EXPLORING BIODIVERSITY PATTERNS AMONG SOUTHERN GONDWANA'S PRIMEVAL FORESTS:

TAXONOMY OF LYCOPOD AND PROGYMNOSPERM FOSSILS FROM THE UPPER DEVONIAN WITPOORT FORMATION (WITTEBERG GROUP, SOUTH AFRICA)

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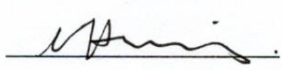
A dissertation submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Master of Science.

Johannesburg, 2020

DECLARATION

I, Christopher Harris, declare that this dissertation is my own work. It is being submitted for the degree of Master of Science at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other university.



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On this 29th day of June 2020.

ABSTRACT

Famennian-aged fossil localities Waterloo Farm and Coombs Hill from the Witpoort Formation (Witteberg Group, Eastern Cape, South Africa) provide unprecedentedly complete Late Devonian plant remains from southern Gondwana, evidencing rich and diverse floras in a high palaeo-latitude setting. These localities present the earliest evidence of high latitude trees. Occurrence of one or more rhizomorphic lycopods together with *Archaeopteris* at the two Witpoort Formation localities suggests an ecological association like that observed across much of Laurussia during the Famennian. With description of four new lycopod species it is shown that of three lycopod species identified at each locality, none occur at both. The only species currently recognised at both localities is *Archaeopteris notosaria*. New lycopod species include the youngest records of *Colpodexylon* Banks, a fertile archaeosigillariid (suggesting inclusion of the family in Protolepidodendrales) and a likely heterosporous form. It is here proposed that protolepidodendralean lycopods persisted at high-latitudes until at least the Upper Famennian (late, Late Devonian), whilst in the tropics its members were replaced by advanced, opportunistic or pioneering taxa around the Middle-Late Devonian boundary. New Coombs Hill derived specimens of *Archaeopteris notosaria* (originally described from Waterloo Farm), allow diagnosis of additional vegetative and fertile characters for the species, permitting re-interpretation of the holotype, as well as detailed comparisons with worldwide records of the genus.

ACKNOWLEDGEMENTS

I give thanks to the following people for the valuable assistance they have provided, without which the project would not have been possible. My parents, Collin and Sandra Harris provided a decent home and an education. My brother, Geoff inspires me to share what has been unearthed. Dr. Marine Wojcieszak has been a constant source of partnership, support and advice on all aspects of life and work over the past few years. The project was conceptualized by Dr. Robert Gess, whose passion and insights on Devonian life are alchemic. Both he and Prof. Marion Bamford kept a diligent eye on the work that was done, ensuring that the project met its aims. The examiners of this dissertation, Prof. Patricia Gensel and Dr. Anne-Laure Decombeix provided numerous useful suggestions which have improved the work. Prof. Bruce Rubidge has been a mentor throughout my postgraduate studies. Dr. Cyrille Prestianni is thanked for useful discussions about the fossils and preparation techniques, and for reading early drafts of the fossil descriptions presented in Chapters 4 and 6. Dr. Christopher Berry critically read a draft of the results presented in Chapter 4, and provided information about the ages and taxonomy of known species of *Colpodexylon*, and an introduction to Dr. Charles Ver Straeten, who gave most up-to-date stratigraphic information on occurrences of *Colpodexylon* in New York State. Dr. Rose Prevec provided access to historical fossil material in the collections at Albany Museum Earth Science Department and the use of facilities. Mr. Gerry Germishuizen manufactured specialized tools for the preparation of fossils. Ms. Prosper Bande assisted with rock maceration and preparation of slides in the fruitless quest for Coombs Hill palynomorphs. Dr. Kudakashwe Jakata assisted with use of the SEM, and Prof. Marion Bamford funded my use of the machine. Mrs. Tandi Scott-Turner is thanked for the gift of a light table. Mr. Viktor Rademacher advised me about graphics programs and art materials. The cooperation and generous assistance of the South African National Roads Agency Limited (SANRAL) in acquiring the fossils for this study is acknowledged. Mr. Steve Beckerling of Bosch Stemele played an important role in facilitating fieldwork on the road construction site. The sponsorship of the DSI-NRF Centre of Excellence in Palaeosciences and the Palaeontological Scientific Trust during this project is gratefully acknowledged. Funding received from the Millennium Trust whilst employed at the Albany Museum is also acknowledged with gratitude.

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GLOSSARY*

Endocortical cast – Some Devonian lycopod axes comprised a cylinder of tough outer cortex, with a less resistant inner cortex which when subject to rapid decay was replaced by sediment. This internal rod of matrix is the endocortical cast, representing a cast of the inside of the outer cortex (Chaloner *et al.* 1980).

False leaf scar – A cross section of a persistent fossil lycopod leaf intersected by parting of rock matrix, distinguished from a leaf scar which occurs after abscission of the leaf (Thomas and Meyen, 1984).

Lateral branch system – Short lived leafy appendages of *Archaeopteris*, comprising a penultimate axis producing numerous ultimate axes and vegetative and fertile leaves (Beck, 1971; Scheckler 1986; Fairon-Demaret *et al*., 2001). Also referred to as 'unit-branch systems' (Phillips *et al*., 1972).

Leaf base – "A 'catch-all' term to include any structure associated with the interface between leaf and axis" (Berry and Edwards, 1995, p. 62), marking the point of attachment of the leaf, particularly regarding fossil lycopod stems.

Leaf base sediment body – A sediment filled cavity in the swollen leaf base of archaeosigillariid lycopods, suggested by Berry and Edwards (1997) to represent originally parenchymatous tissue which after decay was filled by sediment entering from the inside of the stem via a channel associated with the leaf trace.

