



New cyathealean tree ferns from the Cretaceous of South Africa: *Natalipteris wildei* gen. et sp. nov. and *Kwazulupteris schaarschmidtii* gen. et sp. nov.



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ABSTRACT

Two new genera and species of permineralized tree ferns, *Natalipteris wildei* and *Kwazulupteris schaarschmidtii*, are defined and described in detail. *Natalipteris wildei* is a solenostelic stem without well-developed sclerenchyma sheaths in their vascular strands, and has a single vascular strand in the petiole bases, which are somewhat similar to the one present in *Cibotium* and *Nishidacaulis*. On the other hand, *K. schaarschmidtii* is a dictyostelic fern, with petiole bases with fused adaxial arcs and a single isolated meristele in the petiolar pith. Both taxa present features that preclude their placement in the recognized families of Cyatheaes, but may be referred to the “core tree ferns” clade. Fossil specimens were found in the Senckenberg Forschungsinstitut Palaeobotanical Collection and, although they lack precise stratigraphic provenance, it is suggested that they were collected from the Mzinene Formation (Albian–Turonian).

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1. Introduction

The Order Cyatheaes is a clade of ferns that, together with polypods and heterosporous water ferns, comprises the “core leptosporangiate ferns” group (Pryer et al., 2004). One of the most conspicuous features of this group of plants is the development of an arborescent habit, present in many (but not all) representatives of the order. Cyathealean ferns are solenostelic or dictyostelic, with some taxa having accessory medullary and cortical bundles, and have pinnate fronds bearing indusiate or exindusiate sori. Hairs or scales cover the stem and petioles of most tree ferns (Korall et al., 2007; Kramer and Green, 1990). Living Cyatheaes are found in tropical lowland to submontane environments, as well as subtropical and Southern Hemisphere temperate forests, reaching cool latitudes in southern South America, New Zealand and Tasmania (Large and Braggins, 2004). Several schemes for the systematic classification of the cyathealean tree ferns have been

published (e.g., Holttum and Sen, 1961; Korall et al., 2006; Lantz et al., 1999; Smith et al., 2006; Tryon, 1970). Most recent proposals for classification of extant ferns, summarized in Christenhusz et al. (2011), recognize eight families among Cyatheaes: Thyrsopteridaceae, Loxomataceae, Culcitaceae, Plagogyriaceae, Cibotiaceae, Dicksoniaceae, Metaxyaceae and Cyatheaceae.

The fossil record of the cyathealean tree ferns extends back into the Jurassic, and comprises permineralized stems, impression/compression fertile and sterile fronds, and isolated palynomorphs (Tidwell and Ash, 1994). In particular, more than 20 taxa based on permineralized stems have been described worldwide (Lantz et al., 1999; Tidwell and Ash, 1994; Vera, 2009, 2013). Among them, some specimens can be conclusively referred to recognized families of the Cyatheaes. For example, *Dendropteridium cyatheoides* Bancroft, 1932 and *Alsophilocaulis calveloi* Menéndez emend. Vera, 2010 clearly present affinities with the Cyatheaceae s.s., whereas others, described as representatives of the genus *Cibotium* (e.g., *C. oregonense* Barrington, 1983, *C. iwataense* Ogura, 1933), may be attributed to the Cibotiaceae. In addition, many taxa present a mixture of features that make them impossible to place in a particular family, suggesting that the diversity of tree ferns was notably greater than nowadays (Lantz et al., 1999; Stockey and Rothwell, 2004; Vera, 2013).

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In Africa, permineralized tree ferns referable to the Cyatheaales are scarce. In particular, only a single species, *Dendropteridium cyatheoides* (Bancroft, 1932) from the Neogene of Mount Elgon, at present in Kenya, has been described. As was above noted, this taxon is a derived representative of the Order Cyatheaales, and present characteristics which clearly place it in the Family Cyatheaceae.

In this work, we describe two new taxa, referable to the Order Cyatheaales, with a combination of anatomical features not present in any of the cyathealean families recently recognized by Smith et al. (2006). The specimens on which the new taxa are based were identified in the Senckenberg Forschungsinstitut Palaeobotanical Collection, and lack precise information of their provenance, but a tentative age and stratigraphic provenance is also given.

2. Material and methods

2.1. Provenance of the studied materials

Among the rich paleobotanical collection of the Senckenberg Forschungsinstitut (Frankfurt a/Main, Germany) several specimens of Cyathealean ferns were found. They appear to have been collected by Mr. G. Stumke and brought to Senckenberg by Mr. Teuns Erasmus, who in the seventies was studying Osmundaceous ferns on which he wrote his Ph. D. dissertation (Erasmus, 1978). Part of the specimens, in the form of some thick slices, were already mounted in some synthetic cement but not polished. The labels accompanying this material only read: “Hluhluwe District, Natal, Südafrika” and the indicated age only: “Kreide”. With this meager information it is somewhat difficult to establish the exact source or origin of these specimens.

Kennedy and Klinger (1975), for the area of the Hluhluwe District, in Maputaland (Fig. 1), proposed the Zululand Group which includes the Makatini, Mzinene and St. Lucia Formations, ranging in age from the upper Barremian to the lower Maastrichtian. This

nomenclature is accepted in modern South-African stratigraphy (SACS, 1980; Johnson, 1994). Kennedy and Klinger (op. cit., 1975: 305) state that the whole Cretaceous marine sequence (the Zululand Group) is “incredibly rich” in fossil logs and that there is a series of log beds in the Barremian–Aptian. The only clue to precisely identify source sediments could be to associate them to the collection studied by Erasmus (1978) who states that his Osmundales fossils come from the Mzinene Formation, i.e., Albian–Cenomanian (Kennedy and Klinger, 1975). It is possible that they were collected together or at least from the same unit, by the original collector, Mr. G. Stumke. Watkeys et al. (1993) give a short description of the Zululand Group, and mention that the Mzinene Formation was deposited between 112 and 91 Ma ago, thus coincident with the Albian–Turonian interval. This is the stratigraphic source and age accepted provisionally in this paper.

2.2. Methodology and repository

The specimens are all silicified and show an array of colors. Tissue preservation is generally good, showing cellular details, but in some places it is incomplete, making the tissue identification difficult. Some of the rather thick original sections, mainly of transversal surfaces, mounted with some cement, have been thinned and re-mounted with modern techniques. Only one incomplete specimen could be analyzed from a longitudinal section and thus such information is rather scarce. Photographs were taken with a Nikon Coolpix 995 adapted to an Olympus BX-51 or a Nikon SMZ-2 t Microscope. Terminology for describing the vasculature of the petiole bases follows Nishida (1984). Classification scheme follows recent proposals for extant ferns (Korall et al., 2006; Smith et al., 2006; Christenhusz et al., 2011). The specimens are housed at the Paleobotanical Collection of the Forschungsinstitut Senckenberg, at Frankfurt a/Main, Germany, under the acronym SM.B.

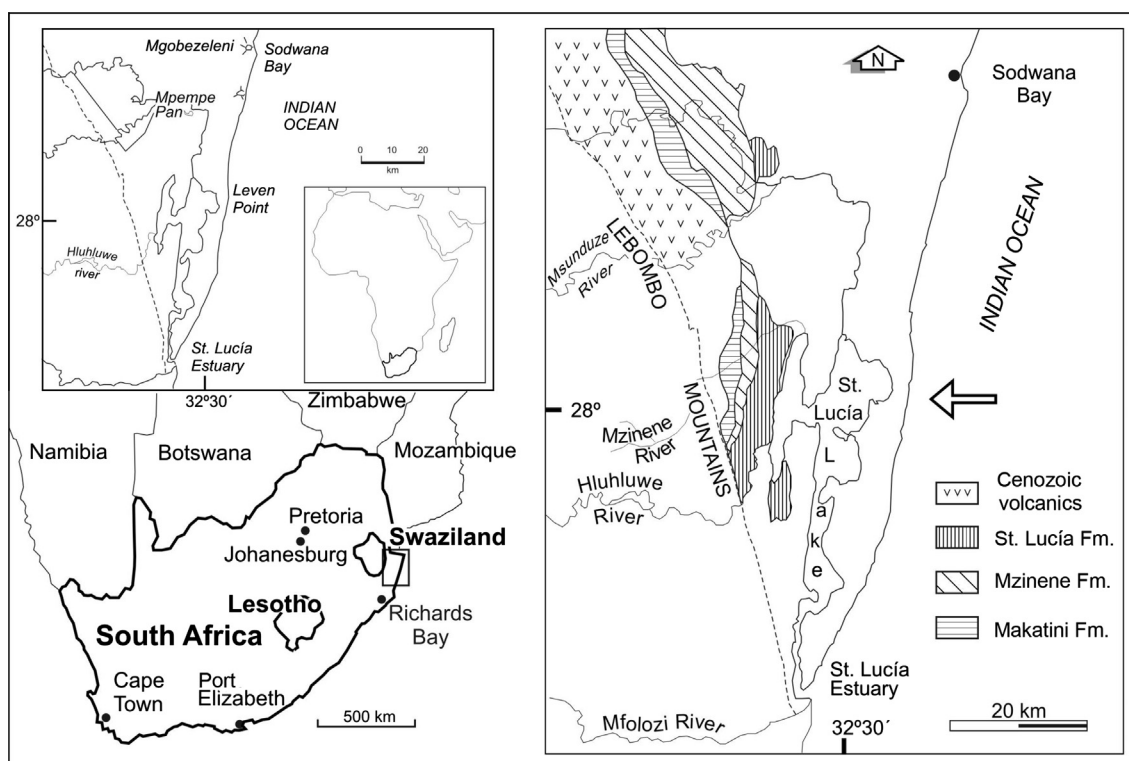


Fig. 1. Location map, showing outcrops of the Mzinene Formation. Modified from Kennedy and Klinger (1975).

