



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



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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 megasporangia 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

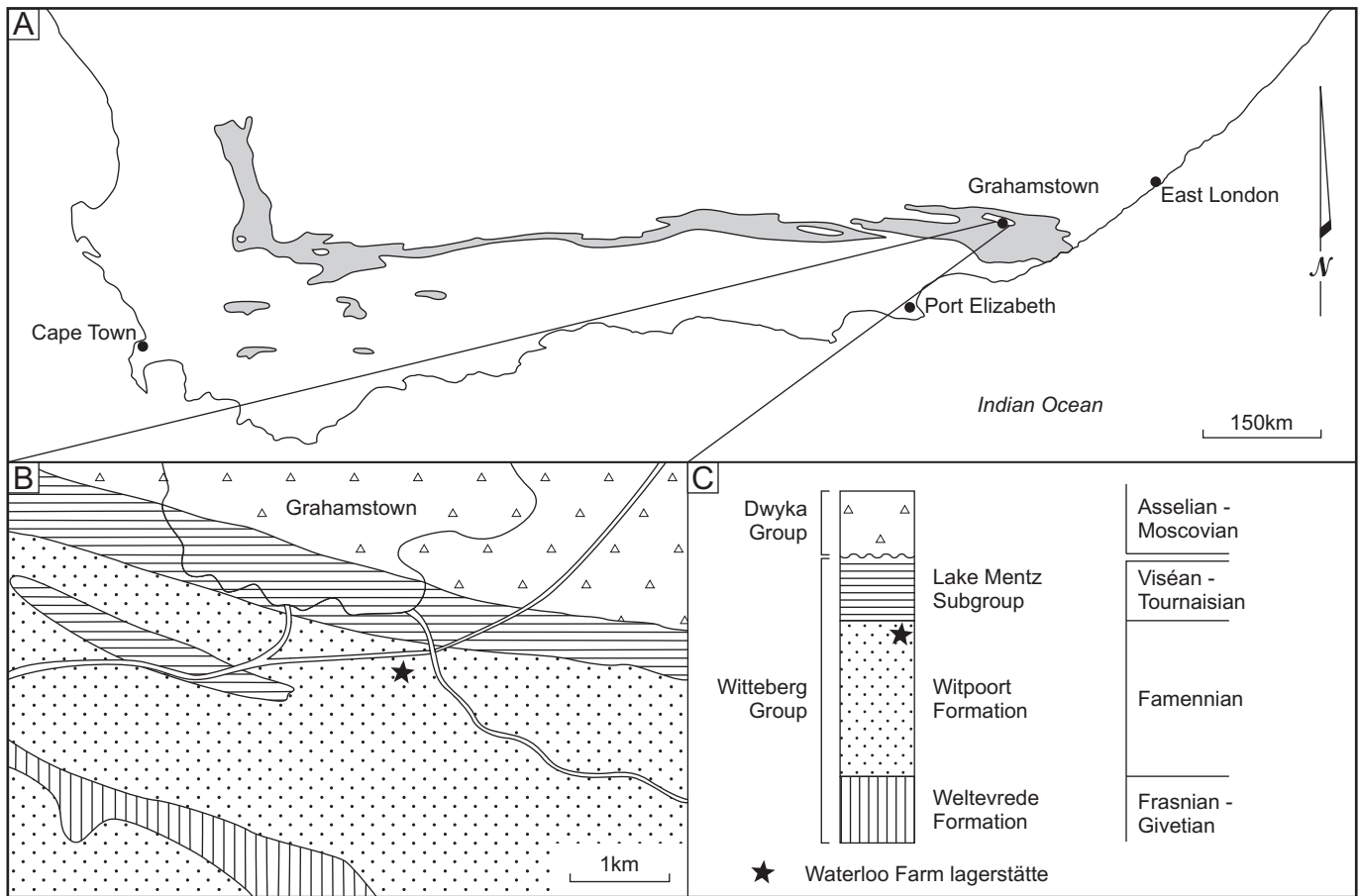
With the exception of AM5300 (collected by Norton Hiller), all specimens were collected by RG from the ‘main fish lens (MFG)’ of the Waterloo Farm lagerstätte, south of the city of Grahamstown (Eastern Cape, South Africa) (Fig. 1). This lens is one of a series of black shale lenses, interbedded within 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 Hiller, 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 Hiller, 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

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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 megasporangia per megasporangium. 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)'.

