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A NEW GENUS OF OVULIFEROUS GLOSSOPTERID FRUCTIFICATIONS FROM SOUTH AFRICA

by

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ABSTRACT

A new genus of Early Permian glossopterid fructifications, *Gladiopomum*, is established to accommodate pedicellate, capitate fructifications with narrow receptacles, apical spines, and very broad wings. Two species recognized within this genus were previously assigned to *Scutum* Plumstead and *Hirsutum* Plumstead, viz., *G. dutoitides* (Plumstead) comb. nov. and *G. acadarense* (Anderson & Anderson) comb. nov. An additional species, *G. elongatum* sp. nov. is established based on material from a new fossil locality at Rietspruit Colliery in the northern Karoo Basin. All species of *Gladiopomum* are confined to the Vryheid Formation; the genus may constitute a useful biostratigraphic index taxon for Artinskian strata throughout the Karoo Basin.

KEYWORDS: Lower Permian, *Glossopteris*, fructification, *Gladiopomum*, Karoo Basin.

INTRODUCTION

Glossopterids remain one of the most enigmatic groups of fossil plants. Although dispersed reproductive structures, now known to be glossopterid, were illustrated as early as 1881 by Feistmantel, a confident relationship between the reproductive structures and the foliage was not established until ovuliferous fructifications attached to the midribs of *Glossopteris* leaves were described by Plumstead (1952, 1956a,b, 1958). However, Plumstead's interpretations and many subsequent analyses have not resulted in broad consensus regarding the structure of glossopterid fertile organs or the phylogenetic relationships of this group as a whole. Two broad hypotheses have been invoked regarding the homologies of the ovuliferous fructifications. The first suggests that these structures represent planated axillary fertile shoots essentially homologous with the seed-bearing axillary branches of cordaitaleans or the ovuliferous scales of conifers (Schopf 1976). The second suggests that the fructifications are leaf-like units (megasporophylls) that are either modified fertile pinnules of the *Glossopteris* leaf proper, or solitary fertile bracts borne on a dormant axillary shoot that is adnate to, or carried up on, the midrib of the subtending sterile leaf (Retallack & Dilcher 1981; Taylor & Taylor 1992). The second hypothesis would make glossopterid ovuliferous fructifications essentially homologous to the megasporophylls of Mesozoic seed-ferns (Crane 1985).

Since the first glossopterid fertile structures were illustrated by Feistmantel (1881, 1886), 34 genera of ovuliferous fructifications have been erected based on differences in gross architecture, receptacle shape, wing dimensions and orientation, seed-scar dimensions, the number of attached seeds and the number of receptacles attached to a subtending leaf. Many of these genera are clearly synonymous, their establishment having been based on misinterpretations of the architecture of the fructifications resulting from workers dealing with fossils having different styles of preservation (McLoughlin 1993a). Four basic architectures are represented amongst fructifications attached to, or associated with, glossopterid foliage: (1) loosely branched, variably planated structures with terminal seeds (Arberiaceae of Anderson & Anderson 1985); (2) variably branched, dorsiventral, fan-shaped fructifications (Rigbyaceae of Anderson & Anderson 1985); (3) capitate, dorsiventral, circular to linear structures [Ottokariaceae of Anderson & Anderson (1985) or Dictyopteridiumaceae of Maheshwari (1990)]; and (4) multicupulate fructifications (Lidgettoniaceae of Anderson & Anderson 1985). The greatest diversity is currently documented for the Dictyopteridiumaceae in which genera are differentiated primarily on receptacle shape, wing morphology, and seed scar size.

A substantial component of our understanding of the diversity of glossopterid fertile structures derives from the study of assemblages from the Karoo Basin, South Africa. Lower Permian Vryheid Formation and Upper Permian Beaufort Group assemblages, in particular, have yielded several hundred specimens providing the basis for the establishment of 13 genera, although not all of these are currently deemed valid. Anderson & Anderson (1985) revised the South African

glossopterid ovuliferous fructifications and recognized 28 species in 10 genera. Among these were two species [*Hirsutum dutoitides* (Plumstead) Plumstead 1958 and *Hirsutum acaderense* Anderson & Anderson 1985] that possessed very broad wings relative to the width of the receptacle. Their elongate receptacles were also extended into a distinctive apical spine. These receptacle and wing features are not accommodated by the original circumscriptions of *Hirsutum* or other established glossopterid fructification genera. The specimens from Vereeniging and Cedara previously assigned to *H. dutoitides* and *H. acaderense* are re-described and, together with conspecific fructifications from Hlobane and closely allied forms from a new fossil locality at Rietspruit, northern Karoo Basin, are placed in the new genus *Gladiopomum*.

MATERIAL AND METHODS

The studied fossil material was preserved primarily as impressions. Fructifications found at the Rietspruit locality contained some carbonaceous residues but no cuticle was recovered. Specimens were photographed under strong unilateral light with a Sony Cybershot digital camera. Measurements were taken using Zeiss Axiovision 2.5 image-analysis software. Line drawings were generated with Adobe Illustrator 8.

Most of the specimens were derived from previous collections housed in the fossil herbarium at the Bernard Price Institute, The University of the Witwatersrand. These included the majority of the Vereeniging specimens, collected by Mr. S.F. Le Roux in collaboration with Dr E.P. Plumstead in the 1940's and 1950's. Additional Vereeniging specimens were loaned from 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. New specimens were collected from the Rietspruit Colliery during an excursion undertaken in 1999 by the first and third authors, together with Mrs R. Renaut (also of the Bernard Price Institute). Specimens cited in the text are housed in various institutions according to the following prefixes: VM – Vaal Teknorama Museum (Vereeniging); NM – Natal Museum (Pietermaritzburg); BP – Bernard Price Institute for Palaeontological Research (Johannesburg).

GEOLOGICAL SETTING

The fossil material was collected from four localities in the Karoo Basin, South Africa: Vereeniging, Hlobane, Cedara, and Rietspruit (Figure 1).

Vereeniging

The town of Vereeniging lies about 60 km south of Johannesburg, Gauteng Province (Figure 1). 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 Leeuwkuil 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. The specimens of *Gladiopomum dutoitides* were collected from the Old Sandstone Quarry, the Shale Quarry and the River Quarry (quarries 1-3, Figure 1A), as outlined by Le Roux & Anderson (1977).

The fossiliferous layers varied from hard, compact, fine-grained, carbonaceous shales to red ferruginous shales and buff-coloured siltstones, with the majority of well-preserved fossils being found in beige or buff-coloured, thinly laminated claystones (Le Roux & Anderson 1977; Anderson & Anderson 1985).

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, Middle Ecca 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 (Millsteed 1994).