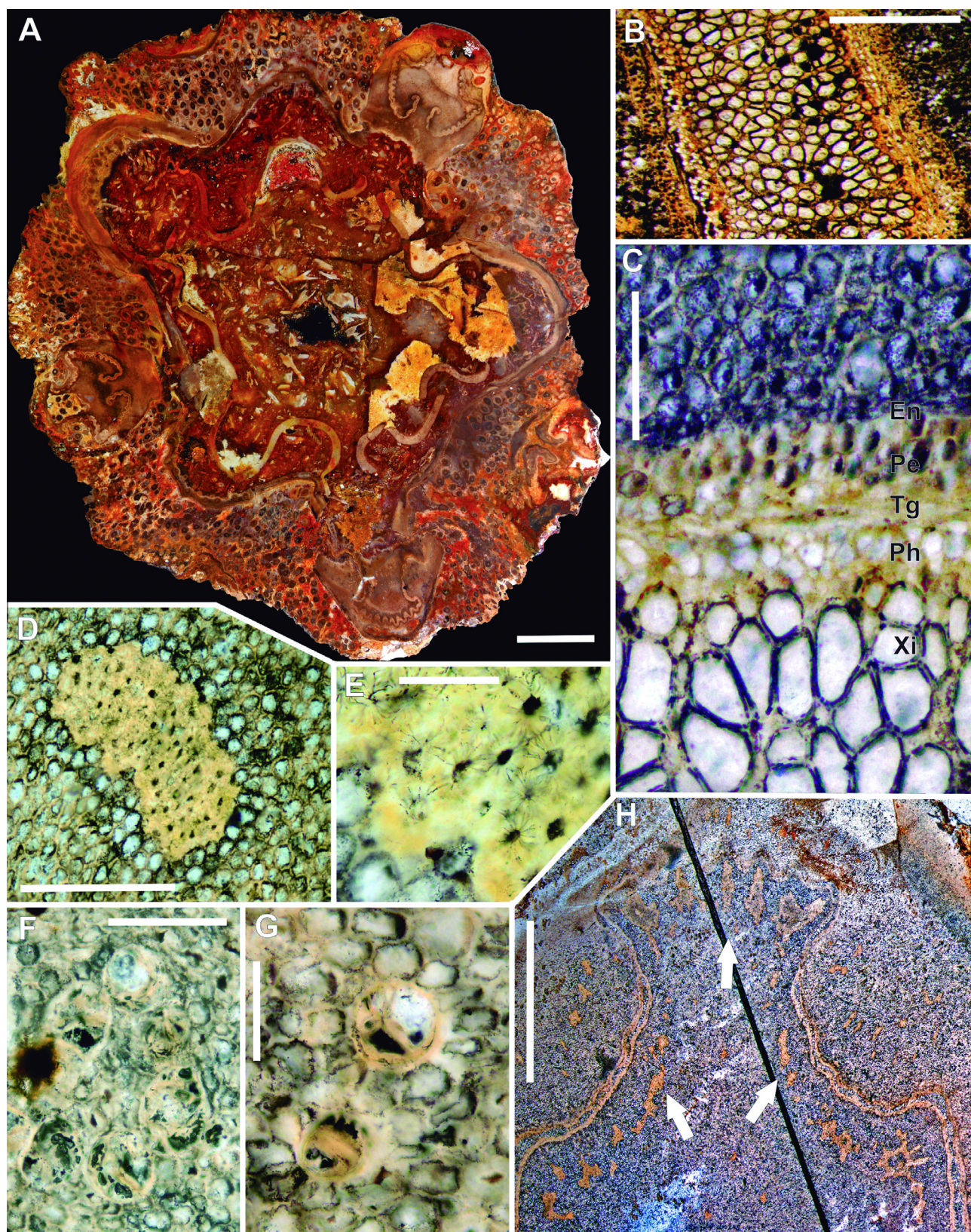


Fig. 2. Anatomy of *Natalipteris wildei* gen. et sp. nov. (A) general view of the stem with attached petiole bases and adventitious roots (SM.B 20635); (B) detail of the cauline vascular strand, showing metaxylem tracheids (SM.B 20633); (C) close-up of the vascular strand, showing xylem (Xi), phloem (Ph), tangential cells (Tg), pericycle (Pe) and endodermis (En); external side up (SM.B 20633); (D) sclerotic nest (SM.B 20633); (E) detail of a sclerotic nest (SM.B 20633); (F) and (G), mucilage cells (SM.B 20633); (H) departing leaf trace. Notice the sclerenchyma strands (arrows) located adaxially to the vascular strand. Scale bar represents 10 mm in A, 5 mm in H, 500 μ m in B and D, 200 μ m in C and F, and 100 μ m in E and G.

