



Rinistachya hilleri gen. et sp. nov. (Sphenophyllales), from the upper Devonian of South Africa

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Abstract

A rich and diverse plant assemblage has been excavated from latest Devonian (Famennian) black shales of the Witpoort Formation (Witteberg Group) at Waterloo Farm, close to the city of Grahamstown (South Africa). Several specimens of a new sphenopsid have been collected. The description of this as a new taxon, here named *Rinistachya hilleri*, gen. et sp. nov., provides an important addition to the scarce early record of the group. *Rinistachya hilleri* presents a novel architecture that include apparently plesiomorphic characters, reminiscent of the organisation of the Iridopteridales (including the production of two types of laterals at one node, the location of fertile parts in loose whorls on lateral branches and an organisation of the fertile parts in which they branch several times before bearing distally elongate sporangia). Other characters unambiguously nest *Rinistachya* within the Sphenopsida (including presence of planate and slightly webbed ultimate appendages and lateral strobili made of successive whorls of fertile leaves with fertile parts located at their axil). This provides strong support for a close relationship between Sphenopsida and Iridopteridales. *Rinistachya* furthermore represents the first record of a Devonian sphenopsid from Gondwana and extends the known distribution of the Sphenopsida from the tropics to very high palaeolatitudes. It is a new sphenopsid with a peculiar organisation. The new taxon allows better characterization of the initial evolutionary radiation at the base of the group.

Keywords Sphenopsid · Famennian · Devonian · Biogeography · Gondwana · Witpoort formation

Introduction

Among euphyllophytes, sphenopsids occupy a peculiar position (Taylor et al. 2009). Currently, they are only represented by the single genus *Equisetum*. They reached a maximum of diversity during the Carboniferous (Taylor et al. 2009; Wang and Guo 2009). They are traditionally composed of three major clades, namely the Sphenophyllales and the Equisetales, both characterized by a whorled organisation of their leaves and/or branches and by complex fertile parts, and the Pseudoborniales (Scott 1909; Taylor et al. 2009).

Sphenophyllales, together with several major clades (e.g. ferns sensu stricto, spermatophytes), originated during the Middle to Late Devonian. This period is marked by a strong landscape partitioning and by increased complexity of biological communities (Bateman et al. 1998; Scheckler 1986). Despite intensive research, the number of Devonian representatives of the Sphenophyllales is very sparse. Up to now, only a few taxa have been described in detail. They are *Eviostachya hoegii* (Leclercq 1957; Wang 1993), *Hamatophyton verticillatum* (Li et al. 1995; Wang and Guo 2009; Wang et al. 2006), *Rotafolia songziensis* (Wang et al. 2005) *Xihuphyllum megalofolium* (Huang et al., 2017a) and species of *Sphenophyllum* (Huang et al. 2017b). These taxa document a wide range of variability among the earliest representatives of the clade.

We redescribe here, as a new sphenopsid genus, specimens that were illustrated in an earlier work by Gess and Hiller as “presumed aquatic plants” due to their superficial resemblance with charophytes (Gess and Hiller 1995, Fig. 12). *Rinistachya hilleri* shows well-defined whorled appendages and complex three-dimensional fertile structures. This fossil plant

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highlights an interesting combination of reproductive and vegetative characters and provides new insights into the earliest steps in the evolution of the sphenopsids.

Geological settings

All specimens were collected by RG from the ‘main fish lens’ of the Waterloo Farm Lagerstätte, south of the city of Grahamstown (Eastern Cape, South Africa) (see Gess and Hiller 1995). 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 composed of graphitic black shale interpreted as having been deposited as anaerobic mud in a back-barrier estuarine lagoonal environment adjacent to the Agulhas Sea (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 references therein), terrestrial (Gess 2013) and aquatic invertebrates (Gess and Hiller 1995) and aquatic vertebrates (Gess and Coates 2015 and references therein). Biogeographic reconstructions indicate that the Waterloo Farm locality was deposited at high latitude, within 30° of the south pole (Torsvic and Cocks 2011) or perhaps at far higher latitude (Scotese and McKerrow 1990; Scotese and Barrett 1990; Mitchell et al. 2012).

Material and methods

Rinistachya is a fairly uncommon element within the Waterloo Farm flora. It is represented by eight specimens. These are all preserved in black, carbon rich, anaerobically derived metashale. The specimens are represented by compressions in which, during diagenesis, organic material was replaced by a silvery white phyllosilicate, which later altered to soft white kaolinite clay (Gess and Hiller 1995).

Systematic Palaeobotany

Rinistachya gen. nov.

Type-species

Rinistachya hilleri sp. nov.

Etymology

Generic name: Rini, after the isiXhosa name for the Grahamstown valley; stáchya: plural form of the Greek word “stáchys” signifying spike.

Generic diagnoses

Axes pseudomonopodial, with nodes and smooth internodes. Vegetative leaves linear divided up to three times, arranged in

whorls of six at axial nodes. Fertile axes lateral at distal nodes. Three fertile axes per fertile node. Fertile axes with nodes and smooth internodes. Each node bearing linear fertile leaves with complex fertile parts at their axils. Fertile leaves arranged in whorls of six, divided two times. Fertile parts complex, made of three successive divisions. Each division produces three equal axes. Second division producing recurved axes each bearing at least two ovate elongate sporangia.

Rinistachya hilleri sp. nov.

Etymology.

Species name: hilleri, after Dr. Norton Hiller, original supervisor of RGs excavations at Waterloo Farm

Specific diagnoses

Same as for genus. Vegetative leaves 12 mm long, ca. 0.5 mm wide at base and up to 6 mm at tip. Internode of fertile axes up to 14 mm long and up to 0.5 mm wide. Fertile leaves up to 8 mm long, 0.2–0.3 mm wide at base and 1.8–1.9 mm wide at tip. Fertile parts up to 3 mm long and 2.5 mm wide. Sporangia 0.6–0.7 mm long and 0.2 mm wide.