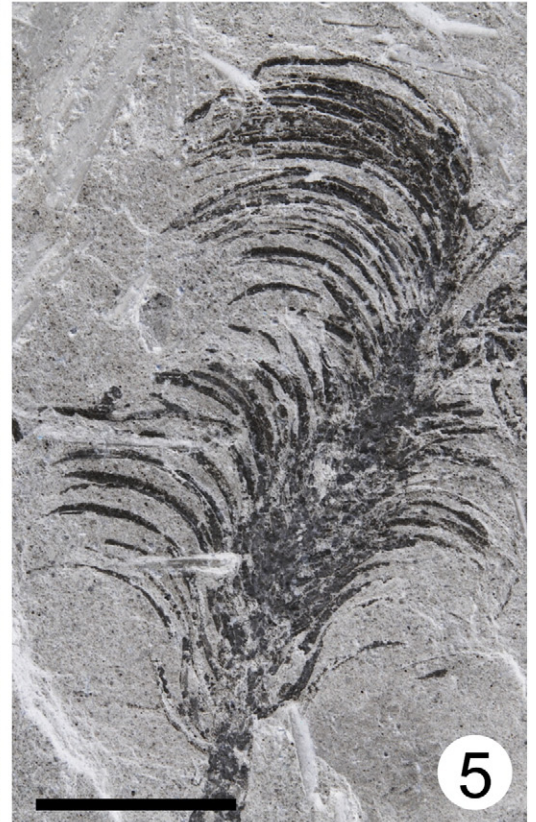
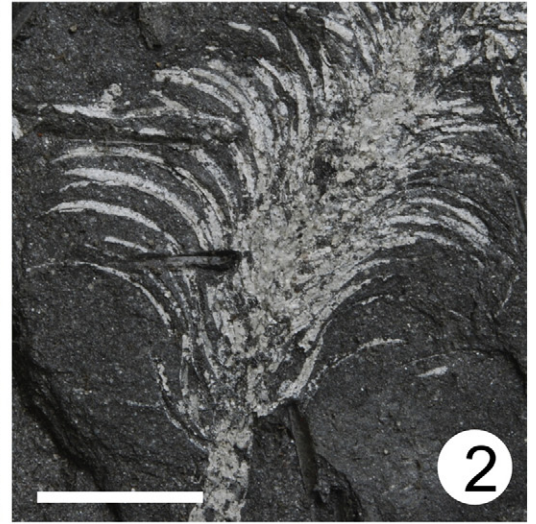
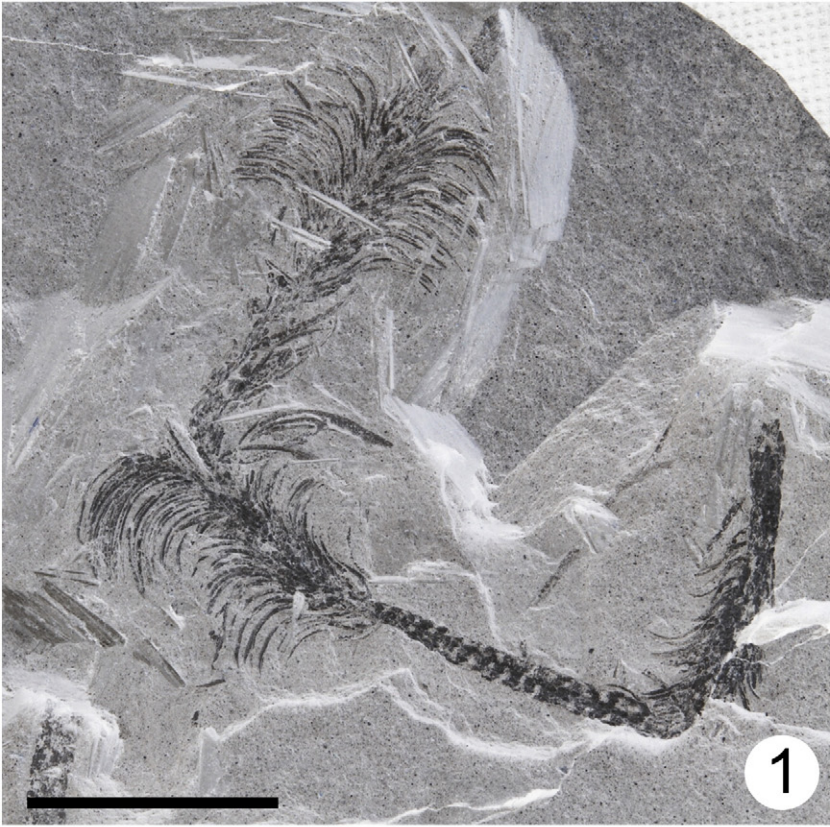
**Age:** Late Famennian.