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 gangamopterid 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 ovulate fructifications in South Africa, many of them preserved in attachment to subtending glossopterid leaves (Anderson & Anderson 1985; Plumstead 1952; 1956a; 1958). We confidently identified six specimens of *Gladiopomum* from the Bernard Price Institute collections.

Hlobane

The Hlobane Colliery is situated near the town of Vryheid, in northern KwaZulu-Natal (Figure 1). The material was collected from an opencast mine-site. Most blocks housed at the BPI are of soft, poorly laminated, light brown to pinkish buff shale. A few of the slabs are dark grey, and rich in carbonaceous material.

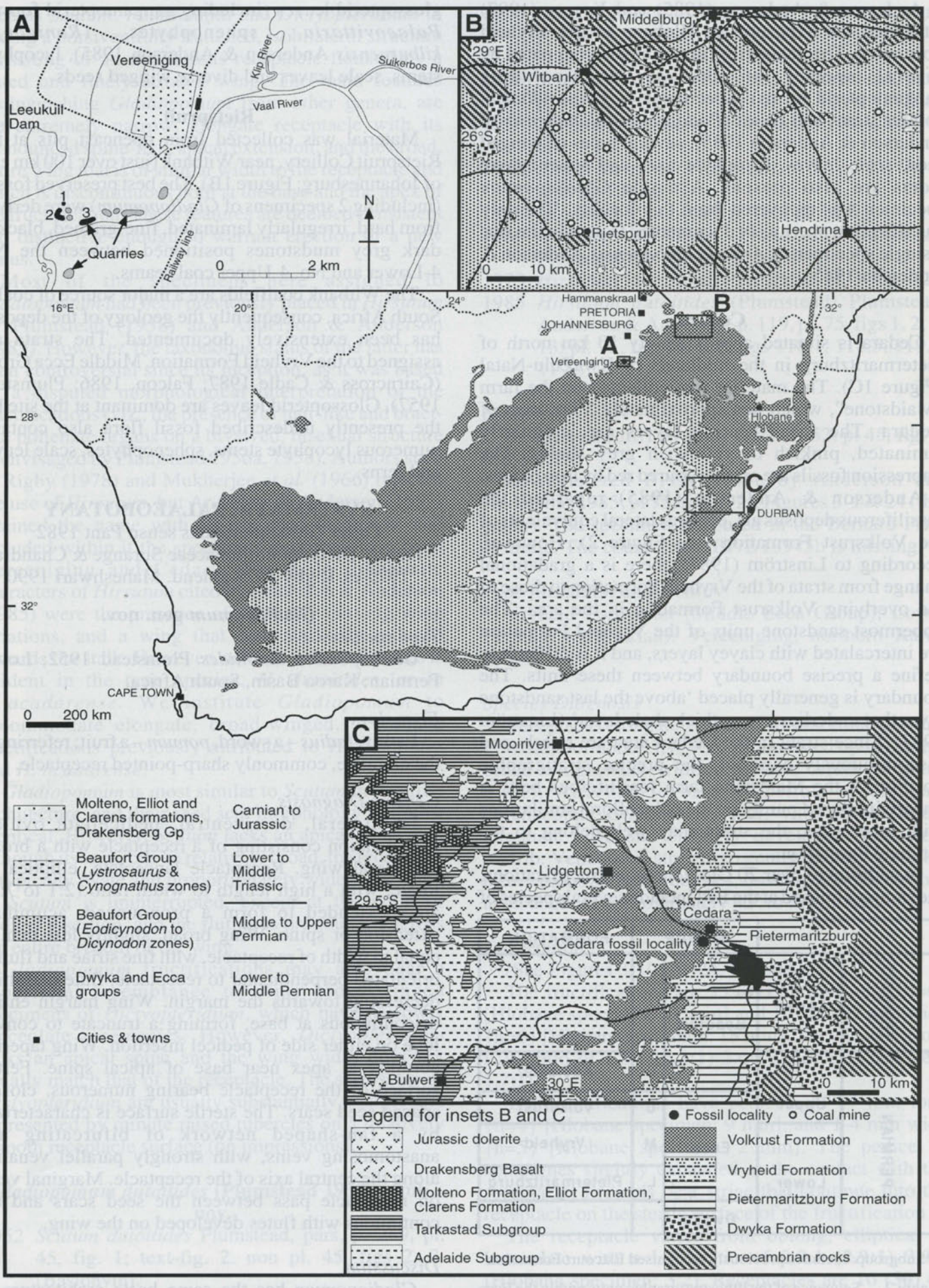


Figure 1. Map of the Karoo Basin showing the distribution of key Permian to Jurassic units and the fossil localities yielding *Gladiopomum* fructifications (after Keyser 1997; Rubidge *et al.*, 1995).

Anderson & Anderson (1985) and Keyser (1997) attributed the exposures at Hlobane to the Vryheid Formation. The palaeoflora at this site is dominated by several species of *Glossopteris* (including gangamopterid 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* Anderson & Anderson 1985.

Cedara

Cedara is situated approximately 10 km north of Pietermaritzburg in the midlands of KwaZulu-Natal (Figure 1C). The material was collected on the farm "Maidstone", which lies approximately 3 km west of Cedara. The fossil-bearing layers are irregularly laminated, pinkish to yellowish grey shales. The impression fossils are often coloured red by iron oxides.

Anderson & Anderson (1985) regarded the fossiliferous deposits at Cedara as lateral equivalents of the Volksrust Formation (see Figure 2). 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.

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

		GROUP		FORMATION
TRIASSIC	Lower	Beaufort		
PERMIAN	Upper		L	Adelaide*
		Ecca	U	Volksrust
	Lower		M	Vryheid
			L	Pietermaritzburg
		Dwyka		

*Subgroup: includes previously recognised Estcourt Formation

Figure 2. Sequence of the lithostratigraphic units within the Ecca Group, in the eastern and north-eastern parts of the Karoo Basin (after Keyser 1997).

Rietspruit

Material was collected from opencast pits at the Rietspruit Colliery, near Witbank (just over 100 km east of Johannesburg; Figure 1B). The best preserved fossils (including 2 specimens of *Gladiopomum*) were derived from hard, irregularly laminated, fine-grained, black to dark grey mudstones positioned between the No. 4-Lower and No. 4-Upper coal seams.

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, Middle Ecca Group (Cairncross & Cadle 1987; Falcon, 1986; Plumstead 1957). Glossopterid leaves are dominant at the site but the presently undescribed fossil flora also contains numerous lycophyte stems, sphenophytes, scale leaves and ferns.

SYSTEMATIC PALAEOBOTANY

Order Glossopteridales sensu Pant 1982
Family Dictyopteridiumaceae Surange & Chandra 1975 ex Rigby 1978 emend. Maheshwari 1990

Gladiopomum gen. nov.