Leaf cushion – A widened, swollen structure at the base of a leaf, which remains on the axis after abscission of the leaf (Thomas and Meyen, 1984).

Monophyletic – A group that includes a common ancestor and all of its descendants, otherwise known as a clade. Compare with paraphyletic.

Orthostichy – A longitudinal row of leaves, after Thomas and Meyen (1984) and Taylor *et al.* (2009).

Paraphyletic – A group that includes a common ancestor and some (but not all) of its descendants. Compare with monophyletic.

Parastichy – A secondary helix in leaf arrangement, in lycopods usually roughly diagonal to the long axis of the stem (Thomas and Meyen, 1984; Taylor *et al*., 2009)

Phyllotaxis – Arrangement of leaves on an axis.

Prophyll – A modified leaf at the base of a shoot. Scheckler (1978) used the term to describe the paired modified leaves at the base of a **lateral branch system** in *Archaeopteris*, which had previously been referred to as ‘stipules’ by Beck (1960).

Pseudowhorl – A single turn about the axis of leaves that are inserted in a tight helix, which, when observed on one side of an axis, appear to be whorled. The term was used by Banks (1944) in describing leaf base arrangement on lycopod axes (See figure 5.2).

Sister taxa– Refers to two taxonomic groups that are the most closely related amongst all known groups of the same taxonomic level.

Strobilus (pl. strobili) – A reproductive cone consisting of modified leaves borne on an axis (Taylor *et al*., 2009), on lycopods characterized by a compact arrangement of sporophylls with modified, enlarged bases, occupying a terminal position on the axis (Berry *et al*., 2003).

*The first in text use of terms defined in the glossary is shown in **bold**.

CHAPTER 1 – INTRODUCTION

The South African fossil record includes a wealth of material of various ages, the study of which has made significant contributions to evolutionary biology (Ardrey, 1961; Selden & Nudds, 2004; McCarthy & Rubidge, 2005). Study of biota from the Devonian Period in South Africa has, in the past, received less attention than coal basin floras, mammalian origins, and hominin evolution. Its main twentieth century contribution is recognition of the cold-water adapted marine invertebrate faunas of the Malvinokaffric realm (Boucot, 1975; Copper, 1986; Hiller, 1990; Penn-Clarke, Rubidge, & Jinnah, 2018). Until recently, Upper Devonian strata in the Cape Supergroup, with a paucity of marine invertebrate remains, were considered as having little palaeontological potential (Thamm & Johnson, 2006). Since the nineteen nineties, however, new discoveries of Upper Devonian marginal marine fossil deposits have provided a wealth of insights on the biota of Gondwana's southern shore (eg. Anderson *et al*. 1995, Gess *et al.* 2006, Gess 2013, Prestianni and Gess, 2014, Gess and Ahlberg 2018, Gess and Whitfield, 2020). This dissertation describes new plant taxa from a locality discovered in 2015, which adds considerably to the growing body of knowledge regarding high latitude floras.

The Waterloo Farm locality, discovered in 1985 to the south of Makhanda (then Grahamstown), is host to 23 new taxa, including plants, invertebrates and vertebrates, part of a diversity which continues to be unearthed and described. The locality provides various fossil evidence for Late Devonian terrestrialization, including remains of Africa's earliest known tetrapods (Gess & Ahlberg, 2018), leafy branches belonging to some of the oldest known trees south of the equator (Anderson, Hiller, & Gess, 1995), and the oldest known land animal from Gondwana (Gess, 2013).

Abundant Devonian plant fossils in South African museum collections derive from more than 150 years of collection in the Cape Fold Belt. However, as much of this material was described long before the 21st century, more in-depth investigation is required for integration with more recent taxonomic work abroad, as well as modern stratigraphic understandings. Devonian floras of South Africa have been the subject of two reviews in the last 50 years. Lycopod dominance was suggested by Dr. Edna Plumstead (1967), who performed the broadest detailed study of the South African Devonian floras to date. She described seven lycopod species, as well as 'psilophytes'

and enigmatic plants. Amendments to Plumstead's work, and further taxa were added by Drs. Heidi and John Anderson (1985). Some of the lycopods described in these reviews belong to genera now regarded as form taxa for lycopod stems without leaves (Berry & Edwards, 1997; Cingolani *et al.*, 2002). Few of the South African species are accepted, given subsequent international progress in Devonian plant taxonomy (see 2.4). Fertile organs are crucial to palaeobotanical classification (Taylor *et al*., 2009), and by the mid-nineteen eighties, only three species exhibiting fertile structures, all ascribed to primitive 'psilophytes' were known from South African Devonian strata. This has contributed to the impression that 'the Devonian macroflora of Gondwana is meagre' (Xu and Berry, 2008, p.1). Cold climates at high-palaeolatitudes have been invoked in explaining the relative poverty of southern Gondwanan floras (Streel *et al.*, 2000).

Discovery in 2015 of a new locality at Coombs Hill, herein discussed, has revealed further fossiliferous shale lenses, providing a comparable flora to Waterloo Farm with important differences in composition. The present dissertation describes additional new lycopod taxa from Coombs Hill and Waterloo Farm, as well as far more completely preserved remains of *Archaeopteris notosaria* Anderson *et al*. 1995 than originally described from Waterloo Farm. As at Waterloo Farm, taxa described from Coombs Hill include specimens with associated leaves, fertile organs, and branching architecture. These allow more in-depth taxonomic study than was permitted by material available to researches prior to discovery of these localities. They contribute to emerging evidence for a rich and diverse high latitude Gondwanan flora from the Upper Devonian.