Holotype

AM 5270 (Fig. 4c, d, g)

Paratypes

AM 5271–AM 5272, AM 5705–AM 5706

Repository

Albany Museum, Somerset Street, Grahamstown, Eastern Cape, South Africa

Type locality

Waterloo Farm, Eastern Cape, South Africa

Horizon

Witpoort Formation, Witteberg Group, Cape Supergroup

Age

Upper (most?) Famennian

Description

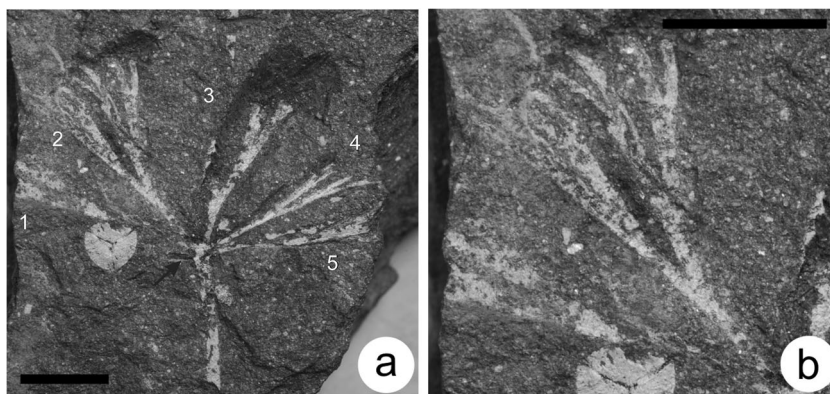
General features

This description is based on five specimens (AM 5270, AM 5271, AM 5272, AM 7505 and AM 7506). They are all incomplete and consist of vegetative remains (1 leaf whorl, AM 7506), main stem fragments (1 main stem, AM 7505) and fertile parts (3 branched fertile parts AM 5270–AM 5272). The proximal part of the plant is unknown.

Vegetative specimen

Only one specimen (AM 7506) appears to document the vegetative organisation of the plant. It consists of a very short stem fragment bearing one single whorl of leaves (Figs. 1a and 2c). The stem is 9 mm long and 1 mm wide. The size of this stem conforms to the main (N) axes described in the next

Fig. 1 Vegetative specimen of *Rinistachya hilleri* gen. et sp. nov. (AM 7506). **a** A general view showing the whorl with five preserved leaves numbered from 1 to 5. Scale bar = 0.5 cm. **b** A detail showing the fan shape of the leaf featuring three dichotomies. Scale bar = 0.5 cm



section. It bears a whorl in which five leaves are preserved. A sixth leaf is suggested but appears to have been broken (see arrow, Fig. 1a). Each leaf is 12 mm long and measures 0.5 mm wide basally. The leaves broaden up to 6 mm distally. They are wedge-shape. Three divisions are observed. The first occurs at one half of the leaf entire length (around 5.5 mm from the base). The second at the half of the remaining distance (around 7.5 mm from the base). The last division at around 9 mm from the base, corresponding approximately to the half of the length separating the second division and the top of the leaf (Figs. 1b and 2c). A total of eight rounded tips per leaf are thus observed.