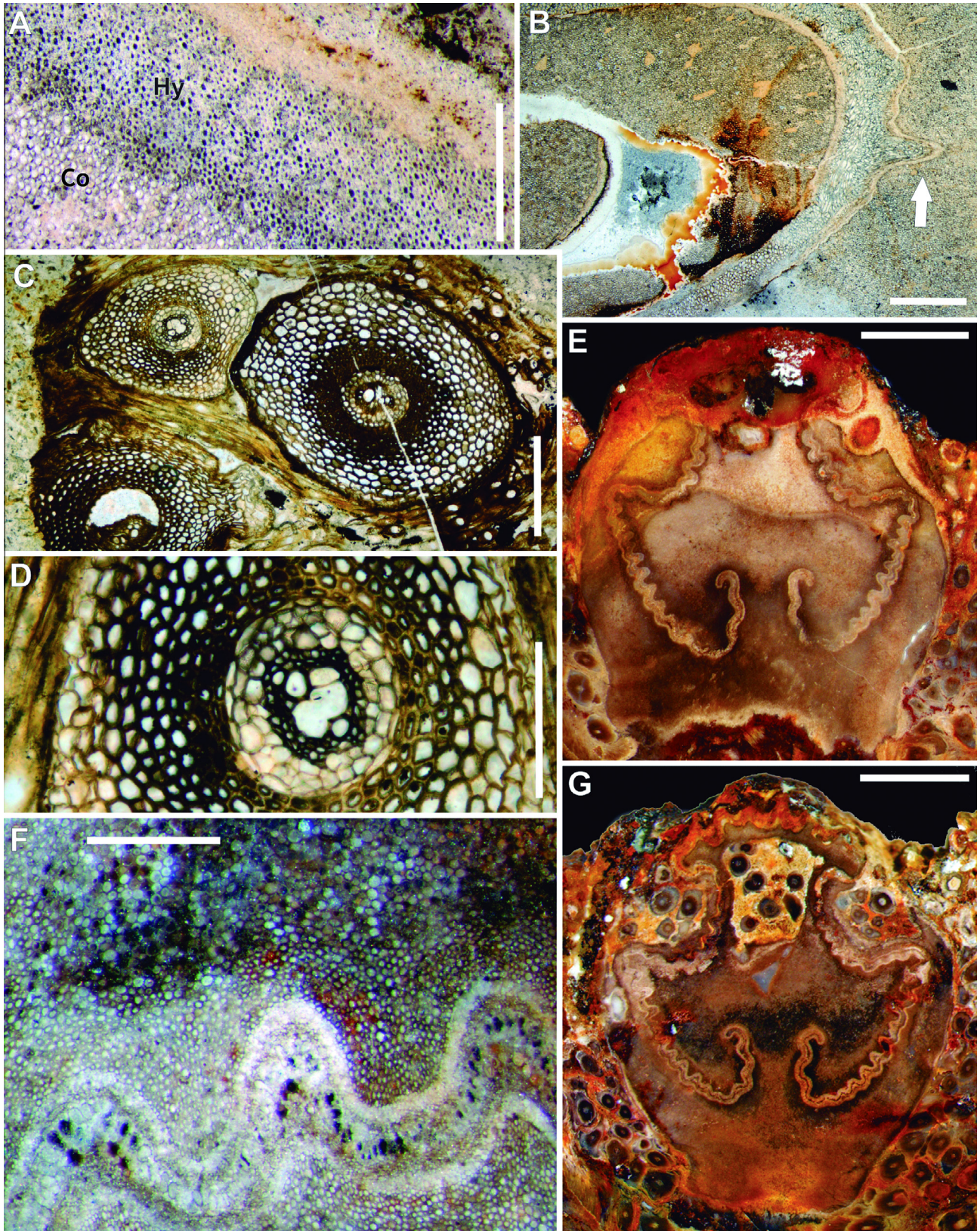


Fig. 3. Anatomy of *Natalipteris wildei* gen. et sp. nov. (A) detail of the hypodermis (Hy) surrounding the cortex (Co). Notice a white area on the hypodermis, representing degenerated sclerenchyma; external side up (SM.B 20633); (B) root traces diverging from cauline vascular strand (arrow); external side right (SM.B 20633); (C) root traces and trichomes; (D) detail of a root trace, showing inner sclerenchymatous and outer parenchymatous cortex; (E) and (G) petiole bases; abaxial side up (SM.B 20635); (F) detail of the vascular strand in the petiole base; abaxial side up (SM.B 20635). Scale bar represents 5 mm in E and G, 2 mm in B, 1 mm in A, 500 µm in C and F, and 200 µm in D.

3. Systematic paleontology

Class Polypodiopsida Cronquist, Takhtajan and Zimmerman 1966

Order Cyatheales A.B. Frank in J. Leunis 1877

Family uncertain

Natalipteris R. Herbst et Vera gen. nov. (Figs. 2, 3, 6A and C)

Type species: *Natalipteris wildei* R. Herbst et Vera sp. nov.

Etimology: After the Natal Province, one of the older names of the KwaZulu-Natal Province of South Africa, and *pteris*, fern.

Referred species: Type species only.

Diagnosis: Same as for species, by monotypy.

Natalipteris wildei R. Herbst et Vera sp. nov.

Etimology: Dedicated to Dr. Volker Wilde, (Curator of the Sengckenberg Paleobotanical Collection) for his many contributions to European paleobotany.

Type locality: “Hluhluwe District, Natal, South Africa” (from accompanying labels).

Stratigraphic horizon: Most probably, Mzinene Formation (Albian–Turonian).

Holotype: SM.B 20635.

Referred specimen: SM.B 20633

Diagnosis: Fossil tree fern stem with attached petiole bases and adventitious roots. Stem solenostelic, without medullary bundles and sclerenchyma sheath; with margins of leaf gap pointing centrifugally. Cortex narrow, surrounded by hypodermis and epidermis, from where an indument of multicellular hairs emerge. Pith and cortex parenchymatous, with interspersed sclerotic nests and mucilage cells. Petiole bases circular to oval; vascular strand single, with a modified omega-shaped morphology, presenting a wavy morphology due to repetition of V-shaped units. Abaxial arc smaller than adaxial arc. Lateral folds in the abaxial half of the strand, with the superior series approximately five times longer than inferior series. Adventitious roots diarch, presenting inner sclerenchymatous and outer parenchymatous cortex.

Description: The description is based on a thin fragment of the stem (SM.B 20635) and a mounted microscope slide (SM.B 20633), which most certainly belonged to the same stem. The specimen is ca. 10 cm wide, and contains a stem (5–9 cm in diameter) surrounded by a mantle of persistent petiole bases and adventitious roots (Fig. 2A).

Internally, the stem consists of a pith 25–50 mm in diameter, which is surrounded by an undulating solenostele. At the leaf gap margin, the meristele slightly curves abaxially. Surrounding the stele is a narrow (0.7–2 cm) cortex, which is completely enclosed by a one-layered hypodermis and the epidermis (Fig. 2A, 3A and 6A). Externally, a mantle of multicellular hairs is present (Fig. 3C).

The pith is mainly composed of parenchyma cells, 68–120 μm in diameter, with thin walls. Interspersed within the pith are sclerotic nests, ranging from 668 to 3600 μm in diameter, with circular to irregular shapes in cross sections. Sclerenchyma cells of this tissue are 60–130 μm in diameter, and have thick (16–32 μm) walls and narrow luminae (Fig. 2D and E). Although the distribution of these sclerenchyma nests seems to be random, these clusters of sclerenchymatous cells are often grouped near the vascular strands, in particular during the development of leaf traces (Fig. 2H). Mucilage cells are also scattered in the pith, singly or in groups of 2–3 (Fig. 2F and G).

The maximum thickness (2100–2768 μm) of the vascular bundle is reached in the middle of the consecutive orthostichies, but they gradually become narrow to both margins. The vascular strand is amphicribal and composed of primary xylem (with tracheids 25–95 μm in diameter), with small interspersed parenchyma cells (Fig. 2B), phloem, 30–200 μm in thickness, including a layer of

tangential cells, and the pericycle, consisting of parenchyma-like cells 16–35 μm in diameter (Fig. 2C). Finally, the endodermis encloses the vascular bundle (Fig. 2C). Externally, no sclerenchyma sheath was identified.

Stem cortex consists of several layers of tissue. The most internal zone is parenchymatous, and presents the same histological characteristics as of the pith, with sclerotic nests and mucilage cells interspersed among thick-walled parenchyma cells. This layer is sheathed by a single-layered sclerenchymatous hypodermis, consisting of cells 15–48 μm in diameter, with thick walls (Fig. 3A and C), which appears partially degenerated in some regions of the stem (Fig. 3A). The degree of preservation of the specimen precludes the identification of other cell types between this layer and the external trichomes (which most certainly emerged from the epidermal layer, Fig. 3C).

Root traces are scarce, and were difficult to identify in the studied specimens. They diverge from the cauline cylinder (Fig. 3B), at the region where the leaf trace is starting to develop. After separation from the central stele, they traverse the stem cortex until they vascularize the adventitious roots.

Leaf trace formation initiates with an outward expansion of the stem vascular bundle, where the xylem becomes thinner than in the adjacent sectors of the stele (Fig. 2H). Distally, the strand expansion continues, exhibiting marginal undulation of the bundle. This progression continues, and two lateral constrictions appear in the structure. At the same time, the leaf trace separates from the cauline vascular cylinder, developing a leaf gap. Finally, the adaxial ends of the produced leaf trace curve inwards (Fig. 6C).

Petiole bases are circular to oval in cross section (Fig. 3E and G), ranging from 1.5 to 2.3 cm in diameter. They have a narrow (1–2 tracheids thick; Fig. 3F), bilaterally symmetrical, vascular strand, which presents a modified omega-shaped morphology, with the adaxial arc larger than the abaxial arc, and with its adaxial margins pointing to the center of the petiole forming the median pair, also developing two small “hooks” (Fig. 3E and G). Along all the length of the meristele, the vascular strand presents a wavy morphology, appearing with a typical corrugated aspect due to repetition of V-shaped units (Fig. 3F). Two lateral folds are present in the leaf trace, with the superior series approximately five times longer than the inferior series. In the studied materials, these constrictions are always present in the abaxial half of the strand (Fig. 3E and G).

Surrounding the petiole vascular trace, several layers of small sclerenchyma cells are present (Fig. 3F), derived from the sclerotic nests present in the stem ground tissue. Petiole pith and cortex are of the same tissue composition as the stem ground tissues.

Adventitious roots are circular to oval in outline, 1000–1780 μm in diameter, and are generally present running vertically parallel to the stem, forming a dense indument. The roots are diarch, with a central xylem surrounded by phloem. This tissue is enclosed by a well-defined pericycle and the endodermis, the latter defined by tangentially elongated cells. The cortex consists of an internal sclerenchymatous layer, with cells 68–232 μm diameter, and a successive external parenchymatous layer, with thin-walled cells (24–65 μm in diameter) with narrow walls. The outermost tissue is the epidermis, consisting of cells 15–35 μm in diameter (Fig. 3C and D).

Comparisons with extant taxa and affinities: A solenostelic stem, surrounded by a mantle of adventitious roots and petiole bases, and petiole bases with wavy contour are characters that link *Natalipteris wildei* with the tree ferns of the Order Cyatheales.

Thyrsopteridaceae, represented by *Thyrsopteris elegans*, have solenostelic stems with medullary bundles, absent in *Natalipteris*. Petiole bases of *Thyrsopteris* are vascularized by a three-parted strand, whereas *Natalipteris* petiole bases have an undivided bundle (Table 1).