This study coincides with a growing interest in Late Devonian palaeoecology, particularly the effects of the spread of plants further into continental areas, facilitated in part by the separate innovations of arborescence and the seed habit. New discoveries of *in situ* forests in North America (Stein *et al.*, 2007, 2020), China (Wang *et al.*, 2019) and Svalbard (Berry & Marshall, 2015) are increasing awareness of their ecology, and indicating surprising complexity of ever older shaded landscapes by the Mid-Late Devonian. A global surge in vegetation changed erosional rates on land (Kenrick *et al.*, 2012), paved the way for vertebrate terrestrialization towards the end of the Period (Clack, 2012) and is considered to be the most likely trigger for the Late Devonian biotic crisis, one of the five most destructive extinction events in earth history (Algeo & Scheckler, 1998; Berner, 2001; Morris *et al.*, 2015; Stein *et al.*, 2020). Studies of the

palaeobotany of the Witpoort Formation have the potential to provide important insights into the earliest forested ecosystems known from cold-climatic regions, which will in turn contribute to a better understanding of Late Devonian palaeo-biogeography.

This dissertation comprises eight chapters, four of which present results gathered in the course of this study. Each 'results' chapter has its own brief introduction, and taxonomic discussion. At the end, a general discussion brings together the key points from each chapter, attempting to integrate their overall significance. Here, a brief description of the remaining chapters:

Chapter 2 presents a literature review, including a brief summary of developments in plant evolution, from the appearance of plants on land, to the global spread of forests. Classification of Devonian lycopods and progymnosperms, and their diversity, is reviewed. Consequences of the Devonian radiation of land plants for Earth systems are then considered.

In Chapter 3, 'Materials' provides an account of how the fossil specimens were collected, and details of their provenance. This includes a short summary of the geological and palaeoecological context of the Coombs Hill and Waterloo Farm localities. 'Methods' describes the techniques used to collect, catalogue, describe and illustrate the specimens.

Chapter 4 – 'Lycopods A + B', describes two new species attributed to the herbaceous lycopod genus, *Colpodexylon* Banks 1944, one of which derives from Coombs Hill, and the other from Waterloo Farm. Palaeogeographic implications of the occurrences are discussed.

Chapter 5 – 'Lycopod C', describes a new genus and species attributed to the problematic lycopod family Archaeosigillariaceae. Among the specimens included in the species, a fertile example sheds light on the ordinal position of this lycopod family. Comparison is made with the holotype of *Archaeosigillaria caespitosa* (Schwartz) Plumstead 1967.

Chapter 6 – 'Lycopod D', introduces a formerly undescribed, probably heterosporous lycopod genus and species. The possible affinities of this taxon amongst the arborescent lycopods, are discussed at length. Further description of a lycopod tree trunk from a

slightly higher stratigraphic horizon confirms that an arborescent lycopod was present at Coombs Hill.

Chapter 7 – Progymnosperm, *Archaeopteris notosaria* Anderson *et al.* 1995. Remains from Coombs Hill are here attributed to a species already described from Waterloo Farm, providing additional morphological information about its vegetative and fertile structures. This study enables more detailed comparison with other *Archaeopteris* species.

Chapter 8 comprises a general discussion, exploring the wider ramifications of new data presented in this study.

The conclusion reviews the contributions of this work and perspectives towards a better understanding of Devonian plant evolution.

CHAPTER 2 – LITERATURE REVIEW

Here, a brief overview of the origin of land plants is presented, followed by a summary of the current state of taxonomy of lycopods and progymnosperms, as well as their Gondwanan occurrences. The great impact of the Devonian plant radiation on Earth systems is then briefly explored.

2.1 The origin and radiation of land plants

The earliest convincing evidence for plants on land (embryophytes) is provided by spores, which have a high preservation potential and are widely distributed (Taylor, Taylor, & Krings, 2009). Plant spores appear in the Early to Mid-Ordovician in Gondwanan strata (Wellman, Osterloff, & Mohiuddin, 2003; Rubinstein *et al.*, 2010; Kenrick *et al.*, 2012). These earliest spore producing plants are thought to have been bryophytes, which have a low preservation potential and are only known from a few Palaeozoic 'body' fossils (Kenrick *et al.*, 2012). Analyses using the molecular clock, however, indicate that embryophytes may have originated as early as the Cambrian (Morris *et al.*, 2018).

Some palaeobotanists proposed that land plants spread in two distinct radiations, the first being the diversification of vascular plants in the Late Silurian and Early Devonian, and the second being the spread of arborescent and seed-bearing plants into upland areas in the Late Devonian (Berry & Fairon-Demaret, 2001). A continuous radiation of land plants during the Siluro-Devonian is an alternative hypothesis (Bateman *et al.*, 1998).

Early vascular plants (tracheophytes) were placed in three groups by H. P. Banks in 1968 on the basis of anatomical differences, which are named Rhyniopsida, Zosterophyllopsida and Trimerophyta (Berry & Fairon-Demaret, 2001). These three pioneering divisions of land plants are supported by phylogenetic analysis (Kenrick & Crane, 1997). Berry and Fairon-Demaret (2001) give a summary of their characters. Rhyniopsida are an extinct group of small, homosporous, primitively vascularized herbaceous plants which were probably restricted to moist environments. The Zosterophyllopsida are today represented by a few living genera of their descendants, the lycopods (Lycopsida). They are united in Division Lycophyta, which is the **sister group** to all other extant vascular plants (Kenrick & Crane, 1997). Lastly, the

trimerophytes are a **paraphyletic** group from which the ancestors of most land plants emerged (Kenrick & Crane, 1997). 'Trimerophytes' and their descendants; ferns, cladoxylopsids, iridopteridaleans, sphenophytes, stenokaleans and progymnosperms are united by primitive characters including dichotomous trusses with paired sporangia. Each group of trimerophyte descendants demonstrates a characteristic modification of this fertile structure bauplan. Together these groups comprise the clade Euphyllophyta. Fossil material since discovered, especially in the Early Devonian of China, includes numerous 'aberrant' taxa which do not conform to Banks' threefold classification, though the scheme remains relevant and widely in use (Berry & Fairon-Demaret, 2001).