### 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.



AM5300 and AM5760 show longer axis fragments (Plate I, figs. 1, 3 and 4). Their axes range from 4.8 up to 10.5 cm long (Plate I, fig. 1) and from 2.7 up to 4.5 mm wide (Plate I, figs. 1–6). Despite the small size of the preserved axis fragments, axis width seems to diminish from proximal to distal. A diminution from 4.5 up to 2.4 mm wide is notably observed on AM7511 (Plate I, fig. 1). The distal part of all preserved axes seems to be much smaller but a reliable measurement is made difficult by the presence of tightly arranged elongated leaves (Plate I, figs. 3–4) or by a strobilus (Plate II, figs. 1, 2 and 5). This size diminution reflects the position, as ultimate axes, of these axis fragments on the original plant.

The preservation does not allow the observation of the shape and organisation of the leaf bases. Some axial parts, devoid of leaves, seem to show a spiral arrangement of what could correspond to simple rounded leaf bases (Plate I, fig. 1). However, more detailed description is impossible. In general, the axial surface appears to be rather smooth characterised by an elongated longitudinal striation (Plate I, figs. 2 and 3). A reliable phyllotaxy is thus impossible to define.

#### 4.2. Vegetative leaves

Many axial fragments are covered with vegetative microphyllous leaves. They have a smooth margin and are characteristically falciform. The organic matter being particularly brittle, preparation could in some cases result in the removal of some fragments giving to the impression of irregular margin to the leaves (Plate I, 6). They measure 13–19 mm long and 0.3–0.6 mm wide (Plate I, figs. 1–4). They form a basal angle of 30°–35° with the axis (Plate I, figs. 1–3). The leaves are always straight in the first 3–7 mm and then markedly curve abaxially. Several axial segments appear to be devoid of leaves (Plate I, figs. 1–3). Interestingly, some bedding planes present dispersed shed microphylls. Plate I, fig. 6 shows an example of three dispersed vegetative leaves. They show some variation in size and present the characteristic falcate shape.

#### 4.3. Strobili and sporophylls

AM7509 (Plate II, figs. 1, 8) clearly shows a strobilus in connection with a short axial segment. Just proximal to the strobilus, the axis measures 2.2 mm in width. The axis presents a similar organisation to that in vegetative specimens but is devoid of vegetative leaves. The strobilus measures 13.5 mm long. Though compressed slightly obliquely, it shows a dense organisation.

In most cases, the strobili are found dispersed (Plate II, figs. 2–3, 5–6). They all show a dense organisation with no vegetative leaves associated. The longest strobilus measures 15 mm long. Except for specimen AM7509b (Plate II, fig. 1) where a short axis is observed, strobilar axes have not been observed.

Sporophylls are borne spirally (Plate II, figs. 2–3 and 5). They are up to 20 mm long and are typically borne at a much wider angle than vegetative leaves. They form a basal angle ranging between 60° and 90° with the axis (Plate II, fig. 2). Sporophylls are attached to the axis by a small 1.5 to 2 mm long straight pedicel. The pedicel is followed by a 4 to 5 mm long adaxially curved segment corresponding to the attachment zone of the sporangium. The end of the sporophyll lamina is curved abaxially and measures up to 10 mm long. The width of the sporophyll lamina is relatively regular from base to top ranging from 0.7 to 1.2 mm in width as measured on specimens with sporophylls preserved in face view (Plate II, fig. 1). They are thus much wider than vegetative leaves.

