



Kowieria alveoformis gen. nov. sp. nov., a new heterosporous lycophyte from the Latest Devonian of Southern Africa



Gess R.W.^a, Prestianni C.^{b,*}

^a Albany Museum and Geology Department, Rhodes University, Grahamstown, South Africa¹

^b Royal Belgian Institute of Natural Sciences, Rue Vautier 23, 1000 Brussels, Belgium

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ABSTRACT

A new lycopsid, *Kowieria alveoformis* gen. et sp. nov., is described from the Famennian Witpoort Formation, Grahamstown, South Africa. It possesses spirally arranged elongated falcate vegetative leaves. Terminal bisporangiate strobili are present and show loosely grouped micro- and megasporophylls. Sporophylls are similar in shape to the vegetative leaves though somewhat wider with a marked expansion to house the sporangium. One sporangium is attached directly to the adaxial surface of the lamina. Each megasporangium contains up to four heavily ornamented hologulate megaspores of the *Lagenicula* type. The combination of both basal and derived characters within this plant places it at an interesting position at the base of the phylogenetic tree of rhizomorphic lycopsids.

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1. Introduction

Late Devonian lycopsid diversity was until recently only represented by a few species, mainly described from Euramerica (Chaloner and Boureau, 1967; Fairon-Demaret, 1991; Grierson and Banks, 1963). The description of abundant and diverse material from China has, however, shed new light on evolution of the group (Berry et al., 2003; Liu et al., 2013; Meng et al., 2016; Meng et al., 2015; Wang et al., 2014a, 2014b; Wang, 2003; Wang et al., 2005; Wang et al., 2003; Wang et al., 2002; Wang, 2001; Wang and Berry, 2003; Wang and Xu, 2005; Wang et al., 2012; Xue et al., 2005). Nonetheless the flora of Gondwana, that constituted the largest contemporary landmass (Scotese, 1999; Stampfli et al., 2013) remains largely unknown. In this context, new information about Late Devonian lycopsids from this continent is both useful and important.

In this paper, a new fossil lycopsid from the Famennian of South Africa is described from many specimens that allow a fairly good understanding of its organisation. This plant is described in the framework of the ongoing effort of characterising in detail the ecosystem recorded within the Waterloo Farm lagerstätte.

2. Material and methods

With the exception of AM5300 (collected by Norton Hillier), all specimens were collected by RG from the 'main fish lens (MFG)' of the Waterloo Farm lagerstätte, south of the city of Grahamstown (Eastern Cape, South Africa) (Fig. 1). This lens is one of a series of black shale lenses, interbedded within quartzitic strata of the Famennian (Late Devonian) aged Witpoort Formation (Witteberg Group, Cape Supergroup). These lenses are comprised of graphitic black shale interpreted as having been deposited as anaerobic mud in a back barrier estuarine lagoonal environment along the high southern latitude margin of Gondwana (Gess and Hillier, 1995). Abundant fossil material is accumulated from both aquatic and adjacent terrestrial environments, and includes both aquatic and terrestrial plants (Prestianni and Gess, 2014 and refs therein), terrestrial (Gess, 2013) and aquatic invertebrates (Gess and Hillier, 1995; Scholtz and Gess, 2017), and aquatic vertebrates (Gess, 2016 and refs therein). Biogeographic reconstructions indicate that the Waterloo Farm lagerstätte was deposited at high latitude, within 30° of the South Pole (Torsvik and Cocks, 2011; Scotese and McKerrow, 1990; Scotese and Barrett, 1990; Mitchell et al., 2012).

The outcrop was originally exposed during construction of a new road bypass in 1985 and initial specimens were collected by RG from *in situ* shale, mainly during excavations between 1993 and 1995. Subsequent cutting back of the fossiliferous roadcutting (in 1999 and 2007) destroyed outcrop of the most important lens. RG however facilitated the rescue of 70 tons of shale in blocks, which are stored in specially constructed sheds to permit continued excavations *ex situ*. Disassociated fertile and infertile

* Corresponding author.