2.2 Classification of Devonian Lycopsida (lycopods)

Recent reviews classify Lycopsida according to various schemes, and their ordinal classification is still a debated matter (Thomas & Brack-Hanes, 1984; DiMichele & Bateman, 1996; Kenrick & Crane, 1997; Berry & Fairon-Demaret, 2001; Gensel & Berry, 2001; Taylor *et al.*, 2009; Xue, 2011). Devonian studies have identified three lycopod Orders, the Drepanophycales, the Protolepidodendrales and the Isoëtales *sensu lato* (or rhizomorphic lycopods) (Table 2.1) (Berry & Fairon-Demaret, 2001; Gensel & Berry, 2001; Xue, 2011), each of which is supported by phylogenetic analysis (Kenrick & Crane, 1997; Xue, 2011). A fourth, extant Order Selaginellales, is considered by some to be basal amongst, and paraphyletic to, Isoëtales, but Devonian fossil evidence is tentative (Xue, 2011).

Table 2.2: Classification of Devonian Lycopsida (continued over page)

Order	Range	Sporangia adaxial on sporophyll?	Spore types	Secondary tissue?	Ligulate?
Drepanophycales Kenrick and Crane, 1997	Silurian (?) – Devonian	no	homosporous	No	No
Protolepidodendrales Pichi-Sermolli 1958	Devonian	yes	homosporous	No	No, except *Leclercqia*

Selaginellales Prantl 1874	Devonian (?) – recent	yes	heterosporous	No (?)	Yes
Isoëtales *s.l.* Meyen 1987	Devonian – recent	yes	heterosporous	Yes	Yes

Drepanophycales are pre-lycopods, having helically arranged spine-like microphylls (primitive leaves), but lacking the lycopod apomorphy of sporangia borne on the leaves (Gensel & Berry, 2001; Matsunaga & Tomescu, 2017). This group is considered as an evolutionary grade transitional between a zosterophyll-like ancestor and the true lycopods (Gensel and Berry, 2001).

The Protolepidodendrales were rhizomatous dichotomizing lycopods lacking secondary tissues, with persistent leaves arranged in low helices (or **pseudowhorls**) (Bonamo, Banks, & Grierson, 1988; Gensel & Berry, 2001). They grew as herbaceous mats in moist environments (Bonamo *et al.*, 1988). The order includes two or three families, the Protolepidodendraceae, the Haskinsiaceae and a 'satellite family' the Archaeosigillariaceae, which are distinguished on the basis of leaf morphology (Berry & Fairon-Demaret, 2001). A protolepidodendralean from China, *Minarodendron*, is considered to have been treelike in stature, indicating that arborescence was attained in this order by the Middle Devonian independently of the line that would give rise to the large Carboniferous tree-lycopods (Liu *et al.*, 2013). Protolepidodendrales were abundant and widespread in the Middle Devonian, and largely disappeared by the Late Devonian (Berry & Fairon-Demaret, 2001). Surprisingly, very little is known about their rooting structures, and fertile structures are only known from a few genera (Gensel & Berry, 2001).

Although heterosporous lycopods are considered to form a clade (Kenrick & Crane, 1997; Xue, 2011), there is currently a lot of ambiguity surrounding their higher-order classification in the Devonian. Heterosporous lycopods first appeared during the Middle Devonian, achieving a considerable diversity by the end of the Devonian Period (eg. Chitaley and Pigg, 1996; Cai and Chen, 1996; Wang and Berry, 2003; Meng *et al*., 2015; Gess and Prestianni, 2018). The early radiation of rhizomorphic, heterosporous lycopods, produced a variety of small to medium sized tree-like forms that are widespread in Mid to Upper Devonian strata (Cai & Chen, 1996; Schweitzer & Li,

1996; Berry & Fairon-Demaret, 2001; Wang *et al.*, 2003). Among them are the precursors of the giant tree lycopods that dominated vast peat swamps over much of Laurasia during the Carboniferous Period (Pigg, 2001; Taylor *et al.*, 2009). Phylogenetic analysis of Devonian lycopods has indicated that heterosporous lycopods are **monophyletic** (Xue, 2011) but their higher relationships remain largely unresolved. Many Devonian lycopods present similar shoot characters to the Isoëtales, but according to current classification systems, lack of preservation of rooting structures precludes confident assignment (Pigg, 2001). Isoëtales *sensu lato* was erected to include satellite taxa, which present features consistent with the Order, but lack understanding of the whole plants (Thomas & Brack-Hanes, 1984; DiMichele & Bateman, 1996). A few genera from the Upper Devonian of China (Xue, 2011), Australia (Evreïnoff *et al.*, 2017) and North America (Cressler & Pfefferkorn, 2005; Gensel & Pigg, 2010), have been included in Isoëtales *s.l.*. Many Devonian heterosporous genera are, however, placed in *incertae sedis*. Disparity of characters, and non-equivalence of preservation presents a major problem for suprageneric palaeobotanical classification. As a result, phylogenetic studies on heterosporous lycopods have focussed entirely on either Devonian or Carboniferous taxa (DiMichele & Bateman, 1996; Xue, 2011).