The middle part of the sporophyll, though in most cases obscured by the presence of the sporangium is characteristically enlarged (Plate II, fig. 6). The base of the sporangium is in all cases covered by a small extension of the subtending leaf (see arrows on Plate II, fig. 7). This extension is particularly visible when sporangia are absent (Plate II, fig. 4). It is 4 to 5 mm long and no more than 1 mm wide at the widest. It starts just after the pedicel, progressively widens and reaches its maximum size

approximately at the middle of the adaxially curved segment. It finally progressively reduces and disappears just before the abaxially curved segment starts.

#### 4.4. Sporangia

Sporangia are nearly always present and occur throughout the strobilus (Plate II, figs. 1–5). A single ovoid sporangium is borne on each sporophyll (Plate II, figs. 6–8). It seems to be sessile and attached to the adaxial side of the sporophyll. Sporangia occur 1.5–2 mm from the axis, just after the straight pedicel (Plate II, fig. 7). They are smooth and measure 3.0–4.5 mm long and 1.7–2 mm wide.

The content of the sporangium is generally unclear, however, several sporangia contain large rounded structures that we interpret as megaspores (see arrows, Plate II, figs. 5 and 7). Two to three megaspores can be observed per sporangium. They measure 100–150 µm in diameter. One specimen partially retains its original carbon (Plate II, fig. 1). Though difficult to observe, this specimen appears to show two types of sporangia in the same strobilus. Most of its sporangia seem to contain two to three large 100–150 µm wide megaspores. By contrast, one sporangium, broken open during preparation, displays numerous small 20–30 µm wide spores, that we interpret as microspores (see arrow Plate II, figs. 1, 8). The preservation mode of this specimen is confusing. The main axis of the strobili is tilted distally up to be perpendicular to the bedding plane. This gives the misleading impression of the microsporangium being basally while it is clearly distally located.