Table 1

Comparison between the new tree fern species and extant Cyatheales. Cyatheaaceae are presented at family level, since selected characters do not differ among genera. Data obtained from [Korall et al. \(2006, 2007\)](#), [Kramer and Green \(1990\)](#), [Lantz et al. \(1999\)](#), [Lucansky \(1974, 1977, 1982, 1984\)](#), [Nishida \(1982\)](#), [Ogura \(1972\)](#), [Qui et al. \(1995\)](#), [Sen \(1968\)](#), [Sen and Rahaman \(1999\)](#), [Smith et al. \(2006\)](#), [White and Turner \(1988\)](#) and works cited therein.

Taxon	Classification (sensu Smith et al., 2006)	Habit	Stele	Pith	Mucilage cells in ground tissue	Medullary bundles	Cortical bundles	Sclerenchyma sheath surrounding cauline meristeles	Cortex	Hypodermis	Indument	Petiole base vasculature	Adventitious roots
<i>Thyrsopteris</i>	Thyrsopteridaceae	Erect	Solenostele	Parenchymatous	Absent	Present	Absent	Absent	Parenchymatous	Two-layered	Uniseriate glandular hairs and hirsute multiseriate to uniseriate hairs	3-parted, modified omega-shaped	Inner parenchymatous, outer sclerenchymatous
<i>Loxoma</i>	Loxomataceae	Creeping	Solenostele	Mostly sclerenchymatous	Absent	Absent	Absent	Absent	Mostly sclerenchymatous	One-layered	Hairs with multicellular base (stem), multiseriate hairs (frond)	Single, U or V-shaped, with margins curved inwards	Inner parenchymatous, outer sclerenchymatous
<i>Loxomopsis</i>	Loxomataceae	Creeping	Solenostele	Mostly sclerenchymatous	Absent	Absent	Absent	Absent	Mostly sclerenchymatous	One-layered	Hairs with multicellular base (stem), uniseriate hairs (frond)	Single, U or V-shaped, with margins curved inwards	Inner parenchymatous, outer sclerenchymatous
<i>Culcita</i>	Culcitaceae	Creeping or ascending	Solenostele	Inner sclerenchymatous, outer parenchymatous	Present	Absent	Absent	Absent	Parenchymatous	Two-layered	Long articulate hairs	Single, U-shaped, margins pointing outwards	Inner parenchymatous, outer sclerenchymatous
<i>Plagiogyria</i>	Plagiogyriaceae	Creeping or erect	Dictyostele, but can protostelic and solenostelic at stolons or branching regions	Inner sclerenchymatous, outer parenchymatous	Absent	Absent	Absent	Absent	Parenchymatous	One-layered	Absent in stem, multicellular in fronds	Single or 3-parted, U or V-shaped	Inner parenchymatous, outer sclerenchymatous
<i>Cibotium</i>	Cibotiaceae	Creeping to erect	Solenostele or dictyostele	Parenchymatous	Present	Absent	Absent	Absent	Parenchymatous	One-layered	Multicellular hairs	Multi-parted, modified omega-shaped	Inner sclerenchymatous, outer parenchymatous
<i>Cyatheaaceae</i>	Cyatheaaceae	Erect	Dictyostele	Parenchymatous	Present	Present	Present or absent	Present	Parenchymatous	Two-layered	Scales	Multi-parted, modified omega-shaped	Inner sclerenchymatous, outer parenchymatous
<i>Calochlaena</i>	Dicksoniaceae	Creeping	Solenostele	Parenchymatous with sclerenchyma strands	Absent	Absent	Absent	Absent	Parenchymatous with sclerenchyma strands	Two-layered	Multicellular hairs	Single, U or modified omega-shaped. Shallow lateral	Inner sclerenchymatous, outer parenchymatous
<i>Dicksonia</i>	Dicksoniaceae	Erect or creeping	Dictyostele	Parenchymatous	Present	Absent	Absent	Present	Parenchymatous	Two-layered	Multicellular hairs	3-parted, modified omega-	Inner sclerenchymatous, outer

(continued on next page)

Table 1 (continued)

Taxon	Classification (sensu Smith et al., 2006)	Habit	Stele	Pith	Mucilage cells in ground tissue	Medullary bundles	Cortical bundles	Sclerenchyma sheath surrounding cauline meristemes	Cortex	Hypodermis	Indument	Petiole base vasculature	Adventitious roots
<i>Lophosoria</i>	Dicksoniaceae	Erect	Solenostele	Parenchymatous	Present	Absent	Absent	Present	Parenchymatous	Two-layered	Multicellular hairs	shaped 3-parted, modified omega- shaped Single, modified omega- shaped Single, modified omega- shaped	parenchymatous Inner sclerenchymatous, outer parenchymatous Inner sclerenchymatous, outer parenchymatous Inner sclerenchymatous, outer parenchymatous
<i>Metaxya</i>	Metaxyaceae	Creeping	Solenostele	Parenchymatous	Absent	Absent	Absent	Absent	Parenchymatous	One-layered	Multicellular hairs	shaped Single, modified omega- shaped Single, modified omega- shaped	parenchymatous Inner sclerenchymatous, outer parenchymatous Inner sclerenchymatous, outer parenchymatous
<i>Natalipteris</i>	?	Erect	Solenostele	Parenchymatous	Present	Absent	Absent	Absent	Parenchymatous	One-layered	Multicellular hairs	shaped Single, modified omega- shaped Single, modified omega- shaped	parenchymatous Inner sclerenchymatous, outer parenchymatous Inner sclerenchymatous, outer parenchymatous
<i>Kwazulupteris</i>	?	Erect	Dictyostele	Parenchymatous	Absent	Absent	Absent	Present	Parenchymatous	One-layered?	Multicellular hairs	shaped 3-parted, modified omega- shaped	parenchymatous Inner sclerenchymatous, outer parenchymatous Inner sclerenchymatous, outer parenchymatous

Loxomataceae (*Loxoma* and *Loxomopsis*) is a clade of creeping solenostelic rhizomes, with mostly sclerenchymatous ground tissues, contrasting with the erect rhizomes with parenchymatous pith and cortex of *Natalipteris*. Mucilage cells, present in the fossil species, are also absent in Loxomataceae (Table 1).

Culcita, only genus of the Culcitaceae, has a pith with a central sclerenchymatous region, not observed in *Natalipteris*. In addition, petiole bases of *Culcita* have a single U-shaped vascular strand, with their margins pointing outwards, not observed in the new species (Table 1).

Plagiogyriaceae, represented by the genus *Plagiogyria*, possess a mass of sclerenchyma in the central region of the pith and lacks mucilage cells in the ground tissue, separating it from *Natalipteris*. Stems of this family lack hairs, which are present in the South African species. In addition, the vascular strand of the petiole bases is arranged in an U or V-shaped structure, different from the modified omega-shaped morphology observed in the new taxon (Table 1).

Living species of the genus *Cibotium*, representative of the Cibotiaceae, may be solenostelic or dictyostelic, being the former easily separable from *Natalipteris*. Petiole vasculature of this genus consists of several vascular strands, arranged in a modified omega-shaped structure. On the contrary, vascular strand of the petiole bases of the new species is undivided (Table 1).

Genera included in the Cyatheaceae (e.g., *Alsophila*, *Cyathea*) have medullary (and sometimes cortical) accessory bundles, absent in *Natalipteris*. Cauline vascular bundles in the Cyatheaceae have well-developed sclerenchyma sheaths, not observed in the new taxon. Furthermore, petiole bases of cyatheacean ferns have multi-parted leaf traces, contrasting with the undivided strand in the South African specimen (Table 1).

Metaxya, sole genus of the Metaxyaceae, is a taxon with creeping solenostelic stems, with ground tissues lacking mucilage cells, and thus different from *Natalipteris* (Table 1).

Dicksoniaceae comprises three genera, i.e., *Dicksonia*, *Calochlaena* and *Lophosoria*. *Dicksonia* and *Lophosoria* can be erect, with well-developed sclerenchyma sheaths surrounding cauline meristemes, which are absent in *Natalipteris*. Petiole bases of these genera tend to have three-parted vascular strands, contrasting with the undivided strand of *Natalipteris*. It is worth noting that some species of *Dicksonia* (e.g., *Dicksonia gigantea*; [Nishida, 1984](#)) have a single vascular strand, but still can be separated from *Natalipteris* by the presence of sclerenchyma sheaths surrounding cauline vascular strands. The third dicksoniacean genus, *Calochlaena*, has creeping rhizomes without mucilage cells in the ground tissue, as well as a two-layered hypodermis, differing from *Natalipteris*. Petiolar vascular strand is U-shaped, or sometimes a modified omega-shaped structure, but with lateral grooves shallower than in the new taxon (Table 1).