Type species

Gladiopomum dutoitides Plumstead 1952; Lower Permian; Karoo Basin, South Africa.

Etymology

Latin; *gladius* – a sword, *pomum* – a fruit; referring to the elongate, commonly sharp-pointed receptacle.

Generic Diagnosis

Isobilateral, dorsiventral, pedicellate ovulate fructification consisting of a receptacle with a broad, peripheral wing. Receptacle lanceolate, elliptical to lorate, with a high length to width ratio (2:1 to 7:1); apex extended to form a pronounced, acuminate extension or spine. Wing broad, slightly less than or equal to width of receptacle, with fine striae and fluting orientated perpendicular to receptacle, flute definition decreasing towards the margin. Wing margin entire, discontinuous at base, forming a truncate to convex lobe on either side of pedicel insertion. Wing tapering abruptly at apex near base of apical spine. Fertile surface of the receptacle bearing numerous, closely spaced seed scars. The 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. Marginal veins on receptacle pass between the seed scars and are continuous with flutes developed on the wing.

Discussion

Gladiopomum has the same basic architecture as other capitate, ovulate, 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 (1958) 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 pollenate organs on a bivalved, bisexual structure as envisaged by Plumstead 1956a, 1958). 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. acadarense*. We institute *Gladiopomum* to accommodate elongate, broad-winged, acuminate fructifications previously attributed to *H. dutoitides* and *H. acadarense*.

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).

Gladiopomum dutoitides (Plumstead 1952) comb. nov.

1952 *Scutum dutoitides* Plumstead, pars, p. 289, pl. 45, fig. 1; text-fig. 2. non pl. 45, figs 2, 3. [Basionym].

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.

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); Figures 3-4 & 24 (this paper). The specimen is housed in the Bernard Price Institute. The counterpart, BP/2/13945b is missing.

Type formation and locality

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

Species Diagnosis

Receptacle elongate elliptical to lanceolate, with a 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 is straight to gently arching with few bifurcations and anastomoses, forming parallel meshes at an angle of approximately 45° to the midrib.

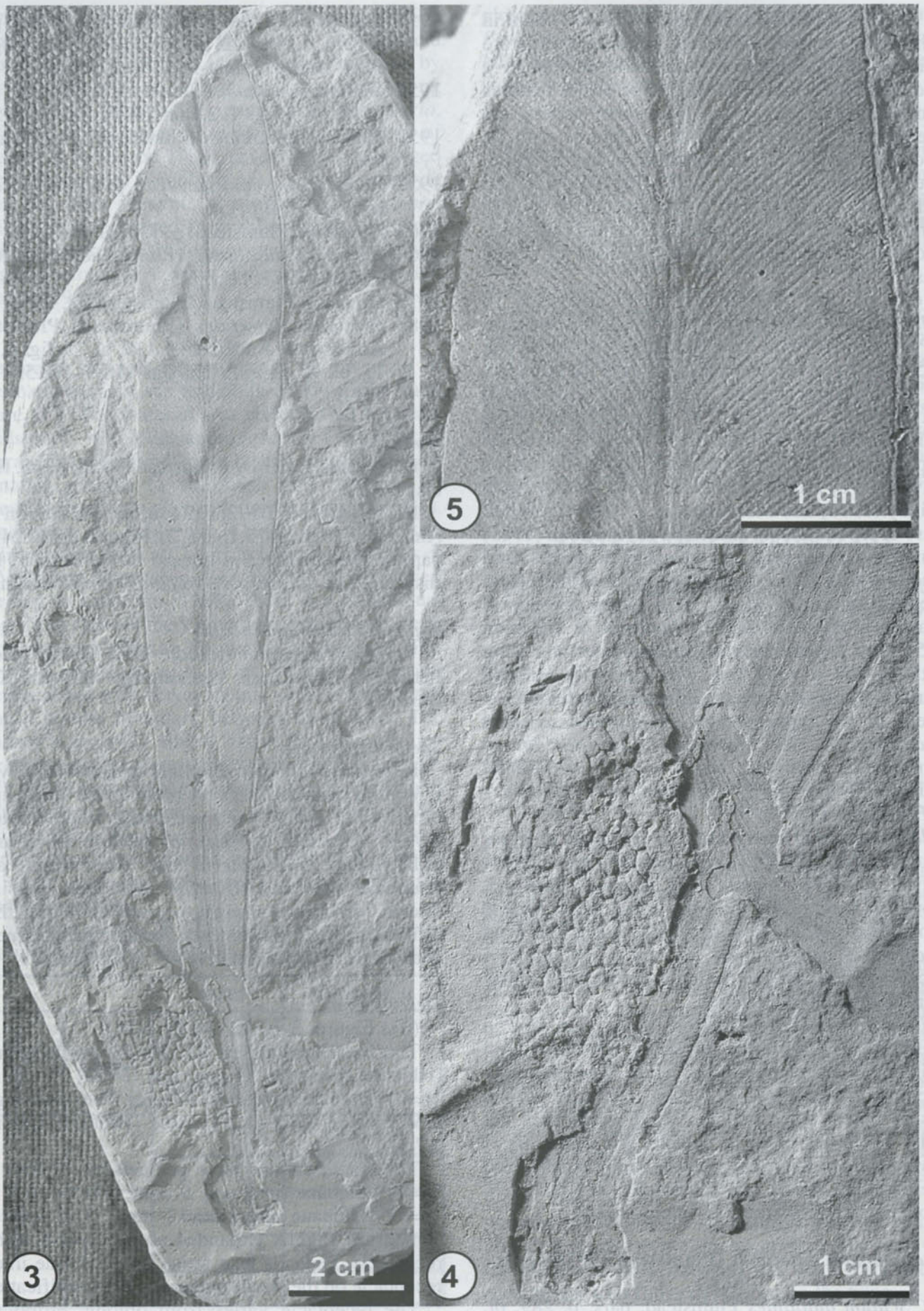
Description

(See Figures 3-10; 21-24, 29, 30A).