Isoëtales are characterized by a rhizomorphic rooting system, secondary growth, simple microphylls, modified sporophylls (fertile leaves) often bearing a ligule and having their fertile leaves arranged in compact cones (DiMichele & Bateman, 1996; Gensel & Berry, 2001; Xue, 2011; Meng *et al.*, 2016). The arborescent habit is a symplesiomorphy of the order, although some members, including the extant genus *Isoëtes*, have become pseudoherbaceous (DiMichele & Bateman, 1996). Derived members bear microspores and megaspores in separate cones (monosporangiate **strobili**) (DiMichele & Bateman, 1996).

The origins of this order are still speculative and remain enigmatic. The search for early isoëtaleans has largely been centred on finding early stigmarian rooting systems, however, evidence in the Devonian is sparse (Pigg, 2001). Recent work in China has identified stigmarian rooting systems in Upper Devonian (Famennian) strata, and this characteristic structure confirms that true isoëtaleans were present by this time (Berry, 2019; Wang *et al.*, 2019).

Recent work has shed much light on the taxonomy of lycopods. It is recognised that Protolepidodendrales cannot be distinguished on the basis of stem morphology and it was suggested that isolated stems of herbaceous lycopods lacking leaves or fertile structures should therefore be designated lycopod indeterminate (Bonamo *et al.*, 1988; Xu & Berry, 2008). Arborescent lycopods however, often have distinctive characters of the stem, including the structure of **leaf cushions** and leaf scars, which may allow generic diagnosis of isolated stems (eg. Wang Qi *et al*. 2003; Gensel and Pigg 2010; Prestianni and Gess 2014).

2.3 A review of Lycopsid diversity of Devonian Gondwana (outside of South Africa)

Despite being considered the dominant plant group of the Devonian (Bonamo *et al.*, 1988; Taylor *et al.*, 2009), the lycopods are represented by few valid taxa for the entire Gondwana. Lycopod stems are common in the fossil record, but their taxonomy is problematic. Recent revisions have abandoned earlier taxonomic work on lycopod stems lacking leaves or fertile material (Bonamo *et al.*, 1988; Gensel & Berry, 2001; Cingolani *et al.*, 2002; Evreïnoff *et al.*, 2017).

The oldest lycopod in the fossil record is the drepanophycale *Baragwanathia* Lang et Cookson 1935, from the Late Silurian/Lower Devonian of Australia. There is some debate surrounding the age of this occurrence, especially since this plant is significantly larger and more advanced than other plants of its reported age (Hueber, 1983; Gensel & Berry, 2001).

Plant remains from the Lower Devonian of Argentina include reported remains of *Baragwanthia*, various unidentified axes and abundant spores, suggesting a well vegetated south-western Gondwana at this early phase of land plant development (Edwards & Wellman, 2001).

Archaeosigillaria piconensis Kräusel et Dolianti 1957 was described from the Lower or Middle Devonian of Argentina, including a single isolated axis with hexagonal swollen **leaf bases** and persistent leaves. It was excluded from the genus by Berry and Edwards (1997).

Leafless axes from the Middle Devonian of Antarctica were attributed to *Haplostigma* (Schwartz) Seward 1932, *Archaeosigillaria* cf. *caespitosa* and *Malazania* Archangelsky, Ascuy et Wagner 1981 (McLoughlin & Long, 1994).

A genus of lycopod from the Middle Devonian of Argentina, identified with clear understanding of its leaf morphology, is *Haskinsia* Grierson et Banks 1983 (Cingolani *et al.*, 2002). This plant is a herbaceous protolepidodendralean with sagittate leaves (Bonamo *et al.*, 1988). Stems bearing characteristic leaves have also been found in lower palaeolatitudes of Gondwana including Venezuela, Morocco and Antarctica, and are additionally known from the Laurussian palaeo-regions of North America, Kazakhstan, China and Siberia (Cingolani *et al.*, 2002; Xu & Berry, 2008). The genus thus had an almost worldwide distribution in the Mid-Devonian, but it has never been reported from South Africa. The Argentinian occurrence represents the only known high latitude *Haskinsia* (Cingolani *et al.*, 2002).

Gondwanan subtropical Mid-Devonian deposits have also produced the widespread protolepidodendralean, *Leclercqia* Banks, Bonamo et Grierson (1972) emend. Bonamo, Banks et Grierson (1988), which occurs with *Haskinsia* (see above) in Morocco (Prestianni *et al.*, 2012). It has also been reported from the Middle Devonian of Australia and Venezuela and is widespread in Laurussia (Meyer-Berthaud *et al.*, 2003).

Floras from north-western South America, which include Middle/Upper Devonian aged remains of *Haskinsia, Colpodexylon* Banks 1944, *Gilboaphyton* Arnold emend. Berry et Edwards 1997 and *Leclercqia* from Venezuela, and Frasnian aged *Colpodexylon* from Columbia, show a strong taxonomic similarity to similar aged floras from New York State (Berry, Casas, & Moody, 1993; Berry *et al.*, 2000). It is uncertain whether the Venezuelan and Columbian deposits formed on Gondwana, or were later sutured onto the South American continent (Berry *et al.*, 2000).

