*, and erected three new species, viz. *L. mooiriverensis*, *L. inhluzanensis* and *L. lawleyensis*. As mentioned earlier, the differences cited by Anderson & Anderson (1985) to distinguish the new species could reasonably be attributed to regional variation within a single taxon, and they have been synonymised with *L. africana*. *Lidgettonia lidgettonioides* has been retained on the basis of its unusual and distinctive scale leaf, and the particularly large capitula, and *L. elegans* is easily distinguished by its spatulate scale leaf and extremely reduced capitula, bearing

only one or two seeds per receptacle, with a wing that is markedly tapered at the base.

Several fructifications from India are attributable to Lidgettoniaceae, the first being described by Surange & Maheshwari (1970) as *Lidgettonia indica*. They partially concurred with Thomas' (1958) interpretation of the genus, but considered the capitula to represent clusters of ovules. In fact the specimens they figured appear to be typical of *Lidgettonia*, with seeds attached to capitula. *Lidgettonia indica* is very similar to *L. cooyalensis*, although the lamina of the scale leaf is more obovate and the capitula lobes are less clearly defined.

Surange & Chandra (1974b) described *Lidgettonia mucronata* from the Upper Permian of India. They reconstructed the fructification as having six or seven ovules borne in a row on the surface of a fan-shaped capitulum near the edge of the undulating margin. They did not distinguish between the receptacle and the wing, although their drawing in text-fig. 3 (p. 123; Surange & Chandra, 1974b) clearly shows the seed scars positioned near the centre of the capitulum. This taxon is very similar to *Lidgettonia africana*, and may be a junior synonym.

Surange & Chandra (1973c) instituted the genus, *Partha* for cupulate fructifications from India that bore multiple capitula on slender pedicels in a single, medio-longitudinal row on the scale leaf, as opposed to the two opposite ranks seen in *Lidgettonia*. They created a new species, *P. spathulata* and transferred Surange & Maheshwari's (1970) *Lidgettonia indica* to *Partha*. These specimens appear to have capitula with lobes, rather than clusters of individual cupules as interpreted by Surange & Chandra (1973c), and *Partha* should probably be synonymised with *Lidgettonia* as suggested by Anderson & Anderson (1985).

*Denkania* is another cupulate fructification described by Surange & Chandra (1973b) that should probably be synonymised with *Lidgettonia*. The fructification has a single row of pedicels arising from the base of an elongated scale leaf. Each pedicel terminates in what Surange & Chandra (1973b; 1975) considered

to be a reduced, completely enclosed, cupular structure containing a single ovule. These structures bear a strong resemblance to the scale-like, reduced capitula of *L. elegans*, even having the three apical lobes and tapering base seen in the latter taxon. There is insufficient evidence to conclude that the capitula in *Denkania* were enclosed structures as Surange & Chandra (1973b; 1975) proposed.

Holmes (1974, 1990) described the only recognised species of *Lidgettonia* from Australia, viz. *L. cooyalensis*, although he initially referred the specimens to the sporangiate genus *Eretmonia*. *Lidgettonia cooyalensis* is distinguished by having a very narrow, elongated, oblanceolate scale leaf with round, campanulate capitula with short lobes. White (1978) described two new species of *Partha* and reported the occurrence of '*Rusangea elegans*' (here called *L. elegans*) from various localities in Australia. It is proposed here that all the *Partha* species created by White (1978) and the purported '*Rusangea*' specimen, belong within *L. cooyalensis*. Of all the known fructifications of the Lidgettoniaceae, *L. cooyalensis* is most similar to *L. elegans*, although the scale leaf is more elongated and capitula are rounded and not reduced as in the latter species.

There are some similarities between the Upper Permian Australian fructification *Cometia biloba* (McLoughlin, 1990a) and capitula of *L. elegans*, although these similarities appear to be fairly superficial, resulting from both structures bearing a reduced number of ovules. The pedicel of *Cometia biloba* is much thicker and more robust than in *L. elegans*, and is not pendulous. In *Cometia*, the pedicel expands to form a fan-shaped lamina which is nearly twice the size of the *L. elegans* capitulum.

Thomas (1958), Lacey *et al.* (1975) and Anderson & Anderson (1985) affiliated *Lidgettonia* with the glossopterids primarily on the basis of association, and on the similarities in venation of the scale leaves and vegetative *Glossopteris* leaves, i.e. the fact that both had reticulate venation. However, the unmistakable similarities in the morphology of the reduced capitula of the Lidgettoniaceae with members of the Dictyopteridiaceae, clearly serve to

identify this family as glossopterid. These similarities were discussed in more detail in section 3.2.1.

It is still unknown exactly how and where fructifications of the Lidgettoniaceae were borne on the *Glossopteris* plant, but White's (1978) work on *Squamella* would indicate that they probably grew in loose, cone-like aggregations at branch termini. *Squamella* is the form-genus White (1978) assigned to Upper Permian scale-fronds aggregated into cones. Some of the specimens she described appear to have been sterile, whilst others are apparently composed of sporangiate, *Eretmonia* scales. No specimens of *Squamella* have been found with capitulum-bearing scales, although this was inferred by White (1978). In White's (1978) descriptions of *Squamella*, she makes the observation that the scales comprising the cone have variable morphology, depending on their position within the aggregation. It is possible that the huge intraspecific variation in the size and shape of the scale leaves of *L. africana* and *L. lidgettonioides* may be accounted for in the context of morphological variation within a cone-like structure.

## CHAPTER 9 DISCUSSION AND CONCLUSIONS

### 9.1 INTERPRETATIONS OF DIVERSITY IN SOUTH AFRICAN GLOSSOPTERID POLYSPERMS

South Africa appears to have an unusually high diversity of glossopterid fructification morphologies concentrated in the Lower Permian (see Table 9.1.1). The Vereeniging locality has yielded 10 out of the 25 taxa of ovuliferous glossopterid fructifications described in this document. Anderson & Anderson (1997) characterised the highly diverse Lower Permian (upper Ecca Group) deposits of South Africa, as being 'about twice as rich' as the flora represented in the Upper Permian, Estcourt Formation deposits. Is this a reflection of diverse localised habitats which encouraged diversification in the Gondwanan landscape that now constitutes South Africa? Perhaps South Africa could be seen as the cradle of the glossopterids! It is also quite possible that South Africa, with its unusually well-represented Permian exposures, and numerous, active stone and clay quarries, has simply provided the best opportunities for the collection of glossopterid material over the years.

A total of nine genera and 15 species of ovuliferous fructification are recognised here from the Lower Permian of South Africa, compared with five genera and nine species from the Upper Permian (see table 9.1.1). Members of the Dictyopteridiaceae are definitely more diverse in the Lower Permian, as highlighted by the recognition of several new morphological features during the course of this study, including a double wing (*Bifariaia*), a hooded wing (*Elatra*) and an apical spine (*Gladiopomum*). However, if we consider the diversity of the glossopterids as a group, at the family level, then the Upper Permian fructifications were more diverse with three families being represented, as opposed to two families in the Lower Permian.

Table 9.1.1 reveals a dramatic switch from a Lower Permian flora in the Ecca Group deposits, to a flora with a very different composition at the generic level in the Upper Permian Beaufort Group.



The only genus common to both the Upper and Lower Permian, is *Plumsteadia*, which is too broadly defined to be a reliable indication of trends in diversity. This change in the flora was probably not as rapid as inferred by Table 9.1.1. There is a dearth of information regarding the Middle Permian glossopterids, mainly because the deposits of the Volksrust Formation, in the otherwise fossil-rich beds of the eastern Karoo Basin, are mostly subaqueous and devoid of fossil material. This is most unfortunate, as the Volksrust Formation was deposited during a time of great glossopterid diversification. According to McLoughlin (1993), it was at this stage that both the Rigbyaceae and Lidgettoniaceae evolved.

### **9.1.1 IMPRESSION FOSSIL INTERPRETATION**

A cornerstone of this investigation was the clarification of what an impression fossil really represents viz. a three-dimensional mould of the original plant structure. This model created a new paradigm for the observation and analysis of the South African material. It was, of course, not an original concept, but one which had been proposed by many authors in the past, dating back to the comments of Harris (p. 322 in Plumstead 1952) and Hughes (p. 224 in Plumstead, 1956b) in the earliest papers describing the famous Vereeniging fossils, and later promoted by authors such as Schopf (1975), Rigby (1978), McLoughlin (1990b) and Chaloner (1999). This is the first time, however, that these concepts have been systematically applied to the fructifications housed in the South African collections, and the exciting and novel results that have emerged have added a new level of intrigue and promise to this controversial plant group.