From the above discussion, it is clear that *Natalipteris* cannot be referred to any of the cyathealean families recognized by [Smith et al. \(2006\)](#), since it possess a mixture of characters which precludes a conclusive familiar classification. [Korall et al. \(2006\)](#) conducted a molecular phylogenetic analysis on Cyatheales, and recognized a “core tree ferns” clade, i.e., (Cyatheaceae (Cibotiaceae (Dicksoniaceae + Metaxyaceae))), separated from the rest of the cyathealean families. Noteworthy, these authors noticed that species included in this “core tree ferns” clade had adventitious roots with inner sclerenchymatous and outer parenchymatous cortices, whereas the cyathealeans outside this clade had inner parenchymatous and outer sclerenchymatous cortices. As a result, these authors suggested that the presence of adventitious roots with inner sclerenchymatous and outer parenchymatous cortices was a character that supported the separation of “core” and “non-core” tree ferns ([Korall et al., 2006](#)). The new taxon, *Natalipteris*, has adventitious roots with inner sclerenchymatous and outer

Table 2

Comparison between the new tree fern species and fossil Cyatheaes stems. Data obtained from Bancroft (1932), Barrington (1983), Gould (1972), Lantz et al. (1999), Nishida (1982, 1984, 1989), Nishida and Nishida (1979), Stockey and Rothwell (2004), Tidwell and Nishida (1993), Tidwell et al. (1989), Vera (2009, 2010, 2013), and works cited therein.

Taxon	Age/ location	Habit	Stele	Pith	Mucilage cells in ground tissue	Medullary bundles	Cortical bundles	Sclerenchyma sheath surrounding cauline meristeles	Cortex (excluding hypodermis)	Hypodermis	Indument	Petiole base vasculature	Adventitious roots cortex
<i>Alienopteris livingstonensis</i>	Aptian / Antarctica	Erect	Dictyostele, Y-shaped meristeles	Inner sclerenchymatous, outer parenchymatous	Present	Absent	Absent	Present	Parenchymatous	Two- layered	Multicellular hairs	9-Parted, modified omega-shaped	Inner sclerenchymatous, outer parenchymatous
<i>Alsophilocalulis calveloi</i>	Late Oligocene / Argentina	Erect	Dictyostele	Parenchymatous	?	Present	Present	Present	Parenchymatous	Two- layered	?	Multi-parted, modified omega- shaped	Inner sclerenchymatous, outer parenchymatous ?
<i>Cibotiocalulis tateiwai</i>	Lower Cretaceous/ Korea	Erect	Dictyostele	Parenchymatous?	Present	Present	Absent	Present	Parenchymatous?	One- layered	Hairs (Multiseriate?)	Multi-parted, modified omega- shaped	?
<i>Cibotium iwataense</i>	Coniacian– Santonian/ Japan	Erect	Solenostele	Parenchymatous	Present	Absent	Absent	Absent	Parenchymatous	One- layered	?	Multi-parted, modified omega- shaped	?
<i>Cibotium oregonense</i>	Upper Eocene/USA	Erect	?	Parenchymatous	Absent	Absent	Absent	Absent	Parenchymatous	One- layered	Multicellular hairs	Multi-parted, modified omega- shaped	Sclerenchymatous
<i>Cibotium tasmanense</i>	Mid- Mesozoic/ Tasmania	Erect	Solenostele	Parenchymatous	Absent	Absent	Absent	Absent	Parenchymatous	One- layered	Multicellular hairs	Single, modified omega-shaped	Sclerenchymatous?
<i>Conantiopteris schuchmanii</i>	Aptian/USA	Erect	Dictyostele	Parenchymatous	Present	Absent	Absent	Present	Parenchymatous	Two- layered	Multicellular hairs	3-Parted, modified omega-shaped	Inner sclerenchymatous, outer parenchymatous
<i>Cyathocaulis</i> spp.	Lower– Upper Cretaceous/ Japan, Korea	Erect	Dictyostele	Parenchymatous	Present	Present	Absent	Present	Parenchymatous	One- layered	Hairs	Multi-parted	Essentially sclerenchymatous
<i>Cyathodendron texanum</i>	Eocene/USA	Erect	Solenostele	?	?	Present	Absent	Present	?	?	Multicellular hairs	Multi-parted, not arranged in omega- shaped structure	?
<i>Dendropteridium cyatheoides</i>	Neogene/ Kenya	Erect	Dictyostele	?	?	Present	Present	Present	?	?	?	Multi-parted	?
<i>Nishidacaulis burgii</i>	Early Cretaceous/ USA	Erect	Solenostele	Parenchymatous	Absent	Absent	Absent	Absent	Parenchymatous	One- layered	Multicellular hairs	Single, modified omega-shaped	Inner parenchymatous, outer sclerenchymatous
<i>Oguracaulis banksii</i>	Mid- Mesozoic/ Tasmania	Erect	Dictyostele	Mainly sclerenchymatous	Absent	Present	Absent	Present	Thick-walled parenchyma	One- layered	Multicellular hairs	Single, modified omega-shaped	Inner sclerenchymatous, outer parenchymatous
<i>Paracyathocaulis ogurae</i>	Turonian– Coniacian/ Japan	Erect	Dictyostele	Parenchymatous	Present	Present	Absent?	Present	Parenchymatous	Two- layered	Multicellular hairs	Multi-parted, modified omega- shaped	Inner sclerenchymatous, outer parenchymatous
<i>Rickwoodopteris hirsuta</i>	Late Campanian/ USA	Erect	Dictyostele	Inner sclerenchymatous, outer parenchymatous	Absent	Absent	Absent	Present	Parenchymatous	One- layered	Uni-and multiseriate trichomes	6- to 10-Parted	Sclerenchymatous?

(continued on next page)

Table 2 (continued)

Taxon	Age/ location	Habit	Stele	Pith	Mucilage cells in ground tissue	Medullary bundles	Cortical bundles	Sclerenchyma sheath surrounding cauline meristemes	Cortex (excluding hypodermis)	Hypodermis	Indument	Petiole base vasculature	Adventitious roots cortex
<i>Yavanna chimaerica</i>	Aptian/ Antarctica	Erect	Solenostele	Parenchymatous	Present	Present	Absent	Present	Parenchymatous	One- layered?	Multicellular hairs?	Single (proximally), three parted (distally), modified omega-shaped	Inner parenchymatous, outer sclerenchymatous
<i>Natalipteris wildei</i>	Albian- Turonian?/ South Africa	Erect	Solenostele	Parenchymatous	Present	Absent	Absent	Absent	Parenchymatous	One- layered	Multicellular hairs	Single, modified omega-shaped	Inner sclerenchymatous, outer parenchymatous
<i>Kwazulupteris schaarschmidtii</i>	Albian- Turonian?/ South Africa	Erect	Dictyostele	Parenchymatous	Absent	Absent	Absent	Present	Parenchymatous	One- layered?	Multicellular hairs	3-Parted, modified omega-shaped	Inner sclerenchymatous, outer parenchymatous

parenchymatous cortex, and thus may be referred to the “core tree ferns”.

Comparisons with fossil Cyatheales: Natalipteris wildei can be separated from fossil taxa referable to the Cyatheaceae (*Alsophilacaulis* Menéndez, 1961, *Dendropteridium* Bancroft, 1932, *Cyathocaulis* Ogura emend. Nishida, 1989, *Cibotiocaulis* Ogura emend. Nishida, 1989, and *Paracyathocaulis* Nishida, 1989) by the presence of dictyostelic stems with sclerenchyma sheaths surrounding cauline meristemes, and petiole bases with multi-parted vasculature in the latter taxa. A stem with accessory medullary bundles, and multi-parted vascular strands in the petiole bases, are also recorded in *Cyathodendron texanum* Arnold, 1945 (Table 2).

Some fossil species included in the genus *Cibotium* (*C. iwatanse* Ogura, 1933 and *C. oregonense* Barrington, 1983) have petiole bases with multi-parted vascular strands, contrasting with *Natalipteris*. In addition, *Cibotium oregonense* and *Cibotium tasmanense* Gould, 1972 lack mucilage cells in ground tissues, whereas these structures are present in *Natalipteris* (Table 2).

The Antarctic *Alienopteris livingstonensis* Vera, 2009 has Y-shaped cauline meristemes, surrounded by sclerenchyma sheaths. In addition, petiole bases have nine meristemes, the features absent in *Natalipteris*. Another species from Antarctica, *Yavanna chimaerica* Vera, 2013, also has sclerenchyma sheaths in its cauline meristemes. Furthermore, this taxon has medullary bundles, absent in the new species (Table 2).

Oguracaulis banksii (Tidwell et al., 1989) and *Rickwoodopteris hirsuta* Stockey et Rothwell 2004 share the presence of abundant sclerenchymatous tissue in the pith, absent in *Natalipteris*. The former species also have sclerenchyma sheaths surrounding cauline vascular strands, not observed in the new species. In addition, *Rickwoodopteris hirsuta* possess six to ten meristemes in the petiole bases (Table 2).

Conantiopteris schuchmanii Lantz, Rothwell et Stockey 1999 is dictyostelic, and possess cauline sclerenchyma sheaths, absent in *Natalipteris*. Petioles of this taxon have three-parted vasculature, contrasting with the undivided vasculature observed in the new species (Table 2).