An isolated, permineralized lycopod strobilus, *Cymatostrobus irvingii* Evreïnoff *et al.* 2017, from the Upper Devonian of Australia, was digitally scanned. This strobilus is bisporangiate, and was identified as a basal isoëtalean (Evreïnoff *et al.*, 2017). It was noted that lycopod diversity from the Devonian of Australia is poorly understood, since remains have been ascribed to a variety of genera which need reassessment. The arborescent lycopod *Leptophloeum* Dawson 1862 is also abundant in the Australian Upper Devonian (Evreïnoff *et al.*, 2017).

Aside from Australian and South American occurrences, reports of Gondwanan Upper Devonian lycopod remains are, to my knowledge, confined to South African strata. Their taxonomy, being highly relevant to this study, is explored in detail below.

2.4 A review of the historic classification of South African Devonian Lycopsida

Plumstead (1967) summarized the then known Devonian floras of South Africa. She reported dominance by lycopods, including the genera *Haplostigma* (Schwartz) Seward 1932, *Drepanophycus* Göppert (two species), *Protolepidodendron* Krejci 1880 (two species), *Archaeosigillaria* Kidston 1901 and *Leptophloeum.* Subsequent taxonomic work abroad has challenged or revised all but the last of these genera.

Drepanophycus schwartzi Plumstead derives from pinkish grey shales from the grounds of the Port Alfred mental hospital (Eastern Cape), attributed to the 'Upper Bokkeveld Series' (Plumstead, 1967), strata which have since been reassigned to the Lower Witteberg Group (Booth, Munro, & Shone, 1999; Johnson, Theron, & Loock, 2006). *D. kowiense* Plumstead occurs at a similar stratigraphic horizon also from the Kowie area near Port Alfred. The latter species was transferred to *'Haplostigma'* by Anderson and Anderson (1985). *Drepanophycus* Göppert is defined by spine-like microphyllous leaves, but lacks the leaf-sporangia association characteristic of Lycopsida (Gensel & Berry, 2001). The genus has been broken up on the basis of leaf morphology with redescription of specimens from New York (Bonamo *et al.*, 1988) and Antarctica (Xu & Berry, 2008) as *Haskinsia.* Lacking fertile material or clear leaf morphology, South African material assigned to *Drepanophycus* is equivocal.

The genus *'Haplostigma',* originally described on the basis of axes from the Devonian of South Africa, included a variety of unrelated lycopod axes (Seward, 1932). Some of the material was redescribed as *Palaeostigma sewardi* by Kräusel and Dolianti 1959. *Haplostigma irregulare* (Schwartz) Seward includes several specimens attributed by Plumstead (1967) to the 'Bokkeveld Series', including the holotype from a graphitic shale horizon on the farm Sweet Waters near Bathurst, now suggested to belong to the Witpoort Formation (R. W. Gess pers. comm. 2019). Numerous localities bearing *'Haplostigma'* are dispersed throughout the Cape Basin. With reassignment of the Upper Bokkeveld Series to the Witteberg Group, it is possible that a number of Plumstead's localities are stratigraphically higher than suggested, and may be Upper Devonian in age. *Haplostigma cf. irregulare* has however been reported from the Wupperthal Fm. (Givetian?) of the Bokkeveld Group (Penn-Clarke, Rubidge, & Jinnah, 2019). A paratype specimen of the genus from the Atherstone quarry in Port Alfred (V.236 of the Natural History Museum in London, Plumstead 1967, Plate XIII, Fig. 4),

was suggested to bear a strong resemblance to *Colpodexylon*, but definite identification was precluded by it having broken leaves (Cingolani *et al.*, 2002). '*Haplostigma'* has become a catch-all term for protolepidodendralean lycopod stems with helically arranged **false leaf scars**, and is not considered a natural taxon (Cingolani *et al.*, 2002).

Protolepidodondron eximum Frenguelli and *P. theroni* Plumstead include specimens from the Upper Witteberg shales near Vondeling (Western Cape). This rock unit is now known as the Lake Mentz Sub-Group (Johnson *et al.*, 2006), and is assigned a Lower Carboniferous age based on palynomorphs and fish remains (Streel & Theron, 1999). *Protolepidodendron* has also been subjected to international revision. It was restricted to the type specimen from Czechoslovakia, since its bifurcated leaves are considered unique, though further preparation of the holotype is required to exclude the possibility that this is an artefact (Bonamo *et al.*, 1988).

The holotype of *Archaeosigillaria caespitosa* (Schwartz) Plumstead derives from an imprecise stratigraphic horizon in the Witteberg Group in the Ceres district (Western Cape). Other specimens that Plumstead attributed to the species derive from Witteberg shales (Lower Witteberg Group?) near Steytlerville and in Port Alfred. One bifurcating specimen collected by J. N. Theron is reliably placed in the 'Main Witteberg Sandstone' (Witpoort Formation) (Plumstead 1967, Plate XI, Figs. 3–4). Anderson and Anderson (1985) added a variety of material to the species, extending its range into the Upper Witteberg Group. *Archaeosigillaria* was however, subsequently restricted to the type species from New York State (Berry & Edwards, 1997).

All South African specimens of *Leptophloeum (australe) rhombicum* Dawson are attributed to the Witteberg Group, and were suggested in the Grahamstown area to have been confined to the Witpoort Formation (Plumstead, 1967). This species is also reported from Witpoort Formation strata near Willowmore (Theron, 1960; Anderson & Anderson, 1985). A specimen from near Touws River has no precise locality info (Anderson & Anderson, 1985). Plumstead (1967) placed a Howieson's Poort specimen in the Lower Witteberg, along with the '*Dutoitia maraisia'* type locality which is now included in the Witpoort Formation (Hiller & Taylor, 1992). Rooting structures and axes of *Leptophloeum rhombicum* were described from Waterloo Farm (Prestianni & Gess, 2014). There is no convincing evidence that *L. rhombicum* occurs stratigraphically below or above the Witpoort Formation.