#### 4.5. Micro- and megaspore

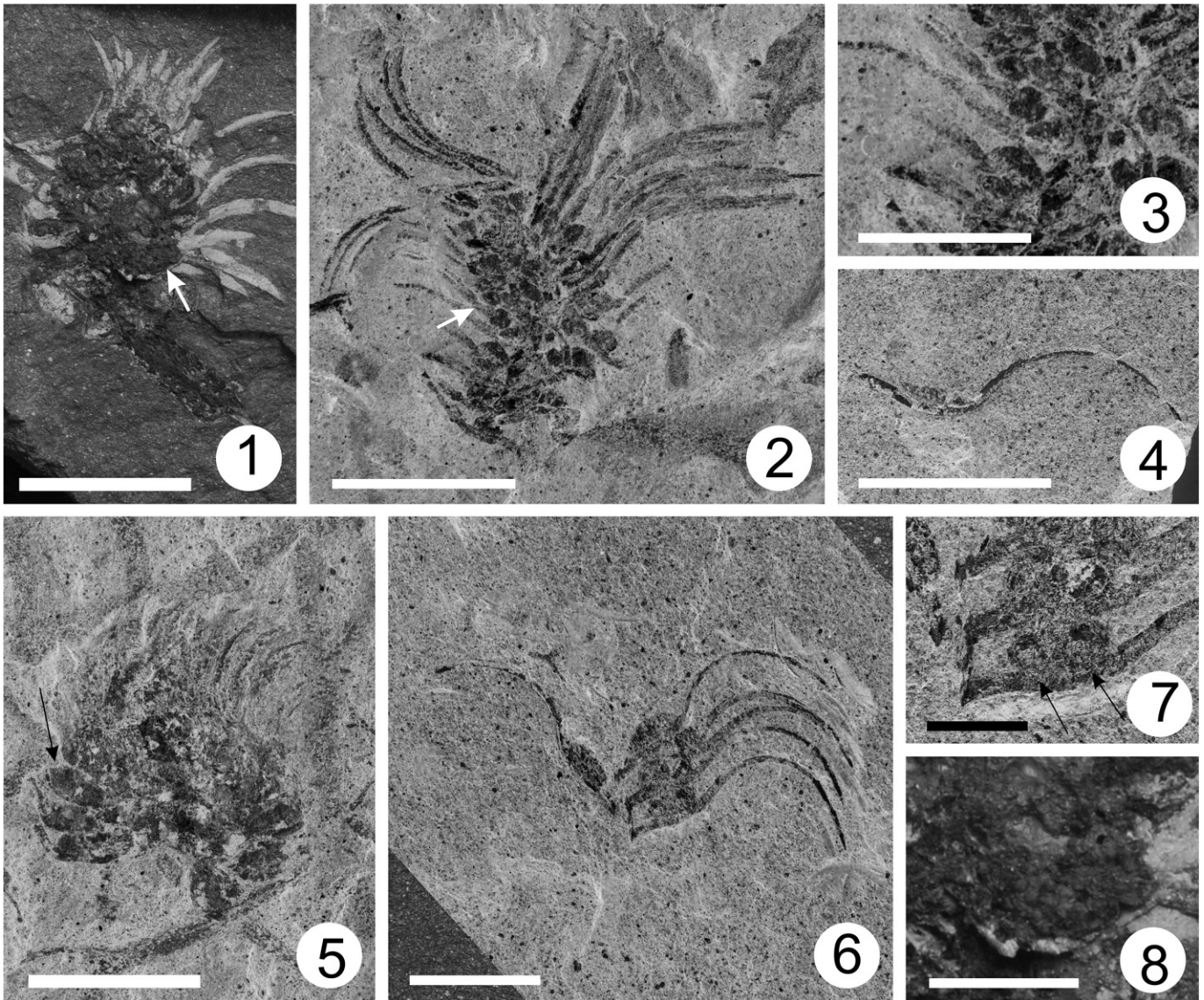
The nature of the preservation of these specimens precludes rigorous identification of the enclosed spores. However, one specimen allows observation of some details of the megaspore organisation (arrow on Plate II, fig. 2; Fig. 2). This megaspore is “hologulate”. Two of the three laesurae can be observed. They measure approximately 200 µm high. The main body of the megaspore is 580–720 µm in diameter and densely covered by perpendicular spines. Spines are at least 150–200 µm long.

A single microsporangium was found (Plate II, figs. 1 and 8). The microspores are unfortunately slightly degraded and a detailed description is thus impossible.

### 5. Partial reconstruction and affinities

*Kowieria alveiformis* is a plant with clear lycopsid affinities as demonstrated by the spirally arranged microphyllous leaves and the organisation of the strobili. Though the parent plant is unknown, we suggest it could have been part of a larger arborescent lycopsid. The presence of megaspores is in our opinion sufficient to suggest that this plant is heterosporous. The observation of a specimen presenting both sporangial types in the same strobilus confirms this statement and highlights the occurrence of bisporangiate strobili. The number of megaspores per sporangium is impossible to assess reliably but a number of four is suggested (one tetrad). All megaspores seem to be equal in size and thus very likely all functional. Megaspores being hologulate and ornamented, they are of the *Lagenicula*-type and are heavily ornamented. These characters all suggest strong affinities with the isoetalean lycopsids (Brack-Hanes and Thomas, 1982; Dimichele and Bateman, 1996). The occurrence of bisporangiate strobili containing *Lagenicula* megaspores is suggestive of a closer relation to the strobilus genus *Flemingites* but other characters such as the general morphology of the strobilus and of the sporophylls do not support this identification.