Natalipteris wildei and *Nishidacaulis burgii* Tidwell et Nishida, 1993 share the presence of a solenostelic stem without sclerenchymatous sheath surrounding the vascular trace, and an undivided vascular trace of the petiole (Table 2). However, *Natalipteris* can be separated from *N. burgii* by the presence of mucilage cells and sclerotic nests in the ground tissue, and petiole bases with deeper lateral folds and a smaller abaxial arc.

Lophosporiorhachis Nishida, 1982, a genus erected for isolated rachides, has shallow lateral grooves in the petioles, which are located in the middle region of the vascular strand (Nishida, 1982), whereas in *Natalipteris* the lateral grooves are deeper, and located in the abaxial region of the strand. Another genus of isolated rachides, *Thyrsopterorachis* Nishida et Nishida 1979 possess deeper and abaxially oriented lateral grooves, as well as a proportionally larger abaxial arc (Nishida and Nishida, 1979).

In summary, the combination of features observed in *Natalipteris wildei* are not present in any of the already described fossil cyathealean stems, supporting its recognition as a new taxon.

Kwazulupteris Vera et R. Herbst gen. nov. (Figs. 4, 5, 6B and D)

Etymology: From Kwazulu, “the land of the Zulu”, and *pteris*, fern.

Referred species: Type species only.

Diagnosis: Same as for species, by monotypy.

Type species: *Kwazulupteris schaarschmidtii* Vera et R. Herbst sp. nov.

Kwazulupteris schaarschmidtii Vera et Herbst sp. nov.

Etymology: Dedicated to the late Dr. Friedemann Schaarschmidt a well-known German paleobotanist.

Type locality: “Hluhluwe District, Natal, South Africa” (from accompanying labels).

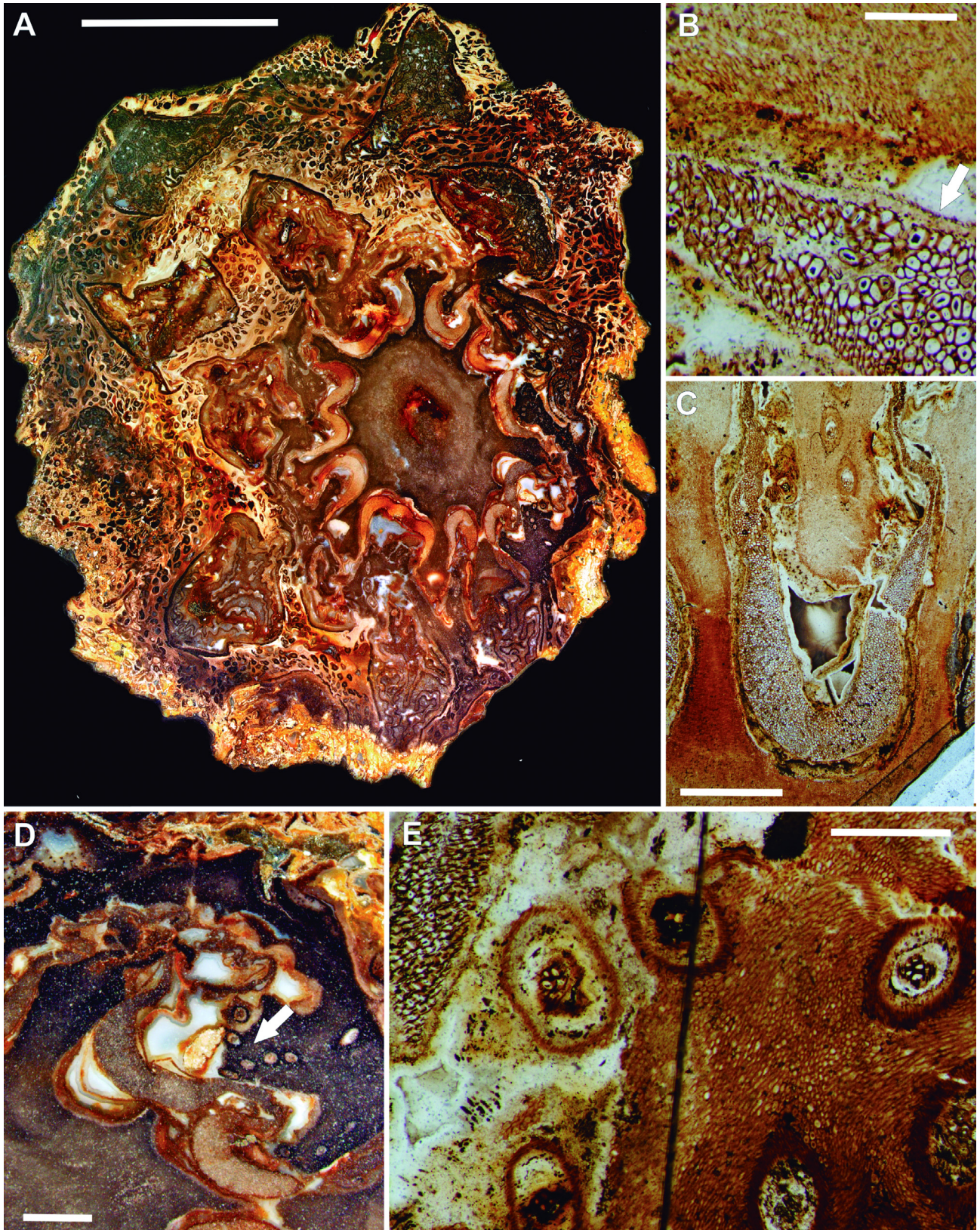


Fig. 4. Anatomy of *Kwazulopteris schaarschmidtii* gen. et sp. nov., SM.B 20628. (A) general view of the stem with attached petiole bases and adventitious roots; (B) detail of a cauline meristele, showing xylem and probable limit of the endodermis (arrow); external side up; (C) U-shaped meristele; external side up; (D) cauline cylinder, showing separating root traces (arrows); external side up and (E) root traces; external side right. Scale bar represents 3 cm in A, 3 mm in C and D, 1 mm in E and 50 μ m in B.

Stratigraphic horizon: Most probably, Mzinene Formation (Albian–Turonian).

Holotype: SM.B 20628, consisting of a stem fragment and a microscopic slide.