Zosterophyllum devriesii, Plumstead 1977 from the Bokkeveld Group in the Warmwatersberg area, was reassigned to *Archaeosigillaria*, based on very well preserved hexagonal leaf bases observed on the specimens (Chaloner *et al.*, 1980). Berry and Edwards (1997, p. 67), in a review of the genus, pointed out that there was 'no conclusive reason to ally these plants with the genus *Archaeosigillaria'*, suggesting that the material should rather be reassessed in light of new material illustrated by Anderson and Anderson (1985; their Plate 9, fig. 7b). Other Bokkeveld Group material was assigned to South American *A. piconensis* as comparison with the holotype of *A. caespitosa* was precluded by its poor state of preservation (suggested to be an **endocortical cast**) (Chaloner *et al.*, 1980). Anderson and Anderson (1985) retained *A. devriesii* and *A. caespitosa*, but considered the material previously assigned to *A. piconensis* to belong to *A. caespitosa*.

In their 1985 review of the Devonian floras of South Africa, Anderson and Anderson (1985) included the (previously) monospecific genus *Palaeostigma* Kräusel and Dolianti 1957 in the Lycophyta. They, added two additional species to the genus, including material that Plumstead (1967) had identified as 'psylophytalean axes'. Anderson and Anderson (1985) described a new lycopod genus and species, *Longicatrix bulbosa* Anderson et Anderson from stem casts from the Msikaba Formation of Port St. Johns (former Transkei, Eastern Cape). A further new genus and species *Howisonia rara* Anderson et Anderson was erected to include a single specimen from the Witpoort Formation at Howieson's Poort near Makhanda (then Grahamstown) bearing a superficial resemblance to a lycopod stem with microphylls attached - though it was not included in the Lycophyta.

Isolated spiny lycopod leaves from Waterloo Farm were illustrated by Gess and Hiller (1995a, Fig. 20. A-E), and these await description, but appear to represent the sporophylls of a heterosporous form (Gess & Prestianni, 2018). Axes identified with the form taxa '*Longicatrix'* and '*Haplostigma'* were also reported from Waterloo Farm (Gess & Hiller, 1995a).

Kowieria alveoformis Gess and Prestianni, 2018 was described from Waterloo Farm derived remains, including axes with attached vegetative and fertile, sporangia-bearing leaves. Fertile material was borne in a terminal strobilus, comprising both megaspores and microspores. On this basis the genus was identified with the heterosporous

Devonian lycopods, but showed both primitive (eg. bisporangiate strobili) and derived features (megaspore morphology) thereof (Gess & Prestianni, 2018).

2.5 Classification of Progymnospermopsida with emphasis on *Archaeopteris* (Dawson) Lesquereux 1880

Numerous studies on all aspects of *Archaeopteris* have made this one of the better understood Devonian plants. A seminal study by Beck (1960) established the connection between *Archaeopteris* vegetation and *Callixylon* wood. He erected the Progymnospermopsida to include plants with pteridophytic reproduction and gymnospermous vascular anatomy. This group includes the Aneurophytales and the Archaeopteridales (Hammond & Berry, 2005) and possibly the Protopityales (Beck, 1976; Taylor *et al.*, 2009). Archaeopteridales have been suggested as a likely precursor group to the seed plants, given that they share the synapomorphy of eustelar anatomy with seed plants (Phillips, Andrews, & Gensel, 1972; Scheckler, 1978; Meyer-Berthaud, Scheckler, & Wendt, 1999). Other phylogenetic analyses have, however, indicated aneurophytalean progymnosperms (Hilton & Bateman, 2006) or Stenokoleales (Toledo, Bippus, & Tomescu, 2018) as sister groups to the seed plants. Detailed studies on *Archaeopteris* vascular anatomy (Carluccio, Hueber, & Banks, 1966; Scheckler, 1978; Kenrick & Fairon-Demaret, 1991; Meyer-Berthaud *et al.*, 1999), root morphology (Stein *et al.*, 2020), leaf morphology (Andrews, Phillips, & Radforth, 1965; Kenrick & Fairon-Demaret, 1991; Fairon-Demaret & Leponce, 2001), and fertile organs (Phillips *et al.*, 1972; Fairon-Demaret, Leponce, & Streel, 2001) have greatly advanced our understanding of this plant. Its ecology has also been explored in some detail (Scheckler, 1986; Algeo & Scheckler, 1998; Fairon-Demaret *et al.*, 2001).

Archaeopteris nomenclature has undergone a complex history, reviewed by Fairon-Demaret *et al*. (2001). Dozens of species have been attributed to the genus, and currently eight species are recognized, following impressive synonymies, most notably by Kräusel and Weyland (1941). According to Phillips *et al*. (1972), the recognised species of *Archaeopteris* include *A. latifolia* Arnold, *A. hibernica* (Forbes) Stur, *A. halliana* (Göppert) Lesquereux, *A. fissilis* Schmalhausen, *A. macilenta* Lesquereux, *A. sphenophyllifolia* Lesquereux, and *A. obtusa* Lesquereux. *A. notosaria* has since been described from Waterloo Farm (Anderson *et al.*, 1995). Species delimitation amongst *Archaeopteris* species continues to be problematic, as not all specimens fit into the

above species (Phillips *et al.*, 1972). The spores of *Archaeopteris* have been of little use in distinguishing between species, as all known examples have very similar spores (Phillips *et al.*, 1972; Fairon-Demaret *et al.*, 2001). Fertile leaves (sporophylls) are of slightly better use, but are similar between species, and are variable within species. Sporophylls usually require the most delicate *dégagement* in order to elucidate their finer details (Phillips *et al.*, 1972; Fairon-Demaret *et al.*, 2001). *Archaeopteris'* sporangia are borne on the upper surface of the sporophylls in two rows (Fairon-Demaret et al. 2001, and refs. therein).