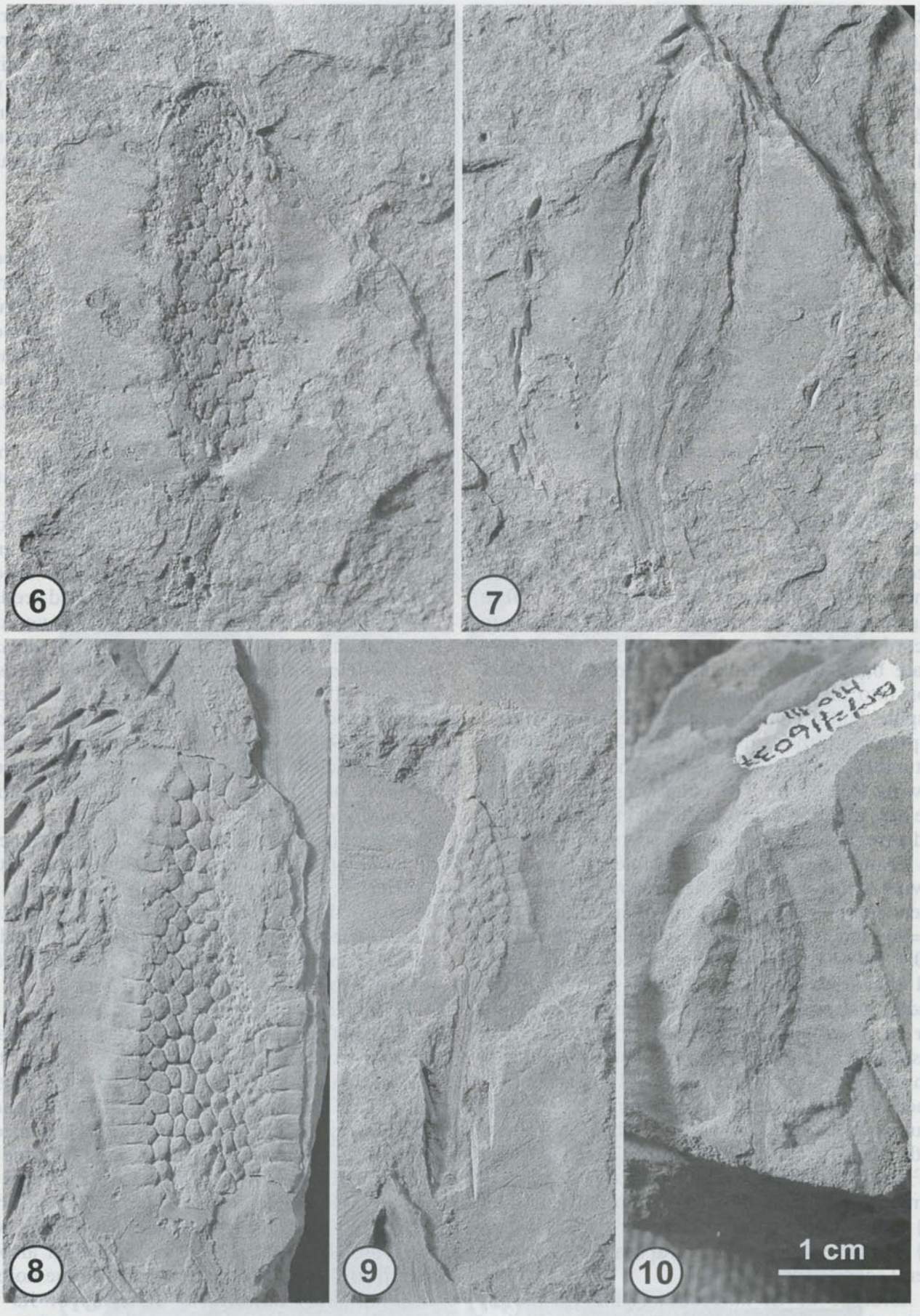
The fructifications are 33 (**47**) 58 mm long {n=6} [Hlobane specimen: 31 mm] and 15 (**22**) 27 mm wide {n=6} [Hlobane specimen: 18 mm]. They have a gross L:W ratio of 1.8:1 (**2.2:1**) 2.6:1 [Hlobane specimen: 1.7:1].

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 sometimes 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].



Figures 3-5: The holotype of *Gladiopomum dutoitides* (Plumstead) comb. nov. (BP/2/13945a) from Vereeniging; 3: *G. dutoitides* fructification attached to the petiole of a *Glossopteris* leaf; 4: Detail of the fructification; 5: Distal portion of the attached leaf, showing venation with parallel meshes.



Figures 6-9: Further examples of *Gladiopomum dutoitides* (Plumstead) comb. nov. from Vereeniging. 6 & 7: Part and counterpart of *G. dutoitides* fructification (BP/2/13936 & BP/2/13937), clearly showing the characteristic apical spine, broad wing and elongated elliptical receptacle. 8: A particularly large specimen of *G. dutoitides* (fertile surface), with well-defined apical spine and wing fluting (BP/2/13941). 9: Fertile surface of the smallest example of *G. dutoitides* from Vereeniging (BP/2/13754). 10: The only specimen of *G. dutoitides* found at the Hlobane locality (sterile surface), showing a broad wing and narrow receptacle (BP/2/16037).

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 (Figures 6, 8, 21). 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 spines are 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; Figures 7, 10, 22). 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 (Figure 8). 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^2 {n=5} [Hlobane specimen: 11.6 per 25 mm^2]. 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 (Figures 3-5, 24). 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