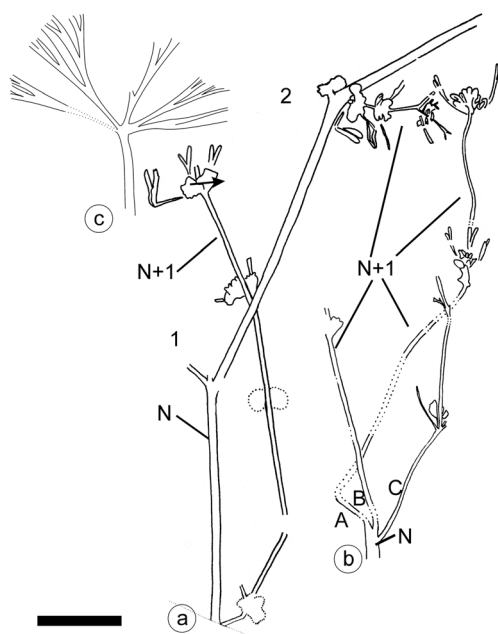


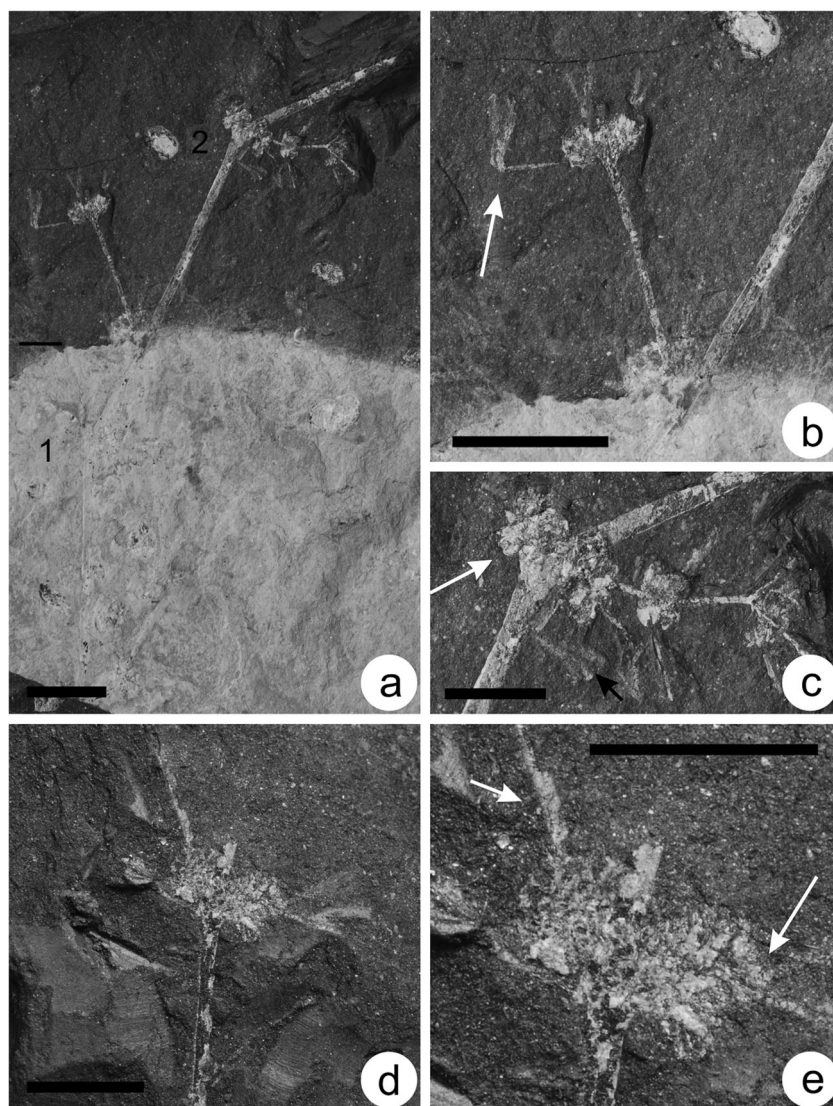
Fig. 2 Line drawing showing the general organisation of the plant. **a** General view of AM 7505 showing the organisation of the N and N + 1 axes. Successive nodes are numbered 1, 2 and 3. **b** General view of specimen AM 5270. Two N + 1 axes numbered 1 and 2 are clearly inserted at one node of the N axis. **c** Specimen AM 7506 showing a whorl of six vegetative leaves. Scale bar = 1 cm

Main (N) axis

The biggest specimen found to date (AM 7505) is illustrated in Figs. 2a and 3a. It is approximately 8 cm long and consists of a main stem of indeterminate order, here called N-order axis (see Fig. 2a). The base of the specimen is unfortunately slightly damaged by weathering that has reduced it and the matrix surface to a light grey clay. The stem is slender and smooth and comprises a succession of nodes (two of which are clearly preserved) and internodes. Internodes range from 0.9 to 1.2 mm in width; one complete internode length is 40 mm. Though two nodes are present, only one is well preserved. The two nodes are labelled ‘1’ and ‘2’ on Figs. 2a and 3a. A slight change of orientation can be observed at the nodes (Fig. 3a). The stem is characteristically slightly wider at nodes (Fig. 3a). No leaves are observed on the N-order axis. The base of two N + 1 axes is observed at node 1 (Figs. 2a and 3a). A more complete portion of an N + 1 axis is preserved at node 2. Internode between nodes 1 and 2 is 40 mm long. The N + 1 axis at node 2 forms an angle of approximately 45° with the N axis and measures 10 mm long. Superficially, only one N + 1 axis seems to be inserted at node 2. However, a closer observation allows the observation of the base of a second N + 1 axis at the opposite side of the N axis (arrow on Fig. 2a). This shows that at least two lateral axes are produced at each node. N + 1 axes on this specimen are fertile. Another N + 1 axis is overlain across the N axis between the two nodes but its origination is obscure. It is proximally poorly preserved due to the weathering of the rock, but appears to be at least 47 mm long and to contain at least three fertile nodes at regular intervals of approximately 14 mm.

The presence of whorls of three N + 1 axes per node is supported by evidence from specimen AM 5270 (Figs. 2b and 4c). This specimen shows a very short fragment (5 mm long and 1.7 mm wide) of the N-order axis (arrow on Fig. 4c) preserving one single node. This node is completely devoid of leaves. A whorl of three N + 1 axes is suggested. These N + 1 axes are labelled from “1” to “3” in Figs. 2b and 4c. They range from 28 to 40 mm in length and are 0.5 mm in width.

Fig. 3 Fertile specimens of *Rinistachya hilleri* gen. et sp. nov. (AM 7505 and AM 5272): **a** general view of AM 7505 showing the articulate organisation of the N and N + 1 axes. Successive nodes are numbered 1 and 2. Scale bars = 2 cm. **b** A detail of the N + 1 axes originating from the second node of AM 5705. It illustrates two successive whorls of fertile leaves. The arrow indicates a bract with a recurved shape. Scale bar = 1 cm. **c** A detail of the third node of the N axis of AM 5705. It shows two N + 1 axes originating on the same node. The white arrow indicates the base of the second N + 1 axis. The black arrow indicates the tip of one bract. Scale bar = 0.5 cm. **d** General view of specimen AM 5272 showing one single fertile whorl. Scale bar = 0.5 mm. **e** Detail of the fertile whorl of AM 5272: the arrows indicate two visible bracts. Scale bar = 0.5 mm