Classically, strobili with lycopsid affinities were named *Lepidostrobus* Brongniart. Later after a re-examination of that genus most bisporangiate strobili have been reclassified in the form genus *Flemingites* (Brack-Hanes and Thomas, 1982; Dimichele and Bateman, 1996). This form genus only refers to the fertile parts which are



**Plate II.** Fig. 1. Strobilus at the tip of a leafless axis. Compressed slightly obliquely it shows the dense organisation. The arrow indicates a microsporophyll. Scale bar: 1 cm. AM7509b. Fig. 2. Isolated strobilus showing the organisation of slightly modified sporophylls. The arrow indicates *in situ* megaspores made visible by the disappearances of the sporangial wall. Scale bar: 1 cm. AM5297. Fig. 3. Detail of the specimen fig. 2 showing sporophyll organisation and exposed megaspores. Scale bar: 0.5 cm. AM5297. Fig. 4. Dispersed sporophyll. Scale bar: 1 cm. AM7510. Fig. 5. Isolated strobilus. The arrow indicates a sporangium. Scale bar: 1 cm. AM5299a. Fig. 6. Fragment of a cone showing superposed megasporophyll. Scale bar: 1 cm. AM5298a. Fig. 7. Detail of a megasporangia of the specimen fig. 6 showing by transparency the shape of two megaspores (arrows). Scale bar: 0.5 cm. AM5298a. Fig. 8. Detail of the specimen fig. 1 showing the microsporangia containing several microspores. Scale bar: 0.5 cm. AM7509b.

suggested to reflect a primitive condition within rhizomorphic lycopsids (Dimichele and Bateman, 1996). Later, the establishment of whole plant based phylogenies showed *Flemingites* to be a rather wide generic concept that very likely encompasses several natural groups (Dimichele and Bateman, 1996). According to these later analyses, the occurrence of bisporangiate strobili is a central characteristic of the Ulodendraceae and Ulodendrinae (*sensu* Dimichele and Bateman, 1996). These two paraphyletic group concepts are mainly defined by the lack of evolved characters, such as monosporangiate strobili (Dimichele and Bateman, 1996). Both the concepts of *Flemingites* and of Ulodendraceae and Ulodendrinae are historic artefacts reflecting the way the field developed and the evolutionary top-down approach that was followed. Most broad taxonomic concepts are based on the wide Late Mississippian and Pennsylvanian lycopsid acme of diversity. In most cases, Devonian forms are simply excluded from the analyses (Dimichele and Bateman, 1996; Stevens et al., 2010). This is largely explained by the poor (preservation and diversity) record of the Devonian rhizomorphic lycopsids. Conversely Devonian centred studies tend to

exclude the Carboniferous diversity, chiefly due to the non-equivalence of preservational modes (Kenrick and Crane, 1997; Xue, 2011).

## 6. Comparison

### 6.1. Comparison with Middle Devonian lycopsids

From this comparison we readily exclude the Protolpidodendrales such as *Leclercqia*, *Haskinsia* or *Minarodendron* (Banks et al., 1972; Berry and Edwards, 1996; Liu et al., 2013) as they are sufficiently different from *Kowieria alveiformis* to prevent any confusion. Likewise we exclude the homosporous arborescent lycopsids, such as *Hoxtoigaya robusta* (Xu et al., 2012).

*Longostachys latisporophylla* is a late Givetian lycopsid from China (Cai and Chen, 1996). It is a small arborescent plant presenting well defined terminal strobili. Strobili are densely packed with spoonlike dentate sporophylls. Whether they are bisporangiate or not is not

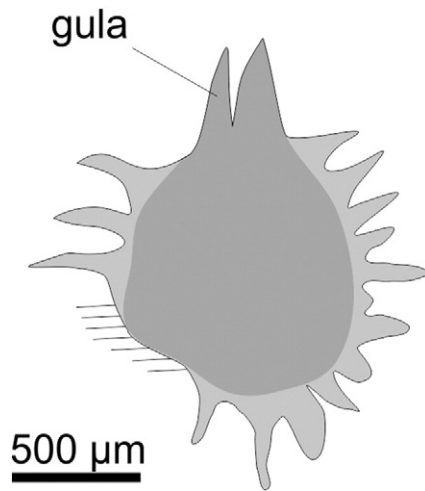


Fig. 2. Camera lucida drawing of the megaspore showing the gula and the spiny ornamentation (see arrow on Plate II, fig. 2).

mentioned in the description. Megaspores are of the *Laevigatisporites* type. This plant thus differs in nearly all aspects from *Kowieria*.