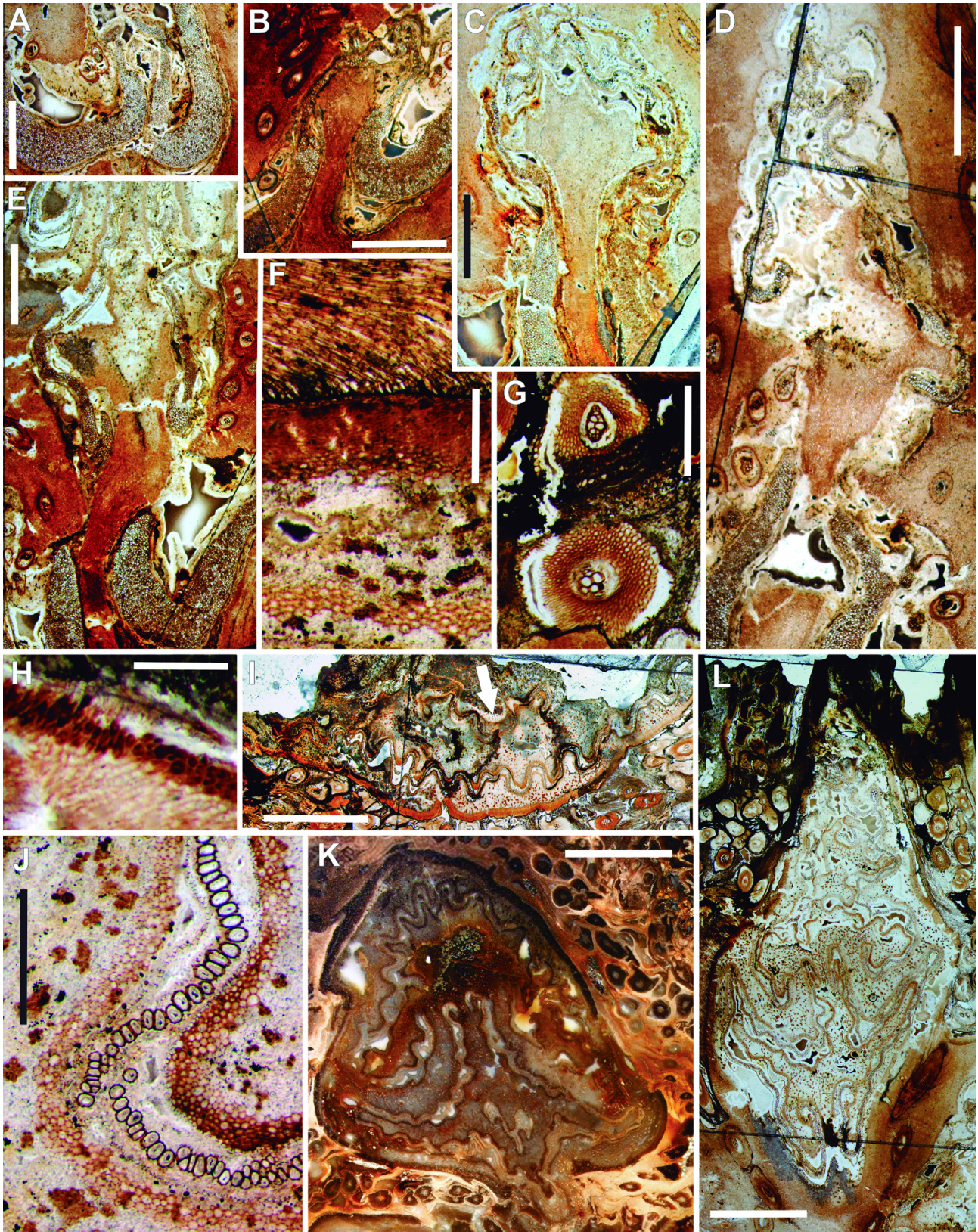


Fig. 5. Anatomy of *Kwazulupteris schaarschmidtii* gen. et sp. nov., SM.B 20628. (A–E) successive series showing leaf trace departure; external side up; (F) hypodermis and indument of trichomes; abaxial side up; (G) adventitious roots; (H) detail of the hypodermis, showing “two layers” of the hypodermal tissue; external side up; (I) partially preserved petiole base, showing central meristele resulting from the fusion of the median pair (arrow); external side up; (J) detail of the petiole vascular strand; external side up; (K) petiole base, showing central meristele and fused adaxial arcs; abaxial side up and (L) petiole base showing three parted leaf trace, with independent adaxial arcs; abaxial side up. Scale bar represents 5 mm in K, 3 mm in A, B, C, D, E, I and L, 1 mm in G, and 500 μ m in F, H and J.

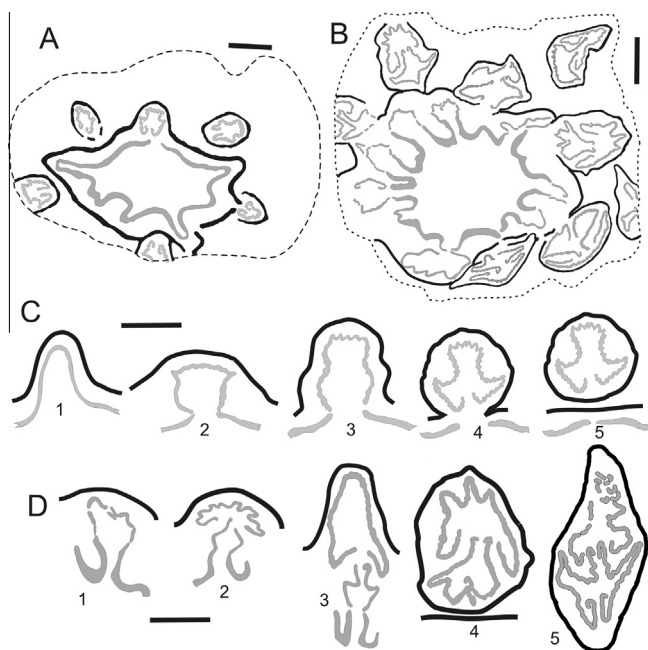


Fig. 6. (A) Sketch of *Natalipteris wildei* gen. et sp. nov. in transverse section; (B) sketch of *Kwazuluopteris schaarschmidtii* gen. et sp. nov. in transverse section; (C) departure of the leaf trace of *Natalipteris wildei* and (D) departure of the leaf trace of *Kwazuluopteris schaarschmidtii*. Scale bars represent 1 cm. Vascular strands shown in grey.

Diagnosis: Fossil tree fern stem with attached petiole bases and adventitious roots. Multicellular hairs on stem surface. Stem dictyostelic, meristemes U or W shaped, surrounded by sclerenchyma sheath; pith parenchymatous; medullary bundles absent; inner cortex composed of thick walled parenchyma cells and outer cortex with thin walled parenchyma, surrounded by sclerenchymatous hypodermis and epidermis. Mucilage cells and sclerotic nests absent. Petiole bases circular to oval; vascular strand a modified omega shape, presenting a wavy morphology due to repetition of U or V-shaped units. Adventitious roots diarch, inner cortex sclerenchymatous, outer cortex parenchymatous.

Description: The specimen is 8.5–11 cm wide, and contains a stem (5–6 cm in diameter) surrounded by a mantle of persistent petiole bases and adventitious roots (Figs. 4A and 6B).

Internally, the stem consists of a pith 20–23 mm in diameter, which is surrounded by 9–10 U or W shaped meristemes, presenting its ends pointing centrifugally. Surrounding the stele is a narrow (2–20 mm) cortex, which is completely enclosed by the hypodermis and the epidermis (Fig. 4A, C and D).

The pith is composed of parenchyma cells. In the central region of the pith, parenchyma cells are thin-walled, 20–53 μm in diameter. Toward the periphery of the pith, parenchyma cells gradually become thick walled, with walls 3.5–7.2 μm thick, while retaining the same size. Neither of mucilage secretory cells, sclerotic nests nor medullary bundles were identified in the specimen.

The stem has a typical dictyostele. The meristeme is thickest at its middle portion (c. 2.2 mm thick), and gradually becomes thinner toward both margins. Each meristeme is composed of several tissue types. It consists of central primary xylem (with tracheids 38–136 μm in diameter, with walls 5.1–9.5 μm thick), containing small interspersed xylem parenchyma cells, and probably of external phloem and pericycle, which are not preserved. Endodermal cells are almost entirely unpreserved, being only represented by remains of the Casparian strips thickenings. Externally, a region devoid of preserved cells surrounds the meristeme. This region is here interpreted as the sclerenchyma sheath, due to its wavy contour, parallel to the contour of the vascular bundles (Fig. 4B and C).

Stem cortex consists of different layers of tissue. The most internal zone is parenchymatous, and presents the same histological characteristics as the pith, with thick-walled cells in the inner cortex near the cauline vascular strands, and near the external region of the stem, and thin-walled cells in the outer cortex. This cortex is sheathed by the sclerenchymatous hypodermis, which in some regions of the stem appear as a layer of several cells in thickness, whereas in other regions it seems to be more “diffuse”, or not clearly differentiated from the cortical cells. Since the hypodermis is generally present in cyathealean ferns, and taking into account that petiole bases have a well-developed hypodermis, we believe that the absence of a differentiated hypodermis in some regions of the stem may be a preservation artifact, not reflecting the features of the original plant. Externally, an indument of multicellular trichomes emerges from a narrow epidermis (Fig. 5F).

Numerous root traces diverge from the cauline cylinder (Fig. 4D and E), and then traverse the stem until they vascularize the adventitious roots. Root traces are diarch, and at the moment of divergence they are sheathed by a layer of sclerenchyma cells, different from surrounding thick walled cells of the cortex (Fig. 4D).

Leaf trace formation initiates with an outward expansion of the vascular strand, where the xylem becomes thinner than in the adjacent sectors of the stem stele. Distally, the strand expansion continues, with its margin starting to undulate. Subsequently, two lateral constrictions appear in the structure. At this point, the leaf trace (which will finally become the abaxial arc of the petiole base) separates from the cauline stele. The free ends of the adjacent meristemes of the stem continue to elongate, generating a pair of symmetrical meristemes composing the adaxial pair, leaving a leaf gap. Finally, the ends of the adaxial pair curve inwards, resulting in a three-parted leaf trace entering the petiole base (Figs. 5A–E and 6D).

Petioles are circular to oval in cross section at the base, ranging from 11 to 25 mm in diameter (Fig. 5K and L). They contain three narrow (1–2 tracheids thick) vascular strands, arranged in a modified omega shape (Fig. 5K–M). Along all the length of the meristeme, the vascular strand presents a wavy morphology, appearing with a typical corrugated aspect due to repetition of U or V-shaped units, as well as some more irregular units. Both adaxial series fuse at the point where the adaxial arc contacts the median pair, resulting in a single adaxial arc, which connects both adaxial corners (Fig. 5K). The remains of the median pair appear as an isolated unit in the pith of the petiole base, between the superior series of the lateral folds and the adaxial arc (Fig. 5I and K). Lateral folds are well developed and abaxially oriented in the petiole vasculature, with the superior series of the lateral fold approximately two times longer than the inferior series of the lateral fold.