Some authors (notably Schopf, 1976; Taylor, 1996) have considered the Vereeniging impression fossils (and impression fossils in general), to be poorly preserved. In fact, as far as impression fossils are concerned, they are beautifully preserved. They may not show the much sought-after anatomical details of permineralized material, but as high resolution, three-dimensional moulds, they show superb details of the surface features of the original plant and general appearance and arrangement of the organs.

The contribution that impression fossils can make to the study of palaeobotany has been increasingly underrated since the discovery of permineralized glossopterid material revealed anatomical details of these plants. As palaeontologists, we often have such limited and fragmented evidence available to us, that every avenue should be enthusiastically and rigorously explored. Rather than bemoaning the difficulties of interpreting preservation types of apparently inferior quality, we should see these as opportunities to glean new types of information which may not be apparent in 'better' preserved specimens.

Admittedly, the three-dimensional structure of paper-thin moulds is very difficult to depict in two-dimensional photographs. This should not, however, diminish the value of these fossils – it should urge us on to develop new methods of extracting the valuable information they contain. In this regard, the future of impression fossil studies may well lie in the application of CT scanning methods (computerised tomography). This technology, which essentially depicts differences in density in a specimen, is ideally suited to the detection of cavities in rock matrix, which is what an impression fossil really represents. With the aid of digital modelling techniques, this technology would allow for the three-dimensional reconstruction of positive images of the original plant structures. An added bonus is that the technique is non-invasive, and would allow for the characterisation of rare and valuable fossils, without causing any of the damage inflicted by physical dissection and preparation of the specimen.

The application of new techniques and three-dimensional depictions of impression fossil material may also help to narrow the gap that has apparently developed between workers studying impressions and those studying permineralized material.

### **9.1.2 COMPARISON BETWEEN PERMINERALIZED FRUCTIFICATIONS AND SOUTH AFRICAN IMPRESSION FOSSILS**

In their landmark paper depicting the first sections through permineralized glossopterid fructifications, Gould & Delevoryas (1977) developed a theory of uniformity amongst all glossopterid fructifications, effectively reducing the



differences between taxa to a matter of length to width ratios. The variety of wing morphologies described in the present study clearly demonstrates that whilst sharing many similarities, the fructifications of *Glossopteris* still exhibited a fair degree of morphological diversity.

It became apparent at the recent IOP<sup>8</sup> congress in Argentina that some workers have been concerned about an apparent incompatibility between permineralized glossopterid fructifications and the reconstructions generated through the observation of impressions fossils (e.g. Prof. Sergio Archangelsky; Dr. E.L. Taylor, pers. com.). This perception may have stemmed from a lack of appreciation of the morphological diversity of the fertile structures of *Glossopteris*, and an underestimation of the information provided by impression fossils. Relatively few permineralized fructifications have been examined because of the rarity of these specimens, as opposed to the well over 700 specimens of ovulate fructification impressions in the South African collections alone, from many different localities of different ages. One would therefore expect a higher degree of diversity to be represented in the impression fossil material.

Impressions of *Dictyopteridium* and particularly *Plumsteadia*, do not conflict at all with interpretations based on permineralized material. The wing is not clearly defined in permineralized specimens, perhaps because the receptacle is a lot thinner than one might think from observing the impression fossils. In cross-section, features such as texture, fluting and striations are not apparent, and these all play an important role in defining the wing in impression fossils. The only clear way to identify the edge of the receptacle and start of the wing in a permineralized fructification, would be to observe the positions of the marginal seed attachment points – the tissue beyond these points would represent the wing. Seeds are not attached immediately adjacent to the margins in any of the permineralized fructifications figured in the literature, and in most cases the presence of a narrow sterile flange is a reasonable assumption.

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<sup>8</sup> 7<sup>th</sup> International Organisation for Palaeobotany Congress, Bariloche, March 2004

It is very difficult to judge the thickness of a plant structure from a compressed mould. The scale in all my schematic sections through fructifications in Chapter 3 has been exaggerated in the y-axis to emphasise the distinction between the wing and receptacle. These structures were probably all a lot thinner, and would have appeared much the same in cross section as the permineralized specimens.

The high degree of infolding of the wing in the permineralized Homevale specimens described by Gould & Delevoryas (1977) has not been observed in South African impressions of members of the Dictyopteridiaceae. Almost all impressions and compressions show a flattened wing lying in a similar plane to the receptacle, although there is a strong tendency in almost all specimens of *Dictyopteridium* and *Plumsteadia* for the wing to be inclined/ arched towards the seed-bearing surface of the fructification. In a few cases fructifications have been preserved with at least one side of the wing folded over the fertile surface of the receptacle [e.g. pl. 87, fig. (h)]. Rigby (1978) accounted for the difference in inrolled permineralized specimens versus flattened specimens observed in compression and impression fossils, in terms of the fructification having a mechanism whereby it was able to open and close depending on the amount of moisture to which it was exposed. He based this theory on the observation by Gould & Delevoryas (1997) that larger cells were present on the non seed-bearing side of the fructification. He postulated that the normal growing state of the fructification was an inrolled one, but under dry conditions the large cells on the sterile side of the fructification contracted, causing the fructification to flatten out. An alternative explanation is that the inrolled state was typical of immature fructifications, which unfurled once their seeds were ready for dispersal.

In the permineralized fructification described by Schopf (1976; p. 59, pl. V, fig. 4) and Taylor & Taylor (1992; p. 11495, fig. 1), the seed-bearing portion of the specimen was divided into a series of mounds and hollows. Taylor & Taylor (1992; fig. 2; p. 11496), reconstructed this fructification with a seed borne in each of these hollows. The relatively narrow wing and prominent seed scars as reconstructed by Taylor & Taylor (1992) correspond well with impression fossils of fructifications such as *Plumsteadia*.

The specimen described by Taylor & Taylor (1992) is small (6 mm wide) for a member of the Dictyopteridiaceae, although it still falls within the lower end of the size ranges for the South African taxa *Plumsteadia lerouxii*, *Plumsteadia gibbosa* and *Dictyopteridium natalensis*. The specimen also falls within the ranges for some of the larger members of the Lidgettoniaceae, which can reach up to 8 mm in width (*L. lidgettonioides*). However, based on evidence from impression fossils, none of the *Lidgettonia* fructifications has structures equivalent to the prominently raised features on the receptacle. A third, intriguing alternative, initially proposed by Schopf (1976), is that the fertile structure may represent a specimen of *Rigbya*. It is almost precisely the same size as the impression fossil of a *Rigbya* specimen Schopf figured from Antarctica in the same paper. The mounds in the permineralized specimen would correspond to the ultimate branches of the fructification, and the thin lamina between the mounds would represent the fan-shaped lamina, which in all specimens of *Rigbya* recovered so far from Antarctica, extends all the way to the seed scars, forming a fused, fan-shaped structure.

Zhao *et al.* (1995) described permineralized structures from Antarctica which they interpreted as belonging to the 'cupulate' type of glossopterid fructification. The 'cupules' were aggregated in groups of four, in a crescent shape, and were described by Zhao *et al.* (1995) as tubular structures, each bearing a single seed. As in the specimen described by Taylor & Taylor (1992), these features are highly reminiscent of the terminal branches of a *Rigbya* fructification. The groups of four fit well with the compact bifurcating structure of a *Rigbya* axis, and the specimen figured in Zhao *et al.* (1995), fig. 1 could easily be interpreted as two secondary branches, with the left branch having undergone a second bifurcation. The tubular walls of the cupules themselves may well be the wing-like scales which extend beyond the seed-attachment point at the branch termini in *Rigbya*. We know from impressions of *Rigbya* that these scales/wings were concavo-convex features, and it is possible that these features were even more inrolled in permineralized specimens. If we compare the degree of inrolling of members of the Dictyopteridiaceae in permineralized material (e.g. Gould & Delevoryas, 1977) versus the relatively flat structures we see in impressions, it makes this theory all the more plausible. The sizes of the

cupules given by Zhao *et al.* (1995) (3.0-3.5 mm long, up to 1.2 mm wide), correspond well to the sizes of the terminal scales in South African *Rigbya arberioides* specimens, which range from 2.5 - 7.6 mm long, and 0.8-3.5 mm wide. The seeds with prominent wings in the Zhao *et al.* (1995) specimens also correspond well to those which have been found attached to or associated with *R. arberioides*, although they may be slightly smaller. It is interesting to note that these specimens were collected from the same locality as the one described by Schopf (1976) and Taylor & Taylor (1992).