#### 6.2. Comparison with Late Devonian Euramerican material

Late Devonian lycopsids are relatively diverse. In Euramerica, previous reports include *Cyclostigma kiltorkense* Houghton, *Barsostrobus famennensis* Fairon-Demaret, *Prolepidodendron breviinternodium* Arnold, *Leptophloeum rhombicum* Dawson, *Clevelandodendron ohioensis* Chitaley and Pigg and *Otzinachsonia beerboweri* Cressler and Pfefferkorn. We can easily exclude *Leptophloeum* and *Prolepidodendron* from this comparison as they differ from our material in plant stature, leaf base organisation and microphyll morphology (Arnold, 1939; Lemoigne, 1982). *Otzinachsonia beerboweri* is only known from the basal part of the plant and is therefore impossible to compare here (Cressler and Pfefferkorn, 2005).

*Barsostrobus famennensis* Fairon-Demaret is a diminutive herbaceous heterosporous lycopsid presenting no particular strobilus-like grouping. The sporophylls are elongated and spiny. They contain megaspores of the *Lagenoisporites*-type with no gula and ornamented by small verrucae. All these characters are inconsistent with our material.

*Cyclostigma (Jurinodendron) kiltorkense* is reconstructed as a small arborescent lycopsid presenting a *Stigmara*-like rooting system and a *Flemingites*-type strobilus (Chaloner, 1968; Johnson, 1913, 1914). The latter is also present in our material. However, megasporophylls in *Cyclostigma* are typically straight and particularly large measuring from 8 cm up to 20 cm long while they are markedly curved and only up to 2 cm long in our material. The margin of the lamina is ciliate while smooth in the SA material. The megasporangium is much bigger measuring up to 4 mm wide and 12 mm long. It also differs markedly in shape, being more triangular. Megaspores are of the *Lagenicula*-type but are twice as big and present smaller spiny ornaments. Similarly *Clevelandodendron ohioensis* presents bisporangiate strobili. They however do not pertain to the *Flemingites*-type as they lack *Lagenicula*-type megaspores. We thus consider our material as different to either *Cyclostigma* or *Clevelandodendron*.

Gess and Hiller (1995) document dispersed fertile sporophylls that were collected in the same layers as *Kowieria* (Gess and Hiller, 1995 fig. 20). They differ from our material by showing much larger leaves measuring up to 4 cm in length. Moreover, these sporophylls are linear in shape, tapering distally and strongly ornamented. They undoubtedly represent a different taxon that will be described separately.

#### 6.3. Comparison with Late Devonian Chinese material

The diversity of Late Devonian lycopsids has considerably increased with description of abundant and diverse material from China. This comprises *Changxingia longifolia* Wang et al., *Lepidostrobus xinjiangensis* Wang et al., *Lobodendron fanwanense* Liu et al., *Minostrobus chaohuensis* Meng et al., *Monilistrobus yixingensis* Wang and Berry, *Sublepidodendron mirabile* Cui and Wang, *Sublepidodendron grabau* Wang and Xu, *Sublepidodendron songziense* Chen and *Wuxia bistrobilata* Berry et al. *Lobodendron* is anatomically preserved with only the axis being known and is thus impossible to compare to our material.

Superficially, *Kowieria* strongly resembles *Changxingia longifolia* Wang et al. This plant has been described as a medium size lycopsid bearing terminal monosporangiate strobili (Wang et al., 2014b). Leaves are spirally arranged measuring up to 25 mm long. Megasporangiate strobili are up to 50 mm long and 9.6 mm wide. The megasporophylls present a keel and alations as well as a heel. Megaspores are of the *Lagenicula*-type. Resemblance to the South African material derives from the characteristic abaxial curvature of the megasporophylls. The two plants however differ strongly in their organisation, in the presence of the keel and heel on the megasporophyll of *Changxingia*, and in its possession of megasporangiate strobili. The latter characteristic places thus *C. longifolia* within the *Dichostrobiles sensu Dimichele and Bateman* (1996) (Wang et al., 2014b). Several other Late Devonian lycopsids from China have also been classified within this group. They are *Lepidostrobus xinjiangensis* Wang et al., 2003, *Minostrobus chaohuensis* Wang (Meng et al., 2013; Meng et al., 2015; Wang, 2001; Wang et al., 2012), *Sublepidodendron songziense* Chen (Wang et al., 2003) and *Sublepidodendron grabau* (Sze) Wang et Xu (Meng et al., 2016; Wang and Xu, 2005).