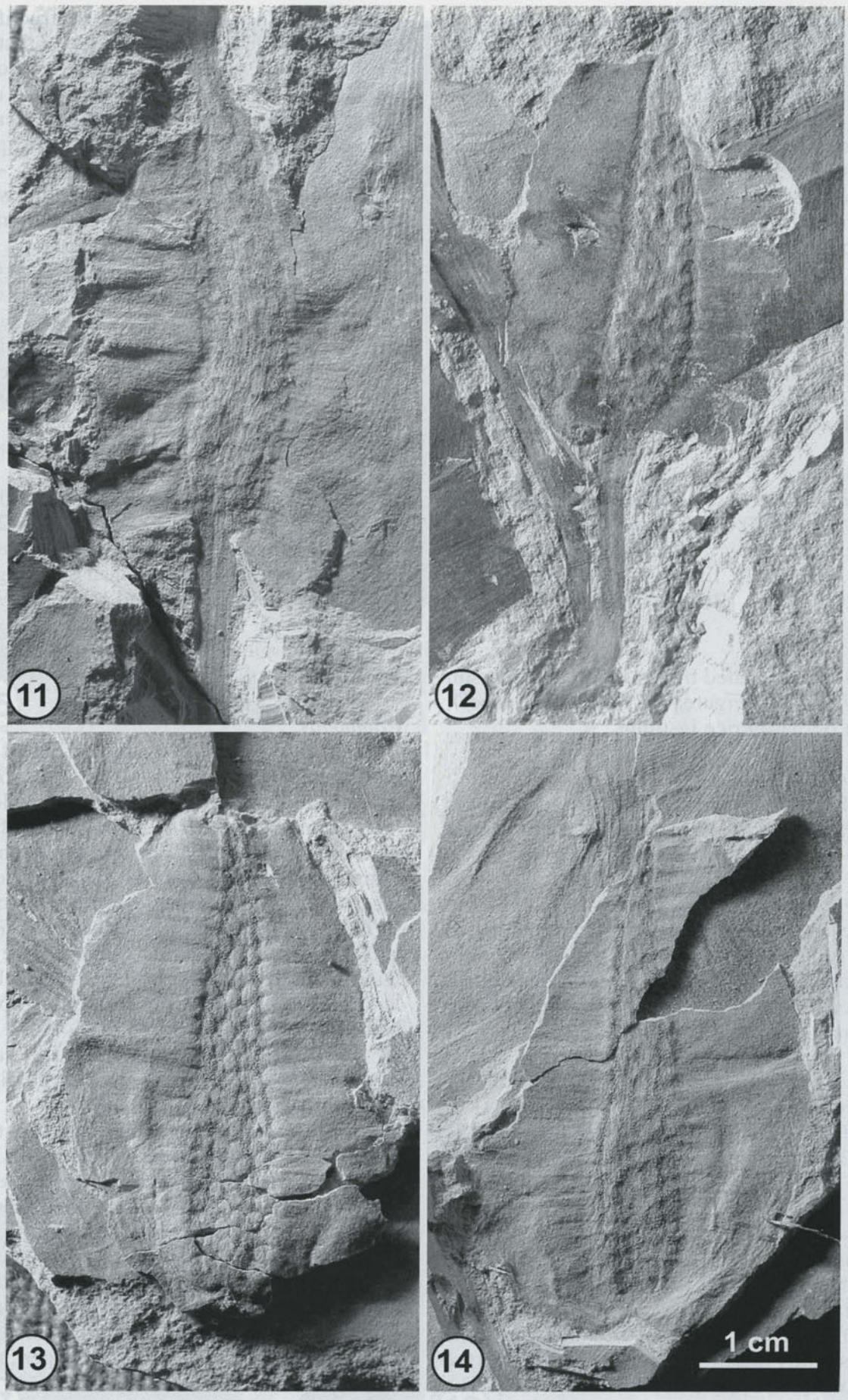
All six specimens are derived from Vereeniging except for a single example from Hlobane (Figures 10 & 25). Measurements of the latter specimen are listed separately for comparative purposes, and were not included in the mean calculations. This specimen falls in the lower part of the range for most measurements but its gross shape and concordant character ratios favour its attribution to *G. dutoitides*.

The type specimen is poorly preserved, but was presumably selected by Plumstead (1952) because it is attached to a glossopterid leaf (Figures 3-5, 24). It does, however, demonstrate the extended apex, the elongated receptacle and the broad wing, which are the most important diagnostic characters of the taxon. No specimens have been found with attached seeds.

Representatives of this species have a lower length:width ratio than specimens of *G. acadarense* 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. acadarense* (Figures 29, 30). 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*.

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 are 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 discernible 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 (1958, p. 55, pl. 7)



Figures 11-14: Specimens of *Gladiopomum acadarense* (Anderson & Anderson) comb. nov. from Cedara with gladiate receptacles, broad wings and long petioles. 11: Sterile surface of a fructification with a well-defined apical extension (BP/2/16329a). 12: Holotype of *G. acadarense* (BP/2/16331a); although the base of this specimen's pedicel overlaps the base of a *Glossopteris* petiole, a physical connection is not convincing. 13 & 14: The fertile and sterile surfaces of a fructification with a particularly high wing width : receptacle width ratio (BP/2/16344a, b).

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*.

Geographic and stratigraphic range

This species has only been found at Vereeniging and Hlobane in the Karoo Basin, South Africa, in sediments of the Vryheid Formation, Middle Ecca Group (Lower Permian). It has not been verified from other parts of Gondwana.

Gladiopomum acaderense (Anderson & Anderson 1985) comb. nov.

1985 *Hirsutum acaderense* Anderson & Anderson, pars, p. 120, pl. 77, figs 6-11; pl. 95, fig. 9; text-figs 120.1, 120.2. [Basionym].

Holotype

BP/2/16331a; designated by Anderson & Anderson (1985, pl. 77, fig. 7); Figures 12 & 26 (this paper); housed at the Bernard Price Institute.

Type formation and locality

?Vryheid Formation (Middle Ecca Group), Lower Permian (Artinskian); Cedara, north-eastern Karoo Basin.

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 Figures 11-18, 26, 27, 30B)

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 (Figures 12, 26). 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 (Figures 11, 27). 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 orientated 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^2. 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

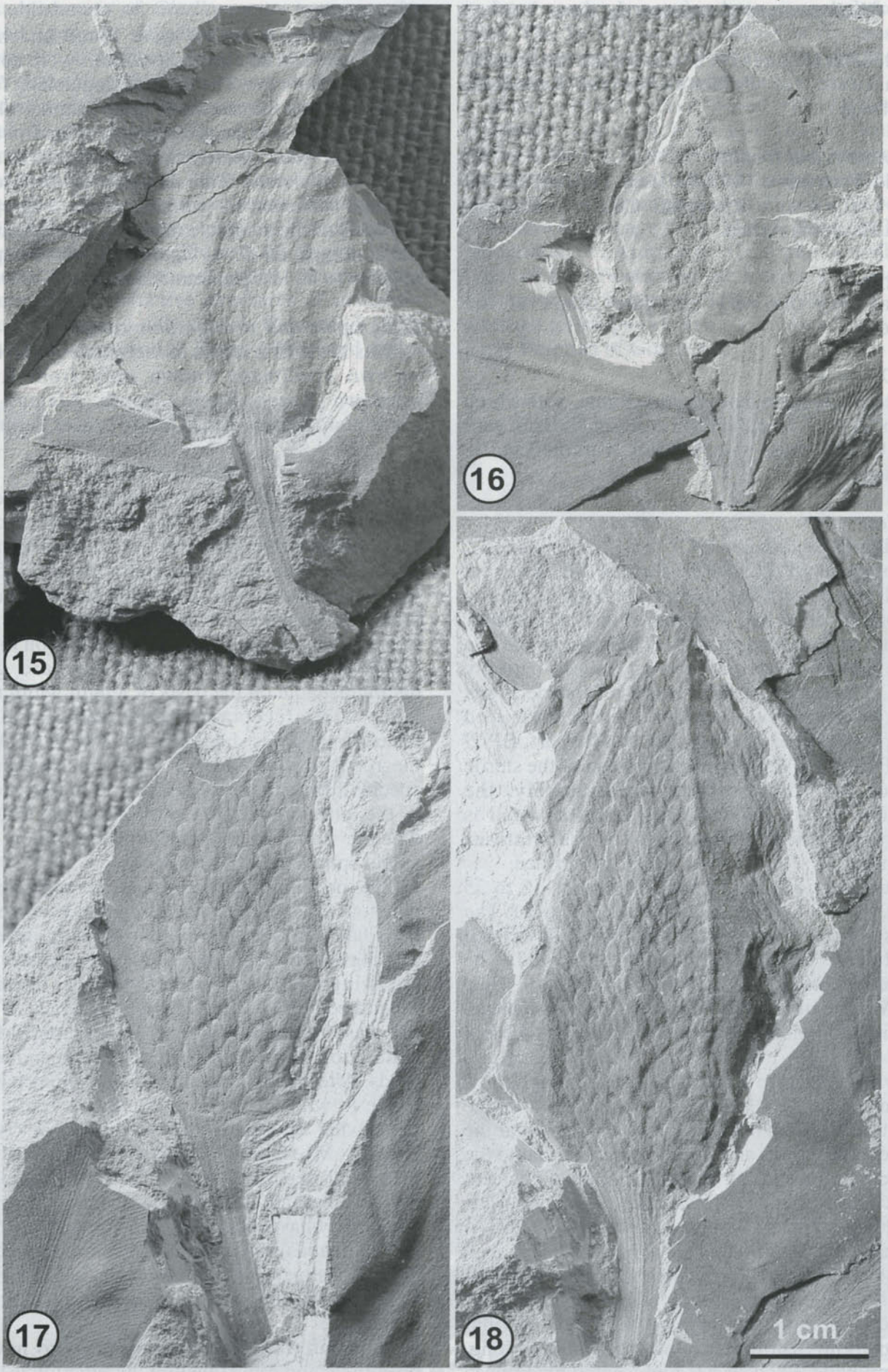
This taxon exhibits the greatest degree of morphological variability of the three *Gladiopomum* species, although this may just be a reflection of the large number (over 20) of available fructifications. The outstanding features of this species are the very broad wing, the sharply pointed, acuminate tip of the receptacle, and the particularly long and robust pedicel.