### **9.1.3 DIVERSE WING STRUCTURES IN GLOSSOPTERID FRUCTIFICATIONS**

The wing present in all members of the Dictyopteridiaceae has been demonstrated in this study to have homologues in members of all the other three families of glossopterid polysperms. It would appear to have been an integral part of the structure of these organs.

Recognition of the three-dimensional nature of impression fossils has facilitated the discovery of some radically new and exciting features in the South African collections of glossopterid fertile structures. The double wing of *Bifariola intermittens* and the covering hood of *Elatra leslii*, have added a new dimension to the interpretation of this group of organs. In section 3.3 I have explained why these wing structures are not just figments of the imagination, but identifying these peculiar structures is just the first step. What implications do they have for our interpretation of the glossopterids as a group?

#### **9.1.3.1 Double wings, hoods and sterile scales**

Gould & Delevoryas (1977) suggested that Plumstead's (1952, 1956 a,b, 1958a) 'bivalve theory' arose from her observation of specimens where cleavage through the edges of the flattened megasporophyll envelope resulted in portions appearing on both part and counterpart. They also suggested that cleavage through the overlapping megasporophyll envelope resulted in theories of a subtending bract such as that proposed by Surange & Chandra (1974a).

The recognition of a double wing in *Hirsutum intermittens*, here reassigned to *Bifaria*, has adequately explained the origins of Plumstead's bivalve theory (section 3.2.2), but this double wing structure as well as the covering hood morphology seen in *Elatra* could also very satisfactorily account for recurring reports of the presence of a sterile bract in members of the Dictyopteridiaceae from India.

The theory that glossopterid fructifications such as *Ottokaria*, *Scutum*, *Dictyopteridium* and *Plumsteadia* have a subtending, veined, sterile bract (see section 3.1.2.3, p. 56), probably originated with Plumstead's compelling vision of a bisexual, bivalved fructification, but has persisted long after most authors have conceded that members of the Dictyopteridiaceae are dorsiventral, ovuliferous structures. Surange & Chandra (1974a, 1975, 1977b,c) have been vigorous proponents of the presence of a sterile bract, and cited instances where they had recovered up to four cuticle layers from a single specimen, apparently favouring the existence of such a structure. They claimed that sequential acetate peels demonstrated the presence of a veined scale covering the seed-bearing surface of the fructification. Retallack & Dilcher (1988) noted, however, that at least three types of cuticle they recovered could have been derived from the fertile surface of the receptacle the sterile surface of the receptacle, and the wing. An alternative explanation for the recovery of multiple cuticle layers is that a hood was present in the fructification – this would allow for the extraction of four large pieces of cuticle with seeds lodged between the two sets.

White (p. 114, figs 146, 147; 1986), who has also been a proponent of the sterile scale, illustrated a curious Australian specimen with a 'covering leaf', from the Upper Permian, Belmont Insect Beds in New South Wales. This fructification appears to have had a very similar wing structure to that of *E. leslii* (see section 3.2.3, p. 92). Chances are very good that removal of the wedge of sediment bearing the impression of the receptacle would reveal the edges of a hood not too dissimilar to the one seen in *Elatra*. If this specimen is all I suspect it to be, then it would prove that the hood was not a curious, isolated occurrence

limited to the Early Permian, but was widespread both temporally and biogeographically.

#### **9.1.3.2 Functional morphology of the wing in members of the Dictyopteridiaceae**

Various authors have considered the possibility that the broad wing present in members of the Dictyopteridiaceae, may have played a role in the dispersal of the seeds, i.e. the entire fructification may have been shed as an aid to seed dispersal (e.g. Plumstead, 1956a; Smithies, 1978; Adendorff *et al.*, 2002). Most of the fructifications have been found isolated from the subtending leaf, perhaps reflecting a tendency to abscise from the leaf once the seeds had matured. It does not seem probable that the polysperms would have travelled great distances themselves, but they would have, in all likelihood, spiralled down to the ground, dislodging any persistent seeds along the way. Retallack & Dilcher (1988) proposed that the small, wingless seeds found in attachment to *Dictyopteridium* were possibly shaken from the fructifications by swaying in the wind, and were then more widely dispersed by wind and water.

Adendorff *et al.* (2002) thought it likely that the principal function of the wing was protective. They hypothesised that it may have been arched over the receptacle in the early stages of development to protect the ovules, opening up later to expose them for pollination and seed dispersal. This would be in keeping with the permineralized fructifications illustrated by Gould & Delevoryas (1977).

The double wing seen in *Bifaria* *intermittens* may have evolved both as a protective organ and as an aid to seed dispersal. The delicate, apparently membranous secondary or scutoid wing may well have had a protective function early in the development of the fructification. The broad lateral wings would have more than adequately covered the fertile surface of the fructification when arched over. The stiffer, narrower primary wing, which is slightly retuse and has an extended apex may have played a role in the dispersal of the seeds, as outlined above.

The larger size of *Elatra* fructifications and the high concentrations of wingless seeds within an individual could be seen as an indication that these structures were dispersed as a unit. It is interesting to note that many of the *Elatra leslii* specimens in the BPI collections contained *in situ* seeds, often *en masse*.

A semi-enclosed structure such as we see in *Elatra*, could have benefits for some seed dispersal strategies:

- 1) the entire fructification may have been dispersed by wind; the low centre of gravity and long pointed wing probably would have resulted in the fructification twirling to the ground, shaking and shedding seeds from the basal opening in the hood;
- 2) the entire fructification could have been a relatively large and inviting snack for megaherbivores, with the seeds being eaten and dispersed by the consumer.

A number of mature fructifications were found still attached to their subtending leaves, which contradicts the theory of the fructification being dispersed as a whole. It is possible that the long, broad, sail-like wing of *in situ* fructifications may have evolved to catch the breeze, shaking loose the seeds which would fall freely through the basal tent-like opening in the hood.

The presence of a covering hood has additional implications for the mechanics of ovule pollination.

Many authors have assumed the glossopterids were wind pollinated (e.g. Schopf, 1976; Melville, 1983b; Meyen, 1987; Retallack & Dilcher, 1988). The structure of *Eretmonia*, the proposed pollen-bearing organ of *Glossopteris*, certainly points towards wind pollination, with its delicate, pendulous bunches of abundant pollen sacs. The bisaccate pollen grains contained within them and ubiquitous to Permian sediments of Gondwana are also suggestive of wind pollination.

Taylor & Taylor (1992) were uncomfortable about the possibility of wind pollination of ovules 'sandwiched between the megasporophyll and a

subtending leaf'. They noted that the protected position of the ovules 'may suggest a relationship with a biotic pollinator of some sort'. Could the highly specialised, enclosed nature of *Elatra leslii* fructifications, which have a hood and which also face the subtending leaf, represent the first glossopterid structure adapted to insect pollination? Retallack & Dilcher (1988) envisioned *Glossopteris* trees producing clouds of dust-like pollen grains, perhaps much as we see in pine trees today. If this was the case, then it probably would not matter too much from a pollination perspective if the ovules were partly shielded from the wind by either a subtending leaf, or by a hood-like structure.

## **9.2 EVOLUTION OF THE GLOSSOPTERIDS**

### **9.2.1 INFERRED HOMOLOGIES AND PHYLOGENY OF OVULIFEROUS GLOSSOPTERID FRUCTIFICATIONS**

Ideally, a system of classification should not only reflect the morphological differences between organisms, but should also be an expression of their phylogenetic relationships. In the case of the fossil plant record, it is particularly difficult to establish these relationships. In most cases our observations are based exclusively on morphological characters.

Establishing the phylogenetic relationships of the glossopterids has been hindered by the lack of a fossil record for the crucial time period when they are thought to have evolved. The Late Carboniferous of South Africa and most of Gondwana, was a period of glaciation, which created a hiatus in the fossil record during this time.

The glossopterids have been affiliated to all the major seed-bearing plant groups at some time or another, as reviewed in section 4.1.1. This confusion has resulted largely from the absence of any clearly recognisable homologies with other plant groups, and has been exacerbated by a general lack of consensus regarding the basic structure of the ovuliferous glossopterid fructifications.

Since Plumstead (1952) demonstrated the attachment of fertile glossopterid structures to *Glossopteris* leaves, most authors have acknowledged that these



polysperms are gymnospermous. They bear naked seeds on a modified leaf or axis. But does the glossopterid fructification represent a modified leaf or stem?