E-mail address: Cyrille.prestianni@naturalsciences.be (C. Prestianni).

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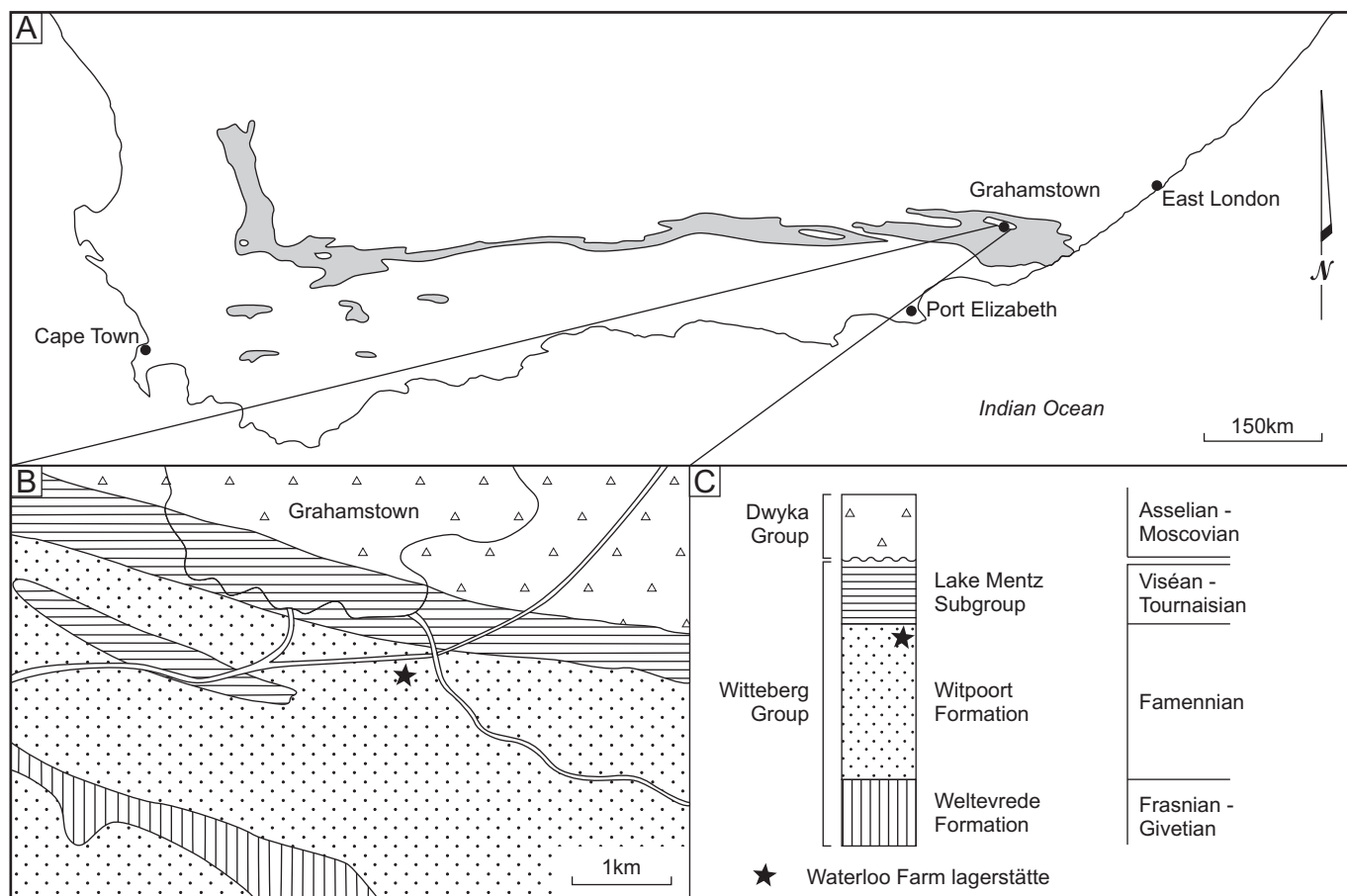