There are many similarities between *G. acadarense* 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. acadarense* receptacle is intermediate between *G. dutoitides* and *G. elongatum*.

No specimens were 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 5mm.

Geographic and stratigraphic range

Only known from the Cedara locality, Karoo Basin, South Africa; ?Vryheid Formation, Middle Ecca Group; Lower Permian (Artinskian).



Figures 15-18: Additional specimens of *Gladiopomum acadarense* (Anderson & Anderson) comb. nov., illustrating the wide range in size and morphology of the fructifications. 15: BP/2/16352, fertile surface. 16: Fertile surface of one of the smallest specimens from Cedara (BP/2/16354a); 17&18: Examples of larger fructifications with more substantial receptacles and large numbers of seed scars evident on the fertile surface (BP/2/16345, BP/2/16346).

Gladiopomum elongatum sp. nov.

Holotype

BP/2/28880b (Figures 20, 28), housed at the Bernard Price Institute for Palaeontological Research, Johannesburg.

Type formation and locality

Vryheid Formation (Middle Ecca Group); Lower Permian (Artinskian); Rietspruit Colliery, northern Karoo Basin, South Africa

Etymology

Emphasizing the very elongate shape of the receptacle.

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 ratio of about 1.

Description

(See Figures 19, 20, 28, 30C)

The holotype, BP/2/28880b (Figures 20, 28) 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. The counterpart, BP/2/28880a (Figure 19) 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^2. 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. acadarense*. 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*.

Geographic and stratigraphic range

This is the first report of the species, which is based on two specimens known only from Rietspruit, northern Karoo Basin, South Africa; Vryheid Formation, Middle Ecca Group; Lower Permian.

DISCUSSION

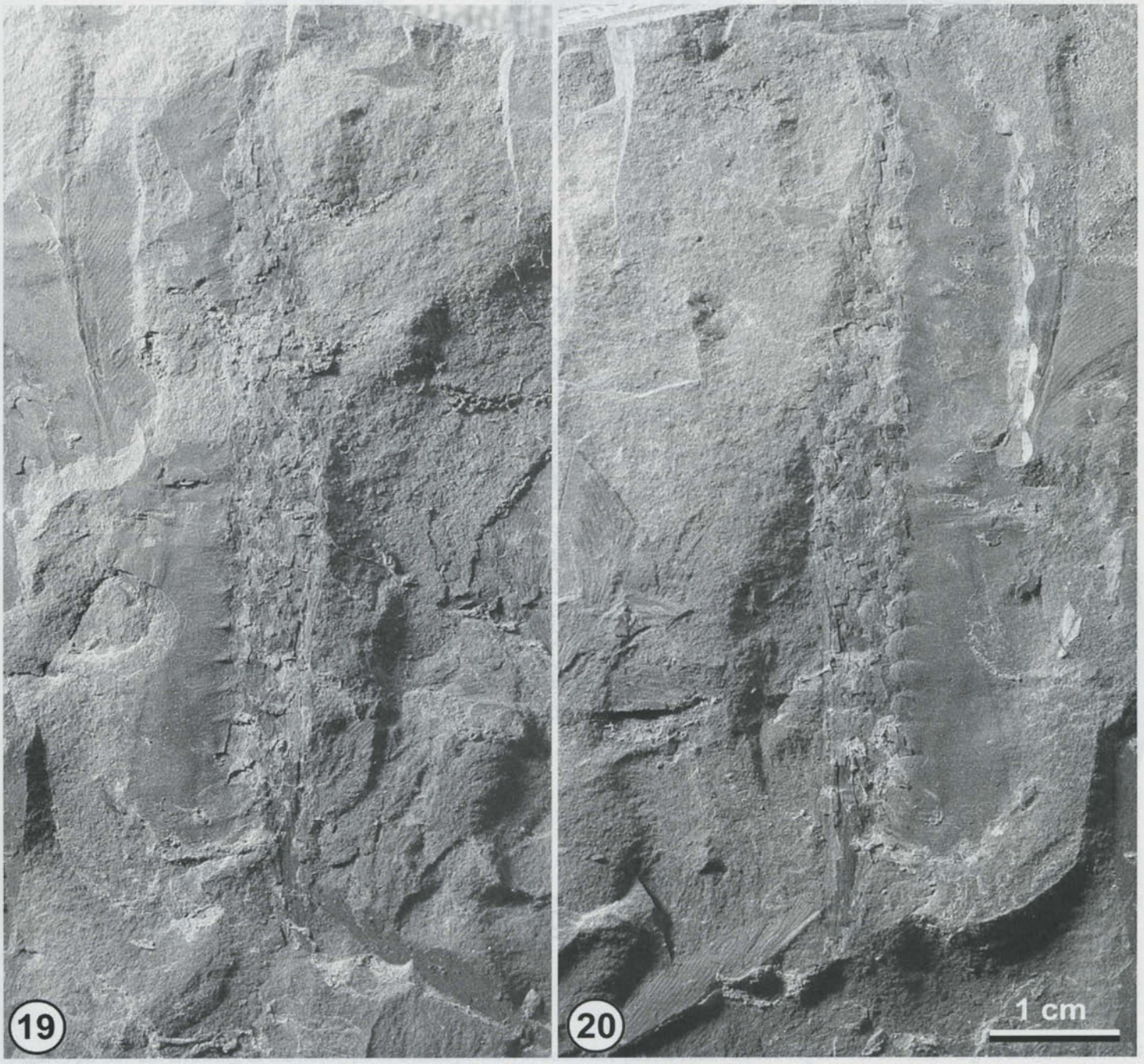
Morphological differences between the three species of *Gladiopomum* might be a consequence of growth under different environmental conditions. Dimensional characters have been principally used to differentiate the species but size is a variable feature amongst the fertile structures of some other plant groups. 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 (Figure 30). The L:W ratio of the receptacle provides 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).