Pigg & Trivett (1994) summarised the various models for homologies of the glossopterid fertiliger suggested by various authors:

- 1) an 'epiphyllous' condition where the sporophyll is fused directly to a subtending leaf;
- 2) a megasporophyll borne on a highly reduced axillary branch
- 3) a flattened axillary branch;
- 4) the entire ovuliferous structure may be a compound sporophyll similar to the structure seen in the ophioglossalean ferns;
- 5) the entire ovuliferous structure could be a modified branch or cladode (Schopf, 1976; Retallack & Dilcher, 1981; Doyle & Donoghue, 1986).

These models can be broadly divided into three groups, viz. the megasporophyll models, the ophioglossalean model, and the cladode model.

#### **9.2.1.1 Megasporophyll models of glossopterid polysperm derivation**

These models are based on the premise that the glossopterid fructifications represent modified leaves, and usually affiliation with the pteridosperms is implied.

Schopf (1976) had grave reservations about the glossopterids being affiliated with the pteridosperms. He considered pteridosperms to have fertile structures with pinnate seed-bearing organs 'not aggregated as cones or flowers', whereas members of the Dictyopteridiaceae certainly do exhibit a concentration of seed-attachment sites into a capitulate structure.

Gould & Delevoryas (1977) played a huge role in promoting the megasporophyll model, with their publication depicting the first sections through a permineralized glossopterid fructification. They concluded that members of the Dictyopteridiaceae represent incurled megasporophylls with gymnospermous seeds attached to the inside surface. The hypothesis that the ovuliferous

glossopterid fructification is a modified megasporophyll is supported by the dorsiventral, leaf-like appearance of members of the Dictyopteridiaceae, which have reticulate venation very similar to that seen in *Glossopteris* leaves. The anatomical features of permineralized fructifications are also leaf-like.

According to some interpretations, the theory that the glossopterid fructifications are megasporophylls makes the awkward assumption that a modified leaf arose in the axis of another leaf, an arrangement that is not seen in other seed plants (Schopf, 1976; Taylor & Taylor, 1992). Taylor & Taylor (1992) were unable to address this issue, other than to suggest that the glossopterids had a unique 'bauplan' that is no longer represented in the plant kingdom today. Retallack and Dilcher (1981) however, had proposed earlier that the glossopterid fertile structure could have been a megasporophyll borne on a short shoot that was adnate to or carried onto the lamina of a *Glossopteris* leaf. They considered the seed-bearing surface of the fructification to face the subtending leaf, but noted it could be either adaxial or abaxial, depending on the position of the lateral meristem.

Despite the input of various authors such as Retallack & Dilcher (1981), Taylor (1981, 1996), Taylor & Taylor (1992) and Zhao *et al.* (1995) have consistently promoted the idea that in glossopterid fructifications, the seeds were borne on the upper or adaxial surface of the leaf-like organ, which faced away from the subtending leaf. Their insistence has apparently stemmed from two assumptions.

Firstly, as noted above, they appear to have regarded the protective position afforded by a fructification with seeds borne on the surface facing the subtending leaf as being obstructive to wind pollination, and therefore untenable (Taylor, 1996). On the other hand, the exposure of ovules borne on the receptacle surface facing away from the leaf was seen to be advantageous. However, a perceived advantage to an ancient plant group about which we know so little, is not really grounds for the construction of scientific fact. By the same reasoning we should dismiss the existence of strobiloid reproductive

structures such as pine cones, because the ovules are too sheltered for pollination to be effective.

Secondly, they perceived the orientation of the xylem tissue in permineralized fructifications such as those figured in Taylor & Taylor (1992), to be closest to the ovule-bearing surface of the vascular bundles relative to the phloem, and on that basis deduced that the seeds were borne on the adaxial surface of the leaf. This was despite the fact that they had no examples of permineralized fructifications in organic attachment to a subtending leaf to substantiate this theory. Although fructifications attached to axes are rare in the fossil record, there are numerous specimens housed in the collections of the Bernard Price Institute which were preserved in attachment to their subtending leaves. Despite the fact that these specimens are only impression fossils, they very clearly, consistently and indisputably demonstrate that in members of the Dictyopteridiaceae, the seed-bearing surface of the receptacle faces the subtending leaf (see section 3.1.1). There is also no evidence to suggest that the fructifications underwent rotation during their development as, when visible, the longitudinal striations on the pedicel of the fructifications could be traced along a parallel path down the pedicel and into the leaf.

#### **9.2.1.2      Ophioglossalean model**

Lam (pp. 227-8 in Plumstead 1956b) drew parallels between the glossopterid fertiliger and *Ophioglossum*. He suggested that the glossopterids were members of the Pteridopsida, thereby pre-dating, in an evolutionary sense, the development of axillary lateral axes which first appeared in the Gymnosperms. Lam regarded the glossopterid fertiliger to be the product of three consecutive dichotomies. He envisaged the first dichotomy to have given rise to a glossopterid leaf on the main axis, the second to have produced one sterile and one fertile branch, the fertile branch being the fructification borne on the midrib, and the third to have produced the sterile half and fertile half of the fructification according to Plumstead's model of a bisexual organ. Lam's model could still be applied to the more modern view of the glossopterid polysperm as a bifacial, dorsiventral structure, by simply excluding the final bifurcation from the model.

Kato (1987) also drew parallels between the arrangement of the sporophore and trophophore seen in the Ophioglossaceae and the epiphyllous fertile structures of the glossopterids.

#### **9.2.1.3 Cladode model**

Schopf (1976) suggested that the glossopterids arose from cordaitan ancestors no later than the Middle Carboniferous. He was a vigorous proponent of the cladode theory, as outlined in point (5) above, with *Arberia* representing the most basal form of the glossopterid fructifications. Bajpai (1992), McLoughlin (1993a), and McLoughlin & Drinnan (1996) supported Schopf's (1976) theories in this regard, as did Meyen (1984, 1987), although this latter author considered the glossopterids to have arisen from primitive gymnosperms of the Calamopityales type.

Schopf (1976) speculated that the stalk and capitulum of *Arberia* could be homologous to the cordaitan ovuliferous spike. The subtending leaf seen in members of the Dictyopteridiaceae would be equable to the foliose bract, with the fructification pedicel partially adnate. Schopf (1976) suggested this would account for the very leafy appearance of the subtending bract in the glossopterids, and would account for the lack of a true midrib in *Glossopteris* leaves and in the scale leaves of *Lidgettonia* and *Eretmonia*. Most authors in the past, however, have regarded the glossopterid fructifications to be axillary structures, which became secondarily adnate to the subtending leaf. Even if the fructification represented a cladode, this arrangement would not be unheard of. The fruits of *Ginkgo biloba* are modified short shoots, and in rare cases are carried up onto the lamina of the adjacent vegetative leaf (Rigby, 1978).

Appert (1977) described *Arberia madagascariensis* fructifications as 'strobili' with lateral branches which were 'megasporophylls'. Like Schopf (1976), he considered the link between *Arberia* and northern hemisphere cordaitalean plants to be strong, in light of the attachment of *Cordaicarpus*-type seeds to the *Arberia* fructifications he described, and the association of these fertile

structures with *Noeggerathiopsis* leaves which are morphologically almost indistinguishable from *Cordaites* leaves. The northern hemisphere cordaitalean fertile structure *Cordaianthus pseudofluitans* was described by Florin (1944, pl. 173/174, fig. 10 and text-fig. 45) as a short shoot bearing megasporophylls.

The cladode model for the evolution of all families of glossopterid fructifications from an arberiid basal form is favoured here. The envisaged transformations required to achieve the morphologies typical of each family are outlined below.

### **9.2.2 A NEW LOOK AT THE CLADODE THEORY AND THE EVOLUTION OF THE FOUR FAMILIES OF GLOSSOPTERID FRUCTIFICATIONS**

This project has demonstrated that although the glossopterid polysperms display a fairly high degree of morphological diversity at the generic and family levels, this diversity embodies variations on basic morphological themes common to all of them (section 3.1.2, p. 48). All the South African ovuliferous fructifications are dorsiventral, with a bifacial arrangement i.e. a fertile side and a sterile side. They all have seed scars, and depending on their position within the organisation of the fructification, at least some of these scars are integral with a scale-like or wing-like feature bearing fine striations radiating away from the seed-detachment site.