Fertile (N + 1) axes

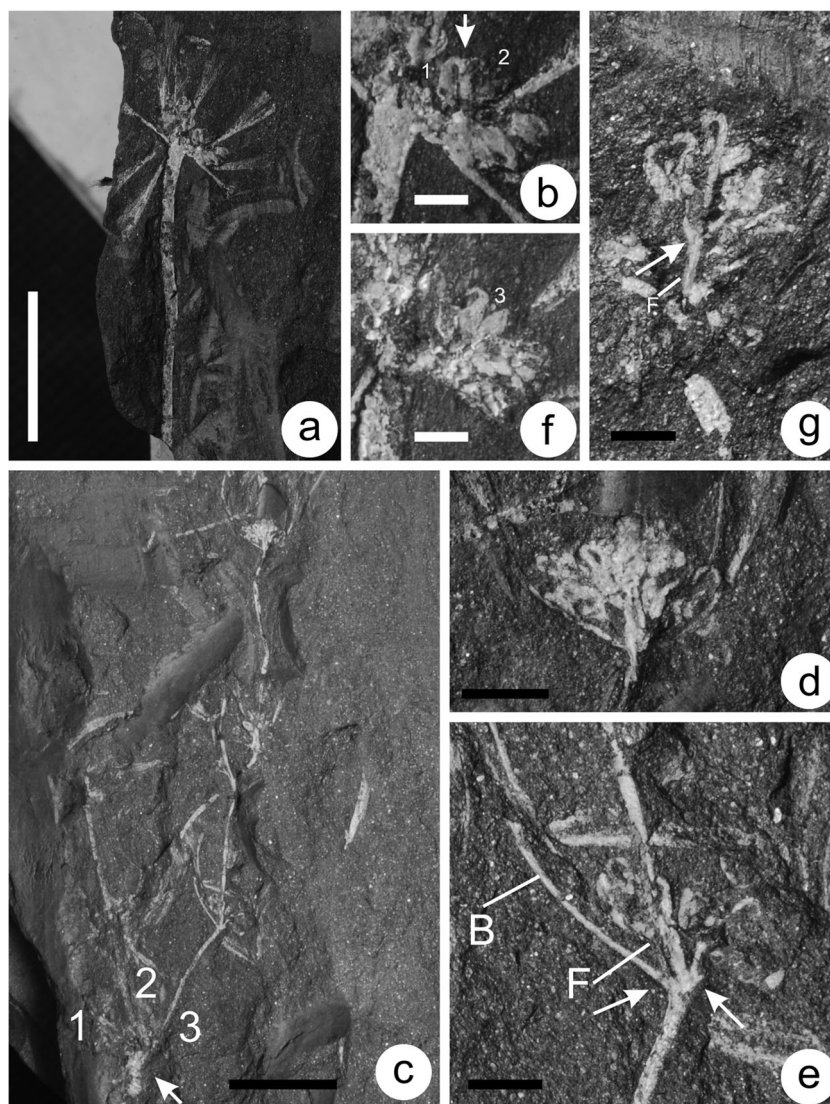
Fertile (N + 1) axes are much more slender than the N axis. They are inserted in whorls of up to three N + 1 axes at each node of the N axis (Figs. 2a, b, 3a–c, 4c). They are up to 47 mm long and range from 0.4 to 0.5 mm in width.

In specimen AM 7505 (Figs. 2a and 3a), a well-preserved section of an N + 1 axis is preserved at node 2. This N + 1 axis is much smaller than the overlain specimen measuring 10 mm long (Fig. 3c). It comprises three successive fertile nodes separated by two internodal axes 3 and 4 mm long and 0.3 mm wide. The initial fertile node occurs very close to the N axis. Each fertile node is similarly organized to those in the overlain axis except that they are much smaller. The fertile leaves have the same shape as those described above; however, only the first whorl of fertile leaves presents a 90° angle with the axis. They are 6.5 mm long.

The other, overlain N + 1 axis is at least 47 mm long and is composed of three successive fertile nodes separated by slender smooth 14 mm long and 0.5 mm wide internodal axes (Fig. 3b). Only the distal two nodes are reasonably well preserved with only the distalmost one yielding useful information. At each node, a whorl of leaves is inserted together with a whorl of fertile parts. In the distal example, fertile leaves are linear in shape and appear to be divided once at approximately 2/3 of their total length (Fig. 3b). Fertile leaves are slightly adaxially recurved. They are approximately 1 cm long. A marked 90° angle is visible between the fertile leaves and the N + 1 axis, though it is impossible to assess whether this feature is taphonomic or representative of the original condition.

In most specimens, the precise number of fertile leaves per node is difficult to assess reliably. The specimen AM 5272 consists of a short N + 1 axis bearing a single fertile node (Fig. 3d, e). This axis is 0.9 mm wide but is slightly enlarged at the

Fig. 4 Fertile specimens of *Rinistachya* gen. et sp. nov. **a** General view of AM 5271 showing a whorl made of six fertile leaves. Scale bar = 1 cm. **b** A detail showing the position of the fertile part at the axil of the fertile leaf, as well as the recurved form of two axes (1–2) produced by the ultimate division of the fertile part. Scale bar = 1 mm. **c** General view of specimen AM 5270. Three $N + 1$ axes numbered 1–3 are clearly inserted at one node of the N axis. Scale bar = 1 cm. **d** A detail of AM 5270 demonstrating the position of the fertile part at the axil of the fertile leaf. Scale bar = 2 mm. **e** Another detail of AM 5270 clearly illustrates the relative positions of the fertile leaves (B) and of the fertile part (F). The bases of the fertile leaves are indicated by two arrows. Scale bar = 1 mm. **f** The counterpart of Fig. 2b (AM 5271) showing the third (3) branch produced by the ultimate trichotomy of the fertile part. Scale bar = 1 mm. **g** A detail of AM 5270 showing the general organisation of the fertile part (F) with two successive trichotomies bearing paired elongate sporangia. Scale bar = 1 mm