Fig. 1. A. Simplified global geological map of South Africa showing in grey the extension of the Witteberg Group and the position of Grahamstown. B. Local geological map of the region of Grahamstown refer to the stratigraphic column for legend. C. Stratigraphic column of the Witteberg Group showing the localisation of the fossil beds.

bracts of the discussed taxon are commonly encountered however bracts associated with axes are rare. All specimens are compressions that have been extensively remineralised to pale secondary metamorphic mica. This has partially broken down to chlorite following uplift. All specimens were photographed using a Nikon digital camera. Only the images of specimens **Plate I** (fig. 2) and **Plate II** (figs. 1 and 8) have been left without treatment. On all other figure, light and dark have been inverted using the Adobe Photoshop CS5 software in the photographic plates to make specimens easier to understand.

3. Systematics

Class—Lycopsidea Pichi-Sermolli 1958

Order and Family—INCERTAE SEDIS

Genus—*Kowieria* gen. nov.

Type species—*Kowieria alveoformis* sp. nov.

Combined diagnosis: Lycopodiaceous plant, only known from terminal axes. Vegetative axes with spirally arranged microphylls. Microphyll pedicels forming an angle of 30°–35° with the axis. Microphylls falciform and markedly curved abaxially, between 13–19 mm long and 0.3–0.6 mm wide. Bisporangiate strobilus terminal. Micro- and megasporophylls arranged spirally, form an angle ranging between 60° and 90° with the axis, are up to 20 mm long. Width regular ranging from 0.7 to 1.2 mm. One adaxial sporangium borne at base of the sporophyll. Sporangia smooth, between 3.0–4.5 mm long and 1.7–2 mm wide.

Megasporangium located proximally within cone, microsporangia located distally. Up to four megaspores per megasporangia. Megaspores hologulate and heavily ornamented, main body between 580 and 720 µm in diameter, gula approximately 200 µm high, ornaments are 150–200 µm long spines.

Etymology: *Kowieria* from the Kowie River that rises along the ridge on which Waterloo Farm is situated; *Alveoformis* referring to the coracle-like simple unkeeled sporophylls, *Alveus* being the Latin word for a simple type of boat.

Holotype: AM5297 (**Plate II**, fig. 2).

Paratypes: AM5298a, AM5299a, AM5300, AM7508, AM7509b, AM7510, AM7511, AM5760a.

Repository: Albany Museum (Devonian lab) Beaufort Street, Grahamstown, Eastern Cape, South Africa.

Locality: Waterloo Farm lagerstätte, south of the city of Grahamstown (Eastern Cape, South Africa) [– 33.323042, 26.536190].

Horizon: 'Main Fish Lens (MFL)'.

Age: Late Famennian.

4. Description

4.1. Axes

Among all collected specimens, no dichotomies have been observed. Only distal portions were recovered. Three specimens, AM7511,

Plate I. Fig. 1. Long axis fragment showing an alternation of leafy segments and leafless fragments, scale bar: 3 cm. AM7511. Fig. 2. Detail of a leafy portion of the axis illustrated fig. 1. This specimen has been reproduced in the original colours. Scale: 1 cm. AM7511. Fig. 3. Moderately well preserved fragment of a vegetative axis. Scale bar = 1 cm. AM5300. Fig. 4. Vegetative axis fragment. Scale bar = 1 cm. AM5760a. Fig. 5. Detail of the axis illustrated fig. 1 showing the dense vegetative leaves organisation. Scale bar = 1 cm. AM7511. Fig. 6. Dispersed vegetative leaves on the bedding surface. Note the characteristic falcate shape of the leaves. Some leaves may show preparation marks. Scale bar = 1 cm. AM7508.

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