Essentially, Appert's (1977) specimens of *A. madagascariensis*, along with his beautiful line drawings and detailed descriptions, have provided us with the perfect basal glossopterid fructification according to the cladode model of glossopterid derivation. We have a pedicellate, longitudinally striated, laminar structure, bearing lateral branches along its margins and additional branches across one face of the lamina; all the seeds are borne on the face bearing the lateral branches. This reflects two of the basic morphological themes common to all glossopterid fructifications: they are dorsiventral and bifacial. The branch termini each bear a single seed-attachment point, with a distal scale-like or wing-like structure, perfectly matching the same arrangement seen in members of all three of the other glossopterid families. It does not require much

imagination to visualise the transformations required to derive members of each glossopterid family from this basal form.

#### **9.2.2.1 Derivation of the Rigbyaceae**

Anderson & Anderson (1985) proposed that *Rigbya* may have been derived from Lower Permian members of the Dictyopteridiaceae, through 'suppression of the central ovuliferous disk and retention of the specialized outer ring of ovules'. They considered it to be most reminiscent of *Ottokaria*. McLoughlin (1995) however, suggested that *Rigbya* fructifications evolved from ancestral *Arberia*-like fructifications with 'relatively compact fertile branches'. This latter view is amply supported by the morphology of *A. madagascariensis*. In text-fig. 3.3.1 (p 107), the similarities between the branch termini in these two taxa removes the need for an evolutionary detour into the Dictyopteridiaceae to explain the terminal scales of *Rigbya*. Derivation of this taxon from an arberiid ancestor would require a reduction in the number of lateral branches, removal of all mid-laminal branches, and aggregation of the branches into a fan-shaped arrangement. The propensity for bifurcation in *Rigbya*, sometimes with several orders of branching, is easily accounted for in terms of a direct transformation from an arberiid form, whereas derivation from an ancestor within the Dictyopteridiaceae would imply that this feature represented an evolutionary reversal or was secondarily derived.

#### **9.2.2.2 Derivation of the Dictyopteridiaceae**

McLoughlin (1995) regarded *Ottokaria* to be the most basal member of the Dictyopteridiaceae, because of its fan-shaped, lobed form, and its early occurrence in the fossil record. *Ottokaria zeilleri* described by Pant & Nautiyal (1984) is certainly highly reminiscent of some species of *Arberia*, with its particularly fan-shaped receptacle and basal lobes with a tendency to curve back towards the pedicel.

The evolution of the capitate polysperms of the Dictyopteridiaceae from ancestral arberiid forms would require the following transformations:

- a substantial increase in number of lateral and mid-laminal branches

- a reduction in branch length and coincident fusion of the branches into a receptacle;
- a loss of the scale-like features in mid-laminal branches (effectively reduced to seed attachment points);
- retention and further development of terminal scale-like features in lateral branches, where they may become fused to varying degrees into a peripheral wing;
- variable fusion of the pedicel of the fructification to the petiole and/or midrib of the subtending glossopterid leaf (the foliose bract of Schopf, 1976).

This explanation for the derivation of the wing possibly makes more sense than other theories regarding its origination from modified ovules, structures which are genetically programmed for dispersal from the parent. But does this model of wing homology and evolution help to explain the peculiar wing morphologies seen in *Bifaria* and *Elatra*?

Formation of a dual wing would be conceivable through the retention of scale-like features in two marginal ranks of modified, fused branches along the periphery of the fructification. The outer ring of scales would fuse to form the primary or hirsutoid wing, and the inner ring of scales would fuse to form the secondary wing. The outermost ring of modified, fused branches would have to be sterile to conform to the evidence provided by impression fossils.

Another possibility is that the primary wing formed through fusion of sterile branches which arose dichotomously from the marginal row of fertile branches. The simplest explanation for the derivation of the primary wing, is that it represents a flange-like extension of the tissues of the receptacle. This could account for the apparent lack of fluting in this wing.

In *Elatra*, the situation is a lot more complicated, and before we fully understand the relationships between the different wing morphologies in this fructification, we should not even begin to speculate on their homologies.

One interesting additional note on the potential stages in the evolution of the Dictyopteridiaceae, is with regard to the possibility of identifying intermediate

forms. What would a fructification look like which had not yet lost the scale-like extensions at the terminus of each mid-laminal lateral branch during the reduction and fusion of the branches into a capitulum? These scales would surely resemble the wings of seeds which were still attached to the fructification. *Ottokaria hammanskraalensis* may well be worth investigating further in this regard.

### **9.2.2.3 Derivation of the Lidgettoniaceae**

The Lidgettoniaceae are almost certainly derived from the Dictyopteridiaceae. This is the most commonly held view in the literature (e.g. Schopf, 1976; Stewart & Rothwell, 1993; McLoughlin, 1993a). The close similarities between individual capitula of members of this family, and the larger capitate forms of the Dictyopteridiaceae have already been addressed (section 3.1.2.4).

Only a few transformational steps would be required to derive members of the Lidgettoniaceae from an ancestor in the Dictyopteridiaceae:

- increase in the number of fructifications per subtending leaf;
- reduction of the size of the fructification with an accompanying reduction in number of ovules produced;
- reduction of the subtending leaf to a scale leaf.

McLoughlin (1993a) and Retallack & Dilcher (1981) suggested that *Jambadastrobus*, a fructification morphologically very similar to *Plumsteadia*, but with multiple fructifications borne on a single *Glossopteris* leaf (Chandra & Surange, 1977a), may represent a phylogenetic link between the solitary capitulate forms of the Dictyopteridiaceae and the multi-cupulate forms of the Lidgettoniaceae. However, Maheshwari (1990) queried the validity of Chandra & Surange's (1977a) interpretation of *Jambadastrobus*, suggesting that the evidence for multiple capitula arising from a single leaf in the specimens they figured was not convincing.



### 9.2.3 GLOSSOPTERIDS AS ANGIOSPERM ANCESTORS

Only a few authors have consistently sought a link between the glossopterids and the angiosperms. Plumstead was the first, and as she stated (p. 233; 1956b): ‘...my belief in Angiospermous affinities was neither a preconceived idea nor, I hope, activated by wishful thinking but a gradual conviction’.

Plumstead (1956a,b, 1958a) cited various reasons in support of an angiosperm connection to the glossopterids, but the majority of these reasons could be attributed to artefacts of preservation. In 1962 (b), she boldly claimed to have found possible angiosperms in the Lower Permian of South Africa. The specimens in question were preserved in white concretions found in a coal seam at the Breyton Colliery in what was then the eastern Transvaal. Plumstead (1962b) interpreted these structures as representing three-dimensional, fleshy structures highly reminiscent of angiosperm fruits. Melville (1983a,b) later named these unusual fertile structures *Breytenia plumsteadiae*, and although he provided a highly interpretive line drawing of the specimen, he did not indicate whether he had examined the specimens in person, or based his descriptions on purely on Plumstead’s (1962b) account of the fructifications. Melville (1983a) described *Breytenia* as a thick-walled, globular fructification with a central cavity filled with seeds, and with a dichotomous network of veins. This vision of an enclosed fertile structure with a thick, fleshy wall, accorded well with his theories of the glossopterids representing possible angiosperm ancestors.

Sadly, after years of searching by Dr. Heidi Anderson and me, not one of the five specimens described by Plumstead could be found in the palaeobotanical collections at the Bernard Price Institute. However, based on my own examinations of the photographs provided by Plumstead (1962b; p. 595, fig. 1), these structures appear to be impression fossils of an ovuliferous glossopterid fructification not unlike *Scutum*. It was not serendipitous that the specimens cleaved along ‘true longitudinal sections’ as noted by Plumstead (1962b) – these were impressions of dorsiventral structures which could only be exposed through cleavage along one plane. The central receptacle bears the venation

pattern typical of the sterile surface of all members of the Dictyopteridiaceae, and there also appears to be evidence of seed scar impressions on the receptacle surface of the uppermost specimen in the photograph, although the preservation of these features may be unusual. Along the periphery of the rounded receptacle, is a smooth wing, with the same type of fluting seen in fructifications such as *Gladiopomum* and *Scutum*. This is the feature interpreted by Plumstead (1962b) and Melville (1983a,b) as a thick wall. Based on the orientation of the venation on the receptacle, the apices of the two fructifications in Plumstead's (1962b) photograph are on the right-hand side. The wing is discontinuous at the apex, and may have an apical spine such as that seen in members of the genus *Gladiopomum*. Melville (1983b) interpreted this latter feature as representing a 'narrow tubular terminal orifice' of the central cavity. It is a great pity that these specimens are not available for further examination, and they may well represent a new genus of ovuliferous glossopterid fructification.