Tissues immediately adjacent to the petiole xylem are unpreserved. As in the stem vasculature, the position of the endodermis can be inferred by the presence of thickenings of the Casparian strips (Fig. 5K). Each meristeme is surrounded by the sclerenchyma sheath. Cortex of the petiole bases is composed of thin-walled parenchyma cells, with abundant interspersed sclerotic nests (Fig. 5J). Externally, petiole bases are enclosed by the hypodermis, composed of two different tissues. The most internal region of the hypodermis is composed of thick walled cells, similar to the ones present in the sheath surrounding the vascular strands. These cells form a thick layer, which in some places appear to be composed of two different layers (Fig. 5H), though we interpret this as preservational artifact. Externally, a narrow epidermis surrounds the petiole bases, and supports trichomes.

Adventitious roots are circular to oval in outline, and are generally present running parallel along the longitudinal axis of the stem, forming a dense indument. Internally, roots are diarch, with a central xylem region surrounded by phloem, pericycle and endodermis. Externally, the most internal cortical region is thick and

sclerenchymatous, with cells 31–53 µm in diameter, but becomes gradually parenchymatous, with cells (30–64 µm in diameter). External to the cortex is a one layered epidermis (Fig. 5G).

Comparisons with extant taxa and affinities: The dictyostelic stem with cauline meristeles surrounded by sclerenchyma sheaths, the mantle of adventitious roots and petiole bases surrounding the stem, and the petiole bases with wavy contour are characters that link *Kwazuluperis schaarschmidtii* with the tree ferns of the Order Cyatheaes.

Thyrsopteridaceae possess solenostelic stems with medullary bundles, and lacks sclerenchyma sheaths surrounding cauline meristeles, which are different from *Kwazuluperis* (Table 1).

Loxomataceae differ from *Kwazuluperis* in having solenostelic stems with ground tissues consisting mostly of sclerenchyma. Petiole bases of this family are vascularized by a single strand, whereas *Kwazuluperis* has a three-parted leaf trace is observed (Table 1).

Culcitaceae are distinct from *Kwazuluperis* in many characters. Petioles of *Culcita* have a single vascular strand with its adaxial margins pointing outwards, different from *Kwazuluperis*. Stems of the living genus are solenostelic and lack sclerenchyma sheaths surrounding cauline vasculature, as opposed to *Kwazuluperis* (Table 1).

Plagiogyriaceae have pith with a big mass of sclerenchyma in the central region, absent in *Kwazuluperis*. Stems of *Plagiogyria* lack indument, present as multicellular hairs in the new species. Furthermore, petiolar vascular strand in *Plagiogyria* is U or V-shaped, contrasting with the modified omega-shaped one in *Kwazuluperis* (Table 1).

Species of the Cibotiaceae have stems without sclerenchyma sheaths surrounding cauline vascular strands, and have multi-parted vasculature in their petiole bases, being in these features different from *Kwazuluperis* (Table 1).

Ferns included in the Cyatheaes have highly dissected vascular strands in the petiole bases, contrasting with the three-parted strand of *Kwazuluperis*. Furthermore, all cyatheaes have medullary bundles, not observed in the new species (Table 1).

Among Dicksoniaceae, *Calochlaena* can be separated from *Kwazuluperis* by having creeping solenostelic stems without sclerenchyma sheaths, and petiole bases with single vascular strands, morphologically different from the structure observed in *Kwazuluperis*. *Dicksonia* and *Lophosoria* share many anatomical features with *Kwazuluperis*, such as the three part modified-omega shaped vascular strand in the petiole bases. *Dicksonia* has a small, flat abaxial arc of the petiole stele (Nishida, 1984) contrasting with the long abaxial arc observed in the new taxon (Figs. 5K, L and 6D). *Lophosoria* has solenostelic stems, different from the dictyostelic cauline stems of *Kwazuluperis*. Mucilage cells, present in *Lophosoria* and *Dicksonia*, are absent in the new species (Table 1).

Metaxyaceae differ from *Kwazuluperis* in having creeping solenostelic stems, which lack sclerenchyma sheaths surrounding cauline meristeles, and an undivided meristele in their petiole bases (Table 1).

Kwazuluperis schaarschmidtii cannot be referred to any family among Cyatheaes, since it presents a combination of characters (Table 1). As discussed above, the presence of adventitious roots with inner sclerenchymatous and outer parenchymatous cortices may suggest that *Kwazuluperis* is a representative of the “core tree ferns” clade (Korall et al., 2006), suggesting that it is more closely related to Cyatheaes, Cibotiaceae, Dicksoniaceae and Metaxyaceae, than with the rest of the Cyatheaes.

Comparisons with fossil Cyatheaes: *Kwazuluperis schaarschmidtii* can be separated from fossil taxa referable to the Cyatheaes (*Alsophilocalis* Menéndez, *Dendropteridium* Bancroft, *Cyathocalis* Ogura emend. H. Nishida, *Cibotiocalis* Ogura emend. H. Nishida, and *Paracyathocalis* H. Nishida), and from *Cyathodendron texanum*

Arnold by the absence of medullary bundles in the new taxa, and by having a three-parted petiolar vascular trace (Table 2).

Fossil *Cibotium* species lack sclerenchyma sheaths surrounding cauline meristeles, contrasting with *Kwazuluperis*. *Cibotium iwataense* Ogura and *C. tasmanense* Gould are solenostelic, whereas the new taxon is dictyostelic. Further differences can be observed in their petiole bases. *C. iwataense* and *C. oregonense* Barrington have multi-parted vascular strands, and *C. tasmanense* Gould has an undivided strand, in contrast to the three meristeles of *Kwazuluperis* (Table 2).

Yavanna chimaerica Vera is solenostelic, and has medullary bundles in its pith, different from the dictyostele without accessory bundles seen in *Kwazuluperis* (Table 2). Another solenostelic stem, *Nishidacaulis burgii* Tidwell et H. Nishida, lacks sclerenchyma sheaths surrounding cauline meristeles, and has an undivided petiolar vascular strand, differing from *Kwazuluperis* (Table 2).

Rickwoodopteris hirsuta Stockey et Rothwell and *Alienopteris livingstonensis* Vera have a central mass of sclerenchyma in the pith, and the petiole bases with more than three vascular strands, contrasting with the features in *Kwazuluperis* (Table 2). *Oguracaulis banksii* Tidwell, H. Nishida et Webster has abundant sclerenchyma in the pith, and also differs from the new taxon in having an undivided vascular strand in the petiole bases (Table 2).

Conantiopteris schuchmanii Lantz, Rothwell et Stockey shares many features with *Kwazuluperis* (Table 2). However, a detailed comparison reveal that the cauline stele differs in both taxa. *Kwazuluperis* has many leaf gaps in cross section, resulting in many U-shaped meristeles. Contrasting, leaf gaps are proportionally less abundant in *Conantiopteris*, resulting in less curved meristeles (Lantz et al., 1999). Furthermore, the latter taxon has mucilage cells distributed in its ground tissue, whereas *Kwazuluperis* lacks these structures.

The vascular system of *Lophosoriorhachis* H. Nishida and *Thyrsopterorachis* H. Nishida et M. Nishida is somewhat similar to the one present in *Kwazuluperis*. However, the adaxial series in these taxa never fuse to produce a pith meristele, as seen in the new species (Nishida and Nishida, 1979; Nishida, 1982).

In summary, the combination of features observed in *Kwazuluperis schaarschmidtii* are not present in any of the already described fossil cyathealean stems, supporting its recognition as a new taxon.

4. Conclusions

Two new representatives of the fern Order Cyatheaes are described from the Cretaceous of South Africa, probably recovered from the Mzinene Formation (Aptian–Turonian).

Natalipteris wildei gen. et sp. nov. has a solenostelic stem without medullary bundles and sclerenchyma sheath surrounding cauline meristeles, mucilage cells randomly distributed in the ground tissue, and petiole bases with a single meristele with a wavy contour, arranged in a modified omega-shape.

Kwazuluperis schaarschmidtii gen. et sp. nov. is a dictyostelic fern, with cauline meristeles surrounded by sclerenchyma sheaths, and with three parted vascular strands in its petiole bases, having a modified omega-shaped morphology. Distally, adaxial arcs fuse resulting a single adaxial arc, a single abaxial arc and the remains of the median pair as a single meristele in the petiolar pith.

The combination of characters observed in both taxa are absent in either extant or extinct species of the recognized families among the Mesozoic cyathealeans with unclear affinities, including other taxa already reported (see Lantz et al., 1999; Stockey and Rothwell, 2004; Vera, 2009, 2013).

As suggested by Korall et al. (2006), the presence of adventitious roots with inner sclerenchymatous cortex and outer paren-

chymatous cortex support the placement of *Natalipteris* and *Kwazuluopteris* in the “core tree ferns” clade, suggesting they are more closely related with the Cyatheaceae, Dicksoniaceae, Cibotiaceae and Metaxyaceae, than with the rest of the Cyatheales.

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