*Lepidostrobus xinjiangensis* consists of an anatomically preserved microsporangiate strobilus (Wang, 2003). It is characterised by small laminate and acute sporophylls characterised by a heel. It differs strongly from our material and will not be discussed further.

*Minostrobus chaohuensis* is another arborescent lycopsid described with monosporangiate strobili (Meng et al., 2013; Wang et al., 2012). The vegetative leaves in *M. chaohuensis* are up to 7.0 mm long and lanceolate in shape, whereas they are straight and up to 19 mm long in *Kowieria*. Both micro- and megasporophylls of *Minostrobus* have alations and a keel; absent in *Kowieria*. *Sublepidodendron songziense* and *Sublepidodendron grabau* are among the best known Late Devonian lycopsids from China (Meng et al., 2016; Wang et al., 2003; Wang and Xu, 2005). These two plants share many morphological similarities with our material but cannot be confused. Their vegetative leaves are spirally arranged and elongated. They measure up to 8.5 mm in length and are always straight. By contrast leaves of *Kowieria* are always abaxially curved and up to 1.9 cm in length. Moreover the presence of monosporangiate strobili in *Minostrobus* and *Sublepidodendron* is a strong distinguishing character.

*Wuxia bistrobilata* Berry et al. has been described as having micro- and megasporophylls grouped into individual strobilus-like structures (Berry et al., 2003). Megasporophylls are spoon-shaped with spiny margins and grouped in strobili that are situated at the dichotomies of axes while microsporophyll strobili are positioned terminally. This organisation is clearly different from that observed in *Kowieria*. Finally, *Monilistrobus yixingensis* Wang and Berry is a small lycopsid that presents indeterminate sporophylls grouped into strobilus-like structures situated at the angle of the dichotomies (Wang and Berry, 2003). Sporophylls are spoon-shaped and present large spiny appendages. None of these characteristics compares favourably to our material.

#### 6.4. Comparison with Late Devonian Russian material

*Kossovella timanica* Petrosjan is a poorly known “arborescent” lycopsid from Russia (Petrosjan and Kossovoj, 1984). Though this material should be restudied in detail before reliable comparison can be

undertaken, it has been recently re-illustrated by Orlova et al. (2016). The vegetative parts consist of spirally arranged elongated straight microphylls somewhat similar to those of our material. The fertile parts consist of a bisporangiate terminal strobilus with loosely arranged sporophylls (Orlova et al., 2016; Petrosjan and Kossovoj, 1984). Megasporophylls are situated basally and contain smooth megaspores devoid of gulae. The microsporophylls are situated distally. Though *Kossovella* superficially resembles *Kowieria alveoformis*, it differs in overall organisation as well as in spore morphology. The latter character is consistently considered as strongly diagnostic (Brack-Hanes and Thomas, 1982; Dimichele and Bateman, 1996).

## 7. Discussion and conclusion

*Kowieria alveoformis* presents an interesting combination of characters and shows many instances of conditions intermediate between those of 'basal forms' and those of more derived ones grouped within *Flemingites* or the Ulodendraceae s.l. The main differences occur in sporophyll morphology. Sporophylls in *Kowieria* are relatively simple with no particular modification. Though wider than vegetative microphylls, they do not exhibit additional modification such as a keel, a heel or an upturned lamina. Not only *Flemingites* but also the other representatives of the Ulodendraceae present clearly modified sporophylls. According to the current classification scheme *Kowieria* could be attributed to the Ulodendraceae s.l. on the basis of possession of bisporangiate strobili with megaspores attributed to *Lagenicula*. We however consider it to represent an, as yet undefined, intermediate evolutionary condition. This new taxon offers new character combinations that can contribute to future phylogenetic analyses. These are increasingly necessary in order to structure and better understand the earliest steps of rhizomorphic lycopsids diversification.

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