Melville (1960, 1962, 1970, 1983a,b) was as tenacious as Plumstead in his quest for proof of the angiosperm-glossopterid connection. Following an investigation of the floral vasculature of extant angiosperms, Melville (1960) concluded that the 'carpel theory' commonly used to explain the evolution of the ovary was inadequate in some respects. He developed the 'gonophyll theory' as an alternative, which portrayed the basal form of the angiosperm ovary as a 'leaf bearing on its midrib or petiole a dichotomous fertile branch'. Melville (1960) based his model of the glossopterid gonophyll on Plumstead's (1952, 1956a,b, 1958a) interpretations of a bisexual fructification with a male and a female half. He interpreted these two halves as representing a bifurcated, epiphyllous branch. He traced the homologies of these organs back to rhyniopsid ancestors in the Devonian.

Retallack & Dilcher (1981) discussed how mounting evidence against Plumstead's (1952, 1956a,b, 1958a) bisexual, bicupulate model of the glossopterid fructification, had taken the wind from Melville's (1960, 1962, 1969, 1970) sails with regard to the incorporation of the glossopterids into his gonophyll model of angiosperm phylogeny. However, they in turn pursued the

relationship between the angiosperms and the glossopterids, diminishing the importance of a bisexual angiosperm ancestor, and shifting the emphasis of their approach to members of the Lidgettoniaceae, as initially proposed by Stebbins (1974). They proposed that the capitulum of single-seeded members of the Lidgettoniaceae was homologous with the outer integument of the angiosperm ovule, and the subtending leaf was homologous with the angiosperm carpel. Their theory relied on the interpretation of an Indian member of the Lidgettoniaceae, *Denkania*, as bearing enclosed, uniovuliferous cupules.

Many authors have considered the capitula of the Indian genus *Denkania* to be enclosed, cupulate structures (Surange & Chandra, 1973b; Meyen, 1987; Stewart & Rothwell, 1993). McLoughlin (1993a) however, questioned this interpretation of *Denkania*, suggesting the cupules may be dorsiventral capitula bearing seeds on one surface, as seen in other members of the Lidgettoniaceae. I consider it likely that these fructifications are similar to the South African species *Lidgettonia elegans*, which has reduced, dorsiventral, spatulate capitulum bearing only a few seeds.

The evolution of an enclosed, cupulate structure such as that proposed in the past for *Denkania*, would involve a fairly dramatic transformation, from a campanulate or flattened dorsiventral structure with a laterally inserted pedicel, to a peltate, deeply campanulate, fused structure. The more likely explanation is the simpler one, that these were flattened, dorsiventral, open structures, for which a precedent has already been set in the South African material. In 1983, Melville was still clinging to his gonophyll theory, and the link it provided between the glossopterids and the angiosperms. He reluctantly conceded to the unisexual nature of the glossopterid fertile structures, and described them as a 'fertile branch epiphyllous upon a leaf-like organ'. He was insistent that the body of evidence pointed exclusively to the glossopterids as the progenitors of the angiosperms, forming 'part of one continuous lineage which stretches back for about 410 My through the Glossopteridae to the Rhyniopsida in the Late Silurian.

Melville (1969) also considered the venation pattern of primitive angiosperms to be comparable to that of glossopterid leaves. However, Alvin & Chaloner (1970), Schopf (1968) and Rigby (1984) noted that a reticulate venation pattern did not serve to affiliate the glossopterids with the angiosperms, as the fossil record illustrates many examples of convergent evolution as far as gross venation patterns are concerned. In addition, the glossopterids do not have a reticulate vein structure in the same sense as the angiosperms. There appears to be only a single order of veins, with individual vascular bundles only crossing paths or approaching each other closely at apparent sites of anastomoses.

No doubt Melville and Plumstead would have been intrigued by the remarkable semi-enclosed form of *Elatra* fructifications!

### **9.3 BIOGEOGRAPHIC AND BIOSTRATIGRAPHIC UTILITY OF THE GLOSSOPTERIDS**

#### **9.3.1 THE BIOGEOGRAPHIC SIGNIFICANCE AND APPLICATION OF SOUTH AFRICAN GLOSSOPTERID POLYSPERMS**

Although the glossopterids as a group are enormously wide-spread, the problems that have been encountered in adequately characterising the foliage material, and the phenomenon of intra-Gondwanic macro-floristic provincialism at the species level (Rigby, 1984; Anderson & Anderson, 1985; McLoughlin, 1993a; Adendorff *et al.*, 2002), have hindered biogeographic correlations across Gondwana. At present, the greatest hope for biogeographic comparisons of the glossopterids lies in the correlation of their ovuliferous structures. McLoughlin (1993a) gave a comprehensive review of the biostratigraphic value of the various known glossopterid organs from Gondwana.

South Africa has elements in common with all the other present-day Gondwanan continents, as reflected in Table 9.3.1.

**Table 9.3.1. Occurrences of ovuliferous glossopterid fructifications common to South Africa and other parts of Gondwana.**

| South African genera   | Other parts of Gondwana with reported occurrences |            |           |               |            |
|------------------------|---------------------------------------------------|------------|-----------|---------------|------------|
|                        | India                                             | Antarctica | Australia | South America | Madagascar |
| <i>Rigbya</i>          | -                                                 | +          | +         | -             | -          |
| <i>Arberia</i>         | +                                                 | -          | +         | +             | +          |
| <i>Vereenia</i>        | -                                                 | -          | -         | -             | -          |
| <i>Bifariola</i>       | -                                                 | -          | -         | -             | -          |
| <i>Estcourtia</i>      | -                                                 | -          | -         | -             | -          |
| <i>Elatra</i>          | -                                                 | -          | ?         | -             | +          |
| <i>Ottokaria</i>       | +                                                 | -          | +         | +             | ?          |
| <i>Scutum</i>          | +                                                 | -          | +         | -             | -          |
| <i>Gladiopomum</i>     | -                                                 | -          | -         | -             | -          |
| <i>Plumsteadia</i>     | +                                                 | +          | +         | +             | -          |
| <i>Gonophylloides</i>  | -                                                 | ?          | ?         | -             | -          |
| <i>Dictyopteridium</i> | +                                                 | -          | +         | +             | -          |
| <i>Lidgettonia</i>     | +                                                 | -          | +         | -             | -          |

+ occurrence reported   - unknown from this region   ? possible occurrence, uncertain

*Arberia* and *Plumsteadia* are the most widespread genera of ovuliferous glossopterid fructification in Gondwana. *Plumsteadia* is a genus with a very broadly defined circumscription, which may well represent a polyphyletic grouping of morphologically similar organs. The widespread occurrence of this taxon may not be of great biogeographic importance. However, *Arberia* is a better constrained genus, and its broad distribution across Gondwana could be seen to support theories that it represents the most basal form of ovuliferous glossopterid fructification. Interestingly, *Ottokaria*, thought by many authors to be the most basal members of the Dictyopteridiaceae, is also widely distributed.

Comments on the similarities in glossopterid polysperm occurrences between different continents may perhaps be more a reflection on which floras have been most thoroughly investigated. Antarctica, which appears to have little in common with South Africa, has vast palaeobotanical resources which have

hardly been touched. Future studies of this continent will undoubtedly yield a more diverse representation of the glossopterid fertile structures.

Madagascar, which appears to have the least in common with South Africa, has barely been explored in terms of its palaeofloral diversity, and both of the taxa listed as confirmed shared occurrences in Table 9.3.1 are exclusive to these regions. There are some close similarities between the floras described by Appert (1977) from the Sakoa Basin in Madagascar and the floras of the Hammanskraal locality, which may point to a more intimate geological relationship between these regions than has been fully appreciated in the past.

From the limited information currently available, South Africa has the most in common with Australia and India, in terms of shared genera of glossopterid polysperms.

### **9.3.2 THE BIOSTRATIGRAPHIC SIGNIFICANCE OF THE SOUTH AFRICAN GLOSSOPTERIDS**

South African palaeontology has a strong tradition of biostratigraphic research using vertebrate fossil taxa for the correlation of geological formations across the Karoo Basin (e.g. Kitching, 1977; Rubidge, 1995). However, the abundant fossil floras found within the Karoo Basin deposits have been enormously underutilized in this respect. Presently, it is possible to differentiate crudely between Lower and Upper Permian strata on the basis of a range of plant taxa. However, the most useful index fossils such as glossopterid ovuliferous fructifications tend to be very rare, and others, such *Trizygia speciosa* have fairly broad ranges, reflecting biostratigraphic trends rather than rules. Of course, as our knowledge of the floras improves, we may be able to detect more subtle biostratigraphic signatures.