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 fructifications illustrated by Gould & Delevoryas (1977). If this were the case then the wings clearly unfolded upon maturation of the polysperm to expose and release the seeds. Alternatively, the broad wings may have played a role in wind dispersal of the entire fertile structure (somewhat analogous to modern *Acer* or *Gyrocarpus* fruits). Most *Gladiopomum* fructifications are preserved separately from their subtending leaves. Enhanced wind dispersal of the fructification as a whole may have aided dissemination of any remaining attached seeds. However, no seeds were found attached to any specimens of *Gladiopomum*, hence the principal function of the wings is deemed to have been protective.

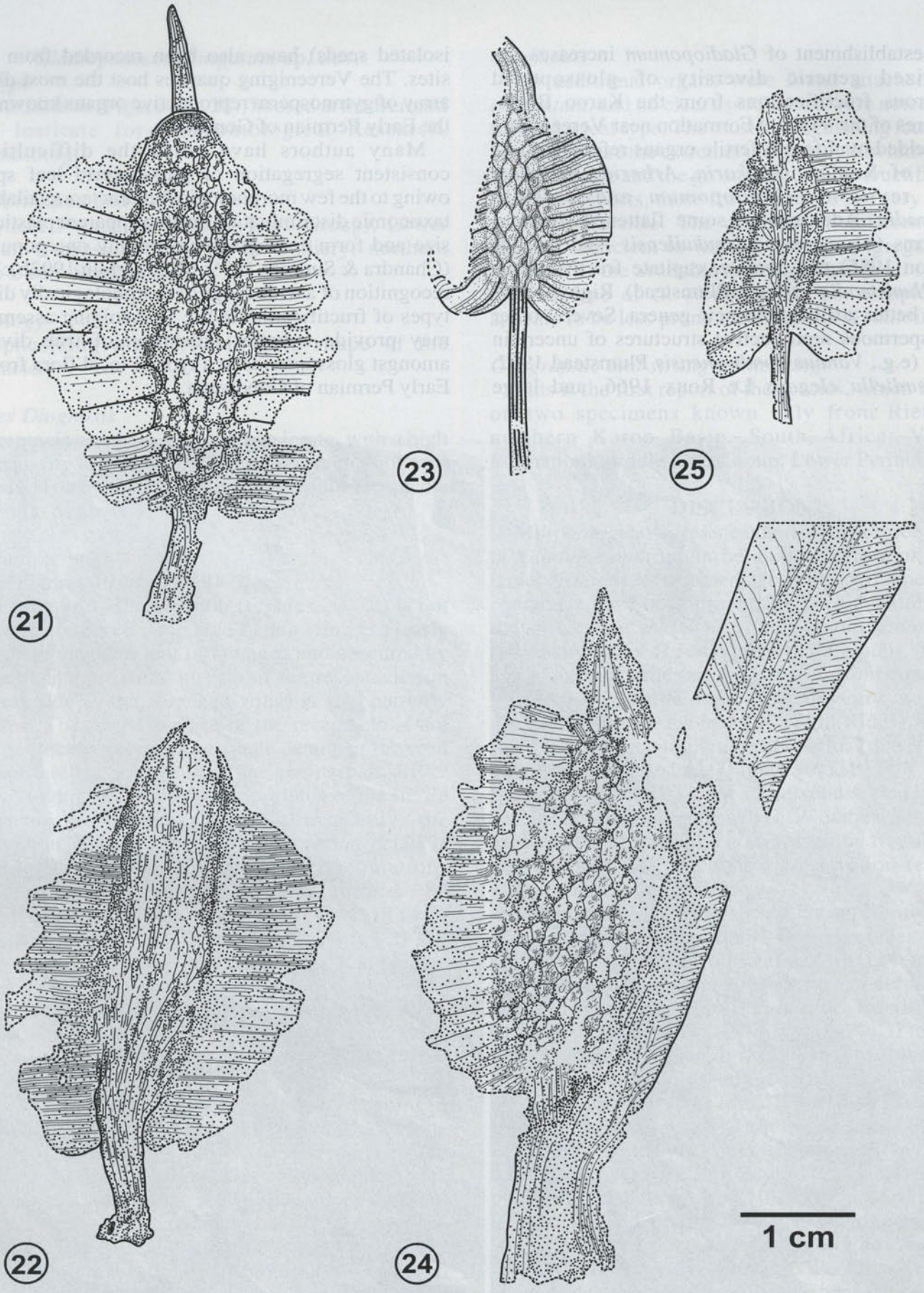
Although the apical spine appears to have been a prominent and robust feature, its function is unclear. It may have been a woody structure that, in conjunction with the wing, acted as a deterrent to herbivory of the seeds.

The establishment of *Gladiopomum* increases the recognized generic diversity of glossopterid ovuliferous fructifications from the Karoo Basin. Exposures of the Vryheid Formation near Vereeniging have yielded ovuliferous fertile organs referable to 12 species of *Scutum*, *Ottokaria*, *Arberia*, *Hirsutum* (under revision), *Gladiopomum* and possibly *Plumsteadia*. Additionally, some flattened *Arberia*-like forms (e.g., *Arberia leeukuilensis* Anderson & Anderson 1985) and cordate, capitate fructifications (e.g., *Plumsteadia stricta* (Plumstead) Rigby 1969) may be better attributed to new genera. Several other gymnospermous reproductive structures of uncertain affinity (e.g., *Vannus gondwanensis* Plumstead 1962, *Plumsteadiella elegans* Le Roux 1966, and large isolated seeds) have also been recorded from these sites. The Vereeniging quarries host the most diverse array of gymnosperm reproductive organs known from the Early Permian of Gondwana.