node, measuring up to 1.2 mm wide. At this level, at least two fertile leaves are visible (arrows on Fig. 3e). They are 3 to 4 mm long (but broken distally) and 0.5 mm wide. It is the specimen AM 5271 (Fig. 4a, b) that provides the most complete information with respect to the organisation of the fertile whorls. This specimen shows a $N + 1$ order axis, 20 mm long and 0.9 mm wide. One fertile node is visible. The $N + 1$ axis enlarges at the point of emission up to a width of 1.2 mm. The whorl of fertile leaves has been preserved slightly tilted, bringing all leaves more or less on the same plane. As a result, it displays their organisation particularly well. Six fertile leaves per whorl are seen. They are fan-shaped and measure up to 8 mm long (Fig. 4b). They are basally very thin, 0.2 to 0.3 mm wide, while distally measuring 1.8 to 1.9 mm in width (Fig. 4b). They dichotomize equally twice. A first division occurs around 1/3 of their length and a second around 2/3. In most other cases, only two opposite leaves are visible in side view (Fig. 4c, f). This orientation obscured

the first division in the other specimens. There is no evidence of the distal bending of the fertile leaves observed in specimen AM 5705 (Fig. 3b) which are slightly recurved adaxially. Fertile parts are borne adaxially to the leaves and are inserted in axillary position relative to the different fertile leaves (arrow on Fig. 4e).

The longest well-preserved $N + 1$ axes are observed on specimen AM 5270 (Figs. 2b and 4c). They are up to 40 mm long, though one poorly preserved axis observed in specimen AM 7505 is at least 47 mm long (Fig. 2a). In AM 5270 with the in situ $N + 1$ axis of AM 7505 (Fig. 3), the first fertile whorl of each $N + 1$ axis is not inserted very close to the point of insertion on the N axis. $N + 1$ axis 3 (Figs. 2b and 4c) best shows the organisation. It measures 35 mm long and bears two fertile whorls with fertile leaves. The first occurs after 14 mm and the second is situated 18 mm more distally. They provide details on fertile part organisation that will be described in the next section.

Fertile parts

The fertile parts are complex. In order to facilitate the understanding of their description, an idealized line drawing is proposed (Fig. 5c). Each fertile part consists of an up to 3.0 mm long and 2.5 mm wide structure composed of an axis that trichotomizes distally. The trichotomy produces three equal axes that in turn trichotomize distally into three equal recurved axes. Finally, each axis divides once again to bear the elongated sporangium.

AM 5270 (Fig. 4e) shows the point of insertion of the fertile part (F), on the main axis, precisely at the axil of the fertile leaves (B) and the N + 1 axis (see arrows on Fig. 4e). In this case, the fertile part organisation is difficult to assess with precision. The main axis of the fertile part (F) is 1 mm long and 0.1 mm wide. The remaining part of this structure is 2 mm long and 1.5 mm wide. A second fertile part (F) axis is visible on the opposite side of the N + 1 axis. It is 0.8 mm long and 0.2 mm wide.

A fertile part is particularly well exposed in another fertile whorl of AM 5270 (Figs. 4g and 5b). The fertile part F axis is 0.9 mm long and 0.2 mm wide (Fig. 5b). At the end of this F axis, a trichotomy is clearly visible (arrow on Fig. 4g). It produces three S1 axes (see Fig. 5b). They measure 1.0–1.2 mm long and 0.1 to 0.15 mm wide. Each S1 axis divides to bear short recurved S2 appendages, each bearing two to three sporangia distally. Each S2 axis is approximately 0.5–0.8 mm long and 0.1 mm wide. The organisation of the S1 and S2 axes is, however, best seen in AM 5271 (Figs. 4a, b, f and 5a), whose part and counterpart are preserved. Figure 4b, f shows part and counterpart of the same fertile structure, with 4f inverted in order to allow an easier comparison with Fig. 4b. The line drawing presented on Fig. 4a shows the combined information of part and counterpart. In this specimen, one fertile part is preserved with its F axis roughly perpendicular to the bedding plane. Three groups of S1 and S2 axes are radiating from a badly preserved central point (Figs. 4b and 5a). One of these groups is particularly clear (see arrow on Figs. 4b and 5a). It

shows one S1 axis 1.0 mm long and 1.8 mm wide. At the end, a trichotomy is visible, producing three recurved S2 axes. The two first S2 axes are labelled “1” and “2” on the part specimen (Figs. 4b and 5a). A third one is visible on the counterpart specimen and labelled “3” (Fig. 4f). The sporangium of the latter is shown in dotted lines on Fig. 5a. The sporangia measure 0.4–0.5 mm long and 0.10–0.15 mm wide. The S2 axes bear at least two sporangia. Sporangia are elongate in shape and are approximately 0.6–0.7 mm long and 0.2 mm wide (Figs. 4b, f, g and 5a–c). They have parallel margins and are distally rounded. Sporangia are pendulous and recurved so that they are borne parallel to the S2 axis that they cover nearly entirely.

Partial reconstruction of the plant

A reconstruction of the plant is proposed in the Fig. 6a. *Rinistachya hilleri* is interpreted as a small-sized herbaceous plant. Only one fragmentary vegetative specimen was observed. As no connection with the fertile parts was observed, it is impossible to be sure of its exact position. Three arguments led us to consider it as a proximal part of the plant: (i) the size of the axis bearing the vegetative leaves conforms to the size range established for the above-described N-order axis. (ii) Vegetative leaves are much larger. (iii) The observation of different maturity stages among the fertile whorls suggests that “younger”, smaller ones are more distally placed. We thus hypothesized here proximally attached vegetative whorls bearing six leaves that dichotomize three times in order to form eight tips. When fertile, the N axis bears nodes comprising three N + 1 branches that are directly inserted on the N axis. Each N + 1 axis bears up to three fertile whorls characterized by fertile leaves similar in shape to the vegetative leaves but notably smaller and simpler, with only one to two dichotomies producing two to four tips. Each fertile leaf bears an axillary complex fertile part (Fig. 6b). Fertile parts divide three times. The ultimate division occurs on a recurved axis and produces two to three elongate sporangia.