Aside from very broad biostratigraphic and biogeographic applications, there has been little progress in establishing the utility of different *Glossopteris* leaf species as index fossils for geological subunits within the Permian. This has largely resulted from the lack of a widely accepted and consistently applied

taxonomic protocol for glossopterid leaves (e.g. Kovács-Endrödy, 1979, 1991; McLoughlin, 1990a). *Glossopteris* leaf taxonomy may never portray an accurate biological representation of the diversity present in the glossopterids, but the variations observed in leaf morphology do have the potential to be useful and consistent indicators of temporal change in the fossil record, particularly since they are so abundant. The much rarer ovuliferous glossopterid fructifications may help in the future to provide a strong framework for the biostratigraphic typification of Permian sediments, around which a useful and more accessible system based on leaf taxonomy may be built. This is an area which urgently needs to be addressed in South Africa.

The perfect index fossil for biostratigraphic applications, would be distinctive, easy to recognise, commonly occurring, would have a broad geographic distribution, and would be entirely restricted to rocks of a narrowly defined age. The glossopterid ovuliferous fructifications vary in the degree to which they fulfil these requirements. Table 9.3.2 summarises some perceptions regarding the biostratigraphic potential of each of the South African genera of glossopterid polysperms, based on the literature referenced in this thesis, and my own opinions. The most useful index taxa for the Lower Permian in South Africa may be *Arberia* and *Gladiopomum*. Other Lower Permian taxa *Bifaria* and *Elatra* have great potential as biostratigraphic indicators, and possibly as biogeographic tools, especially in light of the unmistakable new morphologies which have been identified in this study. The most useful index fossils for the Middle and Upper Permian sediments in South Africa are *Rigbya*, *Dictyopteridium* and *Lidgettonia*. Hopefully this list will grow as our knowledge of the temporal ranges of these fructifications improves.

Comments included in the table pertaining to their rarity or frequency of occurrence should be viewed with caution. Frequency data in the fossil record are potentially very unreliable, as there are so many factors to take into account, particularly taphonomic and collecting biases. The large numbers of *Scutum* and *Bifaria* fructifications probably have more to do with the size of the collection that was made from the Vereeniging locality than their actual frequency of occurrence in the sediments. Stephanus Le Roux spent many

years looking specifically for these structures. However, comparisons of specimen counts between taxa from the same locality might be more appropriate. *Vereenia* really is rare, if only six or so specimens were found in all the years of intensive collecting. Of course, this could just mean that *Vereenia*-producing plants did not grow near water bodies, and were not incorporated into the fossil record very often. For whatever reason though, a useful index fossil can not be a once-off, find of the century, and if very few examples of a particular taxon have been found after many years of collecting, it is worth mentioning in this context.

Table 9.1.1 (p.328) presents all the South African species of glossopterid fructifications and their localities of origin within a lithostratigraphic context. At a generic level, only *Plumsteadia* is common to both the Upper and Lower Permian. It is not terribly surprising that this genus has the most wide-ranging temporal distribution, as it is the most poorly constrained taxon of all the fructifications, and probably encompasses a diversity of polyphyletic organs. This is one of the primary reasons why it is not considered to be a useful index taxon. However, as noted in Table 9.3.2, *P. lerouxii*, with its very distinctive subtending leaf and its characteristic lack of striking features, may prove to be a useful indicator for the Lower Permian on a regional scale.

The stratigraphic range of *Lidgettonia africana* is uncertain at this stage. The oldest occurrence of this fructification is listed in Table 9.1.1 as the Middle Permian. This is entirely dependant on current theories regarding the stratigraphic position of the Lawley locality, which may in the future prove to be younger than currently acknowledged.



Table 9.3.2. Evaluation of South African genera of glossopterid ovulate fructifications as biostratigraphic indicators.

| TAXON                     | RECORDED OCCURRENCE IN SOUTH AFRICA                                                                                 | ADVANTAGES                                                                                                                                                                   | DISADVANTAGES                                                                                                         | SUMMARY EVALUATION                                 |
|---------------------------|---------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------|----------------------------------------------------|
| <b>Arberiaceae</b>        |                                                                                                                     |                                                                                                                                                                              |                                                                                                                       |                                                    |
| <i>Arberia</i>            | Lower Permian only (Artinskian); [note: 'A. allweyensis' transferred to Rigbyaceae]                                 | very distinctive; widespread, found in Lower Permian of India, South America, Australia and South Africa                                                                     | extremely rare; only 2 specimens known from S.A.                                                                      | excellent, very reliable, but rare                 |
| <i>Vereenia</i>           | Lower Permian only (Artinskian)                                                                                     | very distinctive; potentially restricted to the Lower Permian                                                                                                                | very rare; only known from a single locality                                                                          | too rare; insufficient evidence                    |
| <b>Rigbyaceae</b>         |                                                                                                                     |                                                                                                                                                                              |                                                                                                                       |                                                    |
| <i>Rigbya</i>             | Upper Permian only (Lopingian)                                                                                      | very distinctive, immediately recognisable, fairly common and apparently widespread taxon, found in Upper Permian of South Africa, Australia and Antarctica                  | cannot think of one                                                                                                   | excellent, very reliable                           |
| <b>Dictyopteridiaceae</b> |                                                                                                                     |                                                                                                                                                                              |                                                                                                                       |                                                    |
| <i>Bfariata</i>           | Lower Permian only (Artinskian)                                                                                     | very distinctive morphology; may occur elsewhere and has not yet been recognised; apparently restricted to Lower Permian; common within Vereeniging locality                 | only found at a single, South African, locality (Vereeniging)                                                         | excellent potential, but distribution too regional |
| <i>Dictyopteridium</i>    | Upper Permian only (Lopingian)                                                                                      | distinctive morphology; fairly common; characteristic of Upper Permian in South Africa, India and Australia;                                                                 | may be confused with <i>Plumsteadia</i> if seed scar preservation is poor;                                            | excellent, very reliable                           |
| <i>Elatra</i>             | Lower Permian only (Artinskian)                                                                                     | unmistakable morphology, very distinctive; apparently common (within single locality); distribution broad, extending into Madagascar; apparently restricted to Lower Permian | in South Africa only found at single locality; only one specimen found in Madagascar                                  | very good potential                                |
| <i>Escourtia</i>          | Upper Permian only (Lopingian)                                                                                      | possibly restricted to Upper Permian                                                                                                                                         | too rare at this stage to be considered useful; distinguishing features easily overlooked; only found in South Africa | too rare, but with potential                       |
| <i>Gladiopomum</i>        | Lower Permian (Artinskian); possibly Middle Permian (Guadelupian), but challenged by Adendorff <i>et al.</i> (2002) | distinctive diagnostic characters; fairly common; potentially very useful index fossil for the Lower Permian; found at three fairly widely spaced localities in South Africa | restricted to South Africa; superficially similar to wide-ranging taxa <i>Scutum</i> and <i>Plumsteadia</i>           | excellent potential locally                        |