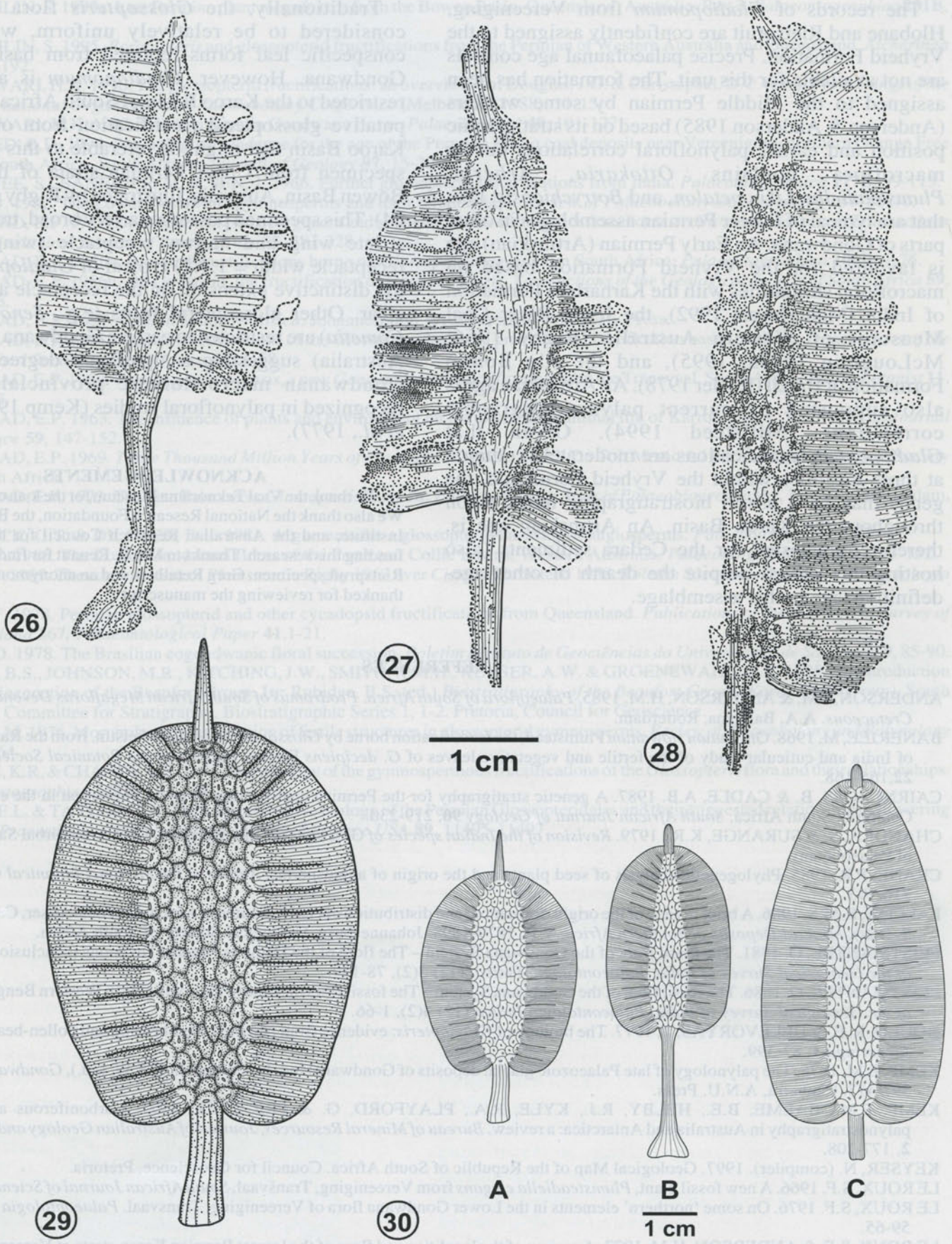
Many authors have noted the difficulties in consistent segregation of glossopterid leaf species owing to the few morphological characters available for taxonomic discrimination and the apparent plasticity in size and form amongst leaves in any one population (Chandra & Surange 1979; McLoughlin 1993b,c). The recognition of a wide range of morphologically distinct types of fructification in the Vereeniging assemblage may provide a better indication of true diversity amongst glossopterids in a typical local flora from the Early Permian of Gondwana.



Figures 19-20: The holotype of *Gladiopomum elongatum* sp. nov. from the Rietspruit locality (BP/2/28880a & b). 19: sterile surface. 20. Fertile surface. Note the very long, narrow receptacle, and broad wing.



Figures 21-25: Drawings of key specimens of *Gladiopomum dutoitides* from Vereeniging and Hlobane highlighting seed scars, wing features, apical spines and pedicels. 21: BP/2/13936 (see Figure 6). 22: BP/2/13937 (see Figure 7). 23: BP/2/13754 (see Figure 9). Holotype BP/2/13945a (see Figure 4). 25: BP/2/16037 (see Figure 10).



Figures 26-30: 26: Drawing of the holotype of *Gladiopomum acadarense* (BP/2/16331a), see Figure 12. 27: Drawing of BP/2/16329a (*G. acadarense)*, clearly illustrating the apical extension (see Figure 11). 28: Line drawing of the holotype of *Gladiopomum elongatum*, BP/2/28880b (see Figure 20). 29: A reconstruction of *Gladiopomum dutoitides*, based on BP/2/13936 (see Figures 6 & 21). 30: Comparative reconstructions of *G. dutoitides* (A), *G. acadarense* (B), and *G. elongatum* (C).

The records of *Gladiopomum* from Vereeniging, Hlobane and Rietspruit are confidently assigned to the Vryheid Formation. Precise palaeofaunal age controls are not available for this unit. The formation has been assigned to the Middle Permian by some workers (Anderson & Anderson 1985) based on its stratigraphic position and earlier palynofloral correlations but its macroflora contains *Ottokaria*, *Arberia*, *Plumsteadiella*, *Liknopetalon*, and *Botrychiopsis*: taxa that are typical of Lower Permian assemblages in other parts of Gondwana. An Early Permian (Artinskian) age is favoured for the Vryheid Formation based on macrofloral similarities with the Karharbari Formation of India (Maheshwari 1992), the Irwin River Coal Measures of Western Australia (Rigby 1966; McLoughlin 1993a, 1995), and the Rio Bonito Formation of Brazil (Rösler 1978). An Artinskian age is also supported by current palynostratigraphic correlations (Millsteed 1994). 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.

Traditionally, the *Glossopteris* flora has been considered to be relatively uniform, with many conspecific leaf forms reported from basins across Gondwana. However, *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, illustrated by 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. Other glossopterid fruits (e.g., *Senotheca* and *Cometia*) are restricted to eastern Gondwana (India and Australia) suggesting a significant degree of intra-Gondwanan macro-floristic provincialism long recognized in palynofloral studies (Kemp 1975; Kemp *et al.*, 1977).

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