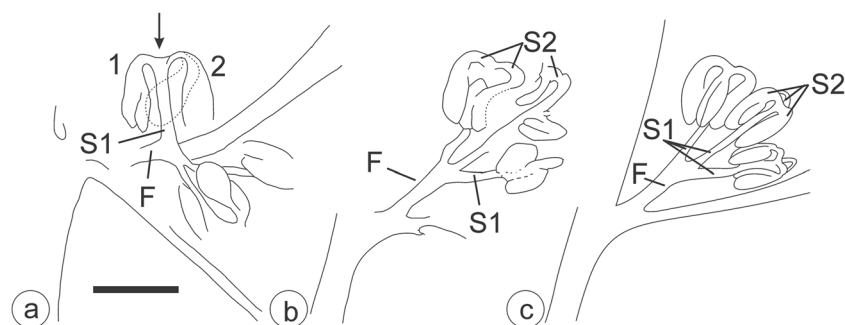


Fig. 5 Line drawing showing details of the organisation of the fertile parts. **a** Detail of specimen AM 5271 showing the organisation of the fertile part. Note the presence in dotted line of a third group of sporangia observed on the counterpart of the

illustrated specimen. **b** Detail of specimen AM 5270. **c** Interpretative reconstruction of the whole fertile part. (F) Fertile part first axis. (S1) Second-order branching of the fertile part. (S2) Third-order branching of the fertile part. Scale bar = 1 mm

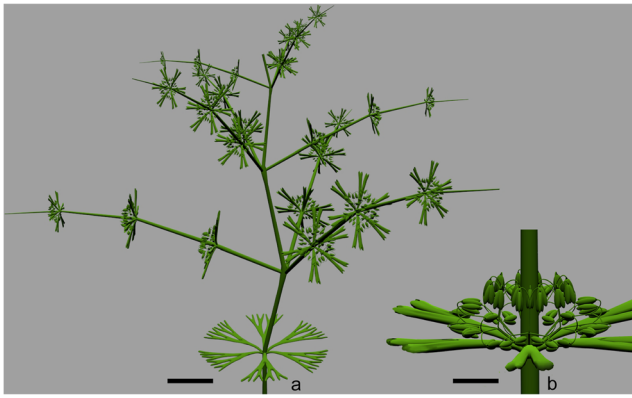


Fig. 6 Suggested partial reconstruction of *Rinistachya hilleri*. **a** The general organisation of the plant, scale bar = 1 cm. **b** A detail of a fertile whorl of fertile parts showing the complex fertile parts at the axil, scale bar = 0.5 cm

Affinities

In an earlier work, Gess and Hiller (1995) illustrated specimens, considered “presumed aquatic plants”, that are here redescribed as *Rinistachya hilleri* (Gess and Hiller 1995, Fig. 12). The confusion was made possible by the presence in the same deposit of several charophyte algae. These remains consist of slender stems bearing whorls of six to eight simple thalli. This latter characteristic makes them superficially similar to *Rinistachya*. However, the thalli in the charophytes present a much simpler organisation with oogonia situated at the abaxial side of the thallus. Three species have been reported from the Waterloo Farm locality. They are *Octochara crassa* Gess and Hiller (1995), *Octochara gracilis* Gess and Hiller (1995) and *Hexachara setacea* (1995). *Octochara crassa* presents eight thalli per whorls that only divide one time and present broad rounded termination. *Octochara gracilis* though following the same basic pattern with eight thalli produced per whorl, the latter are much thinner and may superficially resemble the leaves of *Rinistachya*. They are, however, much simpler dividing only once and ending on very thin tips. Both species present large oogonia that cannot be confounded with the complex fertile parts observed in *Rinistachya*. Finally, *Hexachara setacea* only present simple thalli showing no division. The characeae in Waterloo Farm locality strongly differ with the dichotomous leaves and complex fertile parts observed in *Rinistachya*. Indeed, the occurrence of whorled leaves, whorled fertile leaves, whorled fertile parts (in adaxial position), the rigid appearance of the stems, the articulate architecture and the slightly thickened nodes in *Rinistachya* unambiguously indicate that we are dealing with a member of the Sphenopsida. This group is represented, in the Paleozoic, by the Pseudoborniales, Sphenophyllales and the Equisetales (Taylor et al. 2009). The lack of anatomy preserved on the specimens studied here precludes any definitive

statement of their precise affinities. Nonetheless, the smooth non-ribbed stems, the presence of complex recurved fertile parts as well as the occurrence of repeated trimerous parts indicate affinities of this plant with the Sphenophyllales (Stein et al. 1984).

Comparison

The Devonian record of the Sphenophyllales is markedly poor. Only three other genera are hitherto known in some details (fertile and vegetative parts known). These are *Eviostachya* Stockmans (1948), *Hamatophyton* Gu and Zhi (1974) and *Rotafolia* Wang et al. (2005). The latter two are only known from China, whereas the first is known from both Belgium and China. Other taxa are only known vegetatively. They are *Sphenophyllum lungtanense* (Wang et al. 2008), *Sphenophyllum pseudotenerrimum* (Deng et al. 2016), *Xihuphyllum* Chen emend. Huang et al. (2017a, b) and *Sphenophyllum changxigense* (Huang et al. 2017b). All three were found in China.