| TAXON                  | RECORDED OCCURRENCE<br>IN SOUTH AFRICA                                                     | ADVANTAGES                                                                                                                                                                                                              | DISADVANTAGES                                                                                                                                                                                                                                                                                                                   | SUMMARY<br>EVALUATION                                                                       |
|------------------------|--------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------|
| <i>Gonophylloides</i>  | Lower Permian only<br>(Artinskian)                                                         | may be restricted to Lower Permian; distinctive cordate base                                                                                                                                                            | circumscription of genus very broad; only features distinguishing this genus from <i>Plumsteadia</i> are its very narrow wing, cordate base and low L:W                                                                                                                                                                         | potentially useful                                                                          |
| <i>Oftokaria</i>       | Lower Permian only<br>(Artinskian)                                                         | distinctive taxon; apparently restricted to Lower Permian in South Africa; widespread across Gondwana                                                                                                                   | has been reported from Upper Permian sediments of Australia (McLoughlin, 1990a) and India (Banerjee, 1978); therefore only reliable on regional scale                                                                                                                                                                           | temporally too wide-ranging<br>(may be of regional value)                                   |
| <i>Plumsteadia</i>     | Lower and Upper Permian                                                                    | <i>P. lerouxii</i> is always found attached to its very distinctive <i>Glossopteris</i> leaf, and could prove to be a useful indicator for the Lower Permian in South Africa; widespread across Gondwana; fairly common | bit of a dumping ground for nondescript, lanceolate fructifications with bulbous seed scars; possibly polyphyletic grouping of superficially similar organs; found in both Lower and Upper Permian sediments                                                                                                                    | not useful;<br>temporally too wide-ranging<br>(individual species may be of regional value) |
| <i>Scutum</i>          | Lower Permian only<br>(Artinskian)                                                         | common; widespread across Gondwana                                                                                                                                                                                      | South African members display a high degree of continuous morphological variation; the more lanceolate forms approach the circumscription of <i>Plumsteadia</i> ; taxon may be largely a Lower Permian genus, but the potential for overlap with <i>Plumsteadia</i> –type fructifications makes this an unreliable index taxon. | unreliable; too variable.                                                                   |
| <b>Lidgettoniaceae</b> |                                                                                            |                                                                                                                                                                                                                         |                                                                                                                                                                                                                                                                                                                                 |                                                                                             |
| <i>Lidgettonia</i>     | Upper Permian (Lopingian); possibly Middle Permian (Guadelupian) as well (Lawley locality) | immediately identifiable, common, widespread, found at 7 Upper Permian localities in South Africa; also known from India and Australia                                                                                  | if currently accepted age for Lawley sediments is correct, extension of range into the Middle Permian detracts from the value of taxon                                                                                                                                                                                          | excellent, but temporal range may be broader than hoped                                     |

### 9.3.2.1 The enigmatic Lawley locality

The South African Lawley locality has had a significant impact on the temporal distributions of two glossopterid polysperms which are widely recognised as being important index taxa. The South African species named *A. allweyensis* and *L. lawleyensis* by Anderson & Anderson (1985), apparently represent the latest and earliest occurrences respectively of these genera in Gondwana (McLoughlin, 1985). Unfortunately, the Lawley deposits from which they originated are an outlier of the main Karoo Basin, and cannot be reliably placed stratigraphically on the basis of lithology alone.

Rayner & Coventry (1985) were the first to work on the beautifully preserved Lawley flora. They noted the presence of a peculiar mixture of plants typically associated with both the Upper and Lower Permian strata in South Africa and elsewhere in Gondwana. They equated certain *Glossopteris* leaf taxa with those known from the Lower Permian Hammanskraal locality, although they expressed reservations about the reliability of the taxonomy of these leaves. They also observed that the abundance of *Noeggerathiopsis* leaves at Lawley may support a Lower Permian age for the sediments, as proposed by Maithy (1965). They recovered a single specimen of a fructification which could have been attributed to either *Rigbya*, an Upper Permian index taxon, or *Arberia*, a Lower Permian index taxon. Ultimately, Rayner & Coventry (1985) considered the evidence provided by the presence of typically Upper Permian taxa such as *Lidgettonia africana*, *Eretmonia natalensis*, *Sphenophyllum (Trizygia) speciosum* and *Phyllothea australis*, as well as the absence of typically Lower Permian arborescent lycopods, to outweigh other factors, and regarded the Lawley deposits to be comparable to sediments of the Estcourt Formation (Beaufort Group; Upper Permian).

Anderson & Anderson (1985), when faced with the same dilemma, assigned the controversial branched fructification to *Arberia allweyensis* (see section 5.2, p. 160), and arrived at a compromise regarding the stratigraphic position of the locality, citing the deposits as Volksrust Formation equivalents (Middle Permian). Interestingly, Anderson & Anderson (1985) recorded an 85%

abundance of leaves they considered to belong within their *Lidgettonia lawleyensis* palaeodeme, with *Noeggerathiopsis* making up only 5% of the fossil material examined.

Since then several specimens of the peculiar fern *Liknometalon*, which previously had only been found in Lower Permian sediments of South Africa have come to light from Lawley (Adendorff *et al.*, 2003). Does this mean that the stratigraphic range of *Liknometalon* has been extended, or it is another piece of information pulling the Lawley sediments lower into the Permian?

Here, *Arberia allweyensis* is regarded to be more closely affiliated with *Rigbya*, and has been moved into the Rigbyaceae. This change in familial affiliation has significant implications for the temporal range of *Arberia*, as it becomes entirely restricted to the Lower Permian (Artinskian) on all four continents where *Arberia* has been found. *Lidgettonia lawleyensis* has been synonymised with *L. africana* (section 8.1.4.1, p. 317). These changes could be seen as moves which strengthen the case for an Upper Permian age for Lawley. However, there is a huge danger of being lured into a circular pattern of reasoning when trying to place deposits into a biostratigraphic context. On the one hand we are using information gleaned from the Lawley locality to establish the biostratigraphic ranges of some important index taxa, but the tentative chronostratigraphic position of the Lawley deposits is based almost entirely on subjectively selected pieces of biostratigraphic information.

It is really impossible at this stage to give an unequivocal and entirely objective age for the Lawley deposits. The Lawley flora needs to be intensively re-evaluated, and closely compared with assemblages from other South African sites if we are to make any progress in establishing its stratigraphic position, and most importantly, a palynological study of the site needs to be conducted.

## **9.4 CONCLUSIONS AND THE ROAD AHEAD**

Probably the most important concept that has emerged from what was initially a taxonomic re-evaluation of the South African glossopterid fructifications, is that these structures display a far greater morphological diversity than has been recognised in the past. There is a common morphological theme that affiliates and unifies these fertile structures, but they do not all rigidly conform to the same body plan. In the past, there has been a tendency to oversimplify the group, shoe-horning the fructifications into broad, mutually exclusive, morphological types. It is conceivable that many of the past controversies regarding the morphological interpretation of the glossopterid polysperms may be resolved through careful re-examination of the evidence at hand.

South Africa has vast repositories of fossil plants still waiting to be collected. There are numerous unexplored or superficially collected sites which could add significantly to our knowledge of the glossopterids. Virtually all our knowledge of the Permian floras of South Africa has been accrued from fossil sites in the northern and eastern parts of the Karoo Basin, and not a single glossopterid fructification has been recovered from the Permian deposits of the southern and western parts of the basin. Although the fossil deposits in these regions tend to be sparser and less accessible, they can probably make a very important contribution towards our understanding of the glossopterids, particularly in a biostratigraphic context.

This body of work has focussed exclusively on South African ovuliferous glossopterid fructifications, with only superficial comparisons having been made with those from other parts of Gondwana. The fairly high degree of provincialism exhibited by this plant group has largely accommodated this approach, but there is an urgent need for a broad and consistent revision of these organs on a Gondwana-wide scale<sup>9</sup>.

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<sup>9</sup> A manuscript is currently in preparation, in collaboration with Dr. S. McLoughlin of the Queensland University of Technology (first author), with this very goal in mind.

In the midst of great taxonomic confusion, the ovuliferous fructifications of the glossopterids offer us the greatest hope of reconciling this difficult group of plants and putting them to work for us in the fields of chrono- and biostratigraphy. Although they are relatively rare, they display a useful range of diversity both over time and geographically. If Gondwana researchers could reach a consensus regarding the basic nature of these plants, using all the information available from impression/compression fossils as well as permineralized material, we could make a significant contribution towards the reconstruction of the world as it looked over 250 million years ago.

## CHAPTER 10 SUMMARY

The present study represents the first thorough revision of the South African glossopterid ovuliferous structures to have been undertaken in twenty years. The result was the creation of four new genera and one new species, and the emendation of two families, seven genera and thirteen species.

Some of these taxonomic changes were made to bring diagnoses in line with more modern ideas regarding the morphology of the glossopterid polysperms. Others resulted from the identification of radically new morphologies, revealed through the application of a new approach to the observation of impression fossils as three-dimensional moulds. The nature of these new morphologies, including a double wing structure, a hood and an apical spine, raised numerous questions regarding the homologies of the glossopterids and the pollination and seed dispersal mechanisms employed by the group.

A review of the genus *Arberia* led to an appreciation of the bifacial nature of some of its members, as well as the identification of scale-like features at the branch termini. These features have given impetus to the theory that all the glossopterid fructifications were derived from a basal, arberioid form, through the planation, reduction and fusion of the lateral branches into a cladode. Evolutionary trends in the glossopterids were examined, and transformation series were proposed to account for the morphological diversity seen at the family level.

Biostratigraphic and biogeographic trends apparent from records of glossopterid polysperm occurrences were reviewed from a South African perspective.