Hamatophyton is probably the best known Devonian representative of the group, though there are many differences between the description given in Li et al. (1995) and those of later authors (Wang and Guo 2009; Wang et al. 2006). The most complete specimens have been figured by Wang and Guo (2009). They suggest that the plant presented three axial orders. The first order is pseudomonopodial, the second is alternately arranged and the third order axes occur at the nodes of second order axes, where they are associated with leaves. According to Wang and Guo (2009), leaves are of one type only and consist of simple hooked undivided or simply branched structures. However, Li et al. (1995) mention a strong leaf dimorphism. Their material, however, originated from several localities and could thus represent several taxa (Li et al. 1995). Fertile parts in *Hamatophyton* are grouped into loose strobili consisting of up to ten successive whorls of fertile parts (with up to six parts per whorl). Fertile parts were redescribed in detail by Wang et al. (2006) and convincingly reinterpreted as simple and undivided recurved stalks distally bearing one single ovate sporangium, rather than a complex bisporangiate structure as originally described by Li et al. (1995). A close observation of the illustrated specimens led us to doubt of some interpretations concerning the position of the fertile parts in the plant. We suggest that the latter are always borne by second-order axes. However, as we have not seen the actual specimens, we keep this as an open question. *Rinistachya* nevertheless differs strongly from *Hamatophyton* in the morphology of the leaves, the organisation of the branching and the fertile part architecture. Leaves in *Rinistachya* dichotomize up to three times and do not form a basal sheet. Characters of the vegetative branching system are more difficult to compare as only the two ultimate

branching orders are known in *Rinistachya*. Up to three fertile branches occur at each node in *Rinistachya*, but are not associated with leaf whorls as it is the case in *Hamatophyton*. In general, it is not clear in the different descriptions of *Hamatophyton* whether or not more than one branch could be produced per node though the original photographic plates appear to suggest that it was the case. Fertile axes in *Rinistachya* are more loosely arranged. Fertile parts are more complex with up to three trichotomies and are always associated with fertile leaves.

Rotafolia songziensis Wang et al. (2005) is less completely known than *Hamatophyton*. Only the two ultimate branching orders and the strobili are preserved. All axis orders are striated and covered by small emergences. They bear whorls of six fan-shaped leaves. Leaves dichotomize irregularly up to four times. Strobili are dense and borne by first- or second-order axis. They are always subtended by a whorl of vegetative leaves. They consist of up to 16 whorls of bracts with which fertile parts are associated. Bracts are cuneate and characterized by marginal elongate and recurved segments. Fertile parts are attached at their adaxial face. They consist of numerous stalked pendulous sporangia (Wang et al. 2005). An alternative interpretation could be that the strobilus in this plant is in fact only made of fertile whorls not associated with bracts. The fertile parts in this case would consist of complex three-dimensional structures where each marginal segment represents a sporangial stalk. Nevertheless, *Rinistachya* differs strongly from *Rotafolia*. More precisely, axes in *Rinistachya* are smooth with fan-shaped, regularly divided leaves. Strobili are much more loosely constructed, and fertile parts present a very different organisation.

Another Chinese sphenophyllalean is the recently described *Xihuphyllum megalofolium* (Chen) Huang et al. (2017a). Only the vegetative parts of this plant are known. This plant is much larger than *Rinistachya* and bears whorls of six spatulate to cuneate leaves. This plant cannot be confused with the South African material in which the leaves are up to three times dichotomous. *Xihuphyllum* will thus not be further discussed here. Several species of *Sphenophyllum* have as well been described in China. *Sphenophyllum lungtanense* (Wang et al. 2008), *Sphenophyllum pseudotenerrimum* (Deng et al. 2016). In the case of *Sphenophyllum changxigense* Huang et al. (2017b), a small portion of the plant has been preserved in addition to the vegetative leaves and seems very different from the SA material with branches and leaves being produced by the same nodes. Other differences are the presence of spines on the axes and the occurrence of bilobed leaves (Huang et al. 2017b). *Sphenophyllum lungtanense* presents fan-shaped and spatulate leaves with marginal teeth that are easy to distinguish from the SA African material (Wang et al. 2008). By contrast, leaves of *Sphenophyllum pseudotenerrimum* are very similar to those of *Rinistachya hilleri* (Deng et al. 2016). They are

linear and divided three to four times. They, however, more densely packed on the axes than in *Rinistachya*. The lack of fertile parts in *Sphenophyllum pseudotenerrimum* prevents any further comparison.

Eviostachya hoegii Stockmans (1948) has been reported from Belgium and China (Leclercq 1957; Wang 1993). This plant is described as being rhizomatous with adventitious roots. The stem branches up to three times and shows nodes and internodes. Broad leaves dichotomizing up to seven times are arranged in whorls of six and inserted at nodes. The fertile parts in this plant are organised in whorls of six and grouped within a strobilus. Each strobilus is subtended by a whorl of bracts; however, the strobilus has no intercalary bracts. Bracts are simpler than the leaves and only dichotomize up to four times. The strobili are borne on variably long stem segments. The latter stem segments are inserted on the main stem in whorls of up to three fertile branches and not associated with leaves. The fertile parts in *Eviostachya* are complex and formed by two successive trichotomies forming nine stalks, each bearing three sporangia. *Eviostachya* and *Rinistachya* have six leaves per whorl. Leaves in *Eviostachya* are more complex than those observed in *Rinistachya* where they only dichotomize up to three times. They are overall more regularly organised in *Rinistachya* with three successive dichotomizing levels and a wider lamina. Both plants present fertile branches inserted in whorls of three and not subtended by leaves. The strobili in *Eviostachya* are more densely organised and do not show bracts (fertile leaves) whorls subtending each fertile whorl. The fertile parts in both plants share a similar organisation characterized by two successive trichotomies and up to three sporangia per pedicel (thus 27 sporangia per fertile part). Fertile parts in *Eviostachya* are, however, smaller and characterized by a more compact organisation.

A far wider diversity has been described from Carboniferous and Permian sediments. Most vegetative parts are placed within *Sphenophyllum*, which is characterized by articulated stems bearing whorls of wedge-shaped leaflets. Fertile parts display a wider diversity, but they are, however, most generally attributed to the genera *Bowmanites* (Binney 1871) when anatomically preserved and to *Sphenophyllostachys* when found in compression. They are characterised by several whorls of bracts more or less fused basally. Bracts adaxially bear one to three fertile parts that are distally reflexed and bear a single sporangium. This morphology is very different from that observed in *Rinistachya* in which complex fertile parts are borne at the axil of dichotomous fertile leaves.

Despite similarities between the fertile part of *Eviostachya* and *Rinistachya*, the latter differs from all currently described sphenophyllalean remains. The attribution of the present material to a new genus is thus justified.

Discussion

Scarcity of fossils illustrating the earliest steps of sphenopsid evolution has hampered our understanding of their origin. The strong morphological differences existing between Devonian sphenopsids and both their putative ancestors and comparable Carboniferous forms have led to difficulties in understanding possible homologies (Stein et al. 1984). To date, only a few phylogenies have dealt with fossil ferns (Corvez et al. 2012; Doyle 1998; Kenrick and Crane 1997; Rothwell 1999; Rothwell and Nixon 2006; Xue et al. 2010). Most of them fail to resolve the relationships unifying the putative fern basal groups (e.g. Cladoxylales and Iridopteridales) with younger representatives. Despite this, the description of numerous Middle and Late Devonian fossil (pre?)ferns to fern like plants has confirmed that a strong relationship existed between Sphenophyllales, Iridopteridales and, to a lesser extent, Cladoxylales (Berry and Stein 2000; Stein et al. 1984; Xue et al. 2010).

The euphyllphyte clade diversified considerably during the Devonian, prior to the establishment of more modern lineages (Kenrick and Crane 1997; Bateman et al. 1998; Taylor et al. 2009). Iridopteridales and Cladoxylales constitute two closely allied basal members of the fern clade. They encompass a wide range of morphological and anatomical variations with sometimes tenuous boundaries, resulting in a complex taxonomical history of the group. This led Berry and Stein (2000) to propose a class level Cladoxylales taxon that includes both Devonian Cladoxylales and Iridopteridales. Three features characterizing the Iridopteridales were proposed (Berry and Stein 2000; Cordi and Stein 2005; Meyer-Berthaud et al. 2007). They are (i) the presence of an iterative architecture, (ii) the production of two types of laterals at one node and (iii) the lateral organs that are supplied by one trace originating from one stelar rib. Iridopteridales are further characterized by nodes of loose whorls situated on lateral branches. Lateral fertile parts always branch dichotomously several times and bear distal pairs of elongate sporangia (Berry and Edwards 1996; Berry and Stein 2000; Skog and Banks 1973; Wang 2008).

The absence of anatomical details in *Rinistachya* hampers its inclusion in a cladistic analyses. Interestingly, however, *Rinistachya* presents a combination of both derived and plesiomorphic characters. Characters inherited from its likely ancestors are the presence of an iterative architecture repeating several times the whorled organisation of the main axis, the location of fertile parts in loose whorls on lateral branches and finally the complex organisation of fertile parts that branch several times and bear distally paired elongate sporangia. All of these characteristics strongly link *Rinistachya* to the Iridopteridales rather than to any other fern-like clade known to date. By contrast, *Rinistachya* presents several features that unambiguously recall the sphenophyllales, such as planate and slightly webbed leaves and lateral fertile branches made

of successive whorls of fertile leaves with fertile parts located at their axil. Interestingly, the species *Sphenophyllum tenerrimum* and *S. myriophyllum*, which are often considered the most basal of the genus, have strongly dissected leaves with very narrow segments, exactly as *Rinistachya*. A similar situation is encountered in the Late Devonian Chinese species *Sphenophyllum pseudotenerimum*. *Rinistachya* also sheds new light on the other Devonian Sphenophyllales such as *Eviostachya*. The two plants share closely comparable organisation of their fertile parts, though *Rinistachya* possess a whorl of fertile leaves underlying each fertile whorl.

Further investigation is clearly needed in order to reasonably assess the early evolutionary history of the Sphenophyllales. However, the combination of characters listed here identifies *Rinistachya* as an early member of the Sphenophyllales retaining several plesiomorphic characters. It provides a link between the earliest sphenophytes and their putative ancestors. A character-based comparison further supports a strong relationship of the whole clade with the Iridopteridales though further phylogenetic analyses are necessary (see Xue et al. 2010 for similar discussions).

Rinistachya presents a distinct biogeographic outlier to the known distribution of Devonian sphenopsids, which were formerly only represented by specimens from China and Laurasia, which were situated under the tropics during the Late Devonian. It provides the first record of a Devonian sphenopsid from the Gondwanan continent and extends their range into remarkably high, nearly polar palaeolatitudes.

Conclusions

Rinistachya joins *Eviostachya*, *Hamatophyton* and *Rotafolia* as the oldest fertile representatives of the sphenopsids. Although no anatomical details were observed, the plant documents an unusual combination of both ancestral and derived characters that support a rooting of the whole clade within the Iridopteridales. With the description of *Rinistachya*, *Eviostachya* no longer appears to represent an isolated genus barely allied to Sphenophyllales, but rather appears to be a likely member of the initial evolutionary radiation at the base of the group.

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