Species are usually separated on the basis of vegetative leaf morphology (Phillips *et al.*, 1972). *A. latifolia*, *A. hibernica* and *A. halliana* all have vegetative leaves with nearly entire margins, and have been problematic in their distinction (Phillips *et al.*, 1972). The latter, *A. halliana*, is among the most well understood of *Archaeopteris* species. Synonymy of *A. roemeriana* from Belgium with *A. halliana*, was supported by detailed studies of its vegetative and fertile leaf morphology (Phillips *et al.*, 1972; Fairon-Demaret *et al.*, 2001). *A. halliana* is characterized by fan-shaped sterile leaves with nearly entire margins, and fertile leaves that divide three times isotomously, bearing up to 39 sporangia in two rows on the adaxial surface of the leaf.

A. macilenta is particularly abundant in North America, and hence, it has been well studied (Beck, 1960; Carluccio *et al.*, 1966; Phillips *et al.*, 1972; Scheckler, 1978). The vegetative leaves are unevenly and deeply dissected, having distal segments that taper into delicate hair-like tips. The fertile leaves divide successively three times to produce up to 8 distal tips, and bear a far lower number of sporangia than sporophylls of *A. halliana*. In both *A. halliana* and *A. macilenta*, transitional leaves with intermediate morphologies between vegetative and fertile leaves were described.

A. obtusa has flabelliform vegetative leaves with entire margins or very nearly so, and this is distinctive for the species (Andrews *et al.*, 1965; Taylor *et al.*, 2009).

A. notosaria was described as having deeply dissected, wedge-shaped leaves, and its fertile ultimate branches were considered uniquely compact amongst *Archaeopteris* species (Anderson *et al.*, 1995), though see Chapter 7.

A. fissilis has unwebbed vegetative leaves that are divided once or twice (Andrews *et al.*, 1965). According to the reconstruction (Andrews *et al.* 1965, their Figure 2), *A. fissilis* has fertile leaves that are isomorphic to vegetative leaves, and bears the majority

of sporangia on the proximal undivided segment of the leaf. There is disagreement about whether *A. fissilis* belongs to *Archaeopteris* or to *Svalbardia*, as the latter also bears unwebbed vegetative leaves, and distinction between them is unclear (Carluccio *et al.*, 1966). Some authors favour synonymizing *Svalbardia* with *Archaeopteris* because the genera are indistinguishable in terms of fertile structures, leaf morphology and vascular anatomy (Beck, 1971; Scheckler, 1978; Berry & Fairon-Demaret, 2001). Matten (1981) considered the leaves of *Svalbardia* to divide in a three-dimensional manner, unlike the planate leaves of *Archaeopteris*. Some in favour of retaining their distinction suggest that *Archaeopteris*-like plants (i.e. *A. fissilis*) with unwebbed leaves should be transferred to *Svalbardia* (Carluccio *et al.*, 1966; Jurina & Raskatova, 2012, 2014). There is general agreement, however, that *Svalbardia* appears earlier and is a likely precursor to *Archaeopteris*, with unwebbed leaves being the plesiomorphic state.

Much of what is known about *Archaeopteris* **lateral branch systems** is derived from anatomical studies (eg. Carluccio *et al*. 1966; Beck 1971; Scheckler 1978; Kenrick and Fairon-Demaret 1991) which are not always in agreement with observations on external morphology. The apparent planation of *Archaeopteris* 'fronds' was once considered a fern-like character, but this was placed in doubt when Beck, (1960) demonstrated attachment between *Archaeopteris* and *Callixylon* wood (then considered of gymnospermous affinity). Carluccio *et al.* (1966) highlighted the three-dimensional arrangement of *Archaeopteris* leaves and their vascular supplies, forcefully dispelling the earlier notion that the leafy lateral branches were compound leaves. They indicated that leaves and sporophylls in *A. macilenta* were helically arranged about a 6-7 ribbed, radially symmetrical xylem column, with sporophylls arising in opposing pairs from alternating sympodia. From a small sample of compressed remains, Beck (1971) could not reconcile his observations with those of Carluccio *et al*. (1966), instead suggesting that *A. macilenta* sporophylls were consistently paired, with successive pairs alternating perpendicularly. This was interpreted as representing a decussate pattern, otherwise understood as a 1/2 helix (Beck, 1971). Phillips *et al.* (1972) also noted the paired arrangement of sporophylls but were undecided whether *A. halliana* sporophylls were arranged in a decussate or helical pattern. Kenrick and Fairon-Demaret (1991), like Carluccio *et al*. (1966), noted in fertile ultimate branches a radially symmetrical xylem column with 6-7 (or more) sympodia. Fairon-Demaret *et al*. (2001) carefully *dégaged* an *A.* (*roemeriana*) *halliana* fertile ultimate branch to reveal the insertions of

sporophylls, and suggested a helical arrangement, finding no evidence for pairing of sporophylls. Sterile ultimate branches of *A.* (*roemeriana*) *halliana* suggest a less dense helical arrangement of leaves than on fertile ones (Kenrick & Fairon-Demaret, 1991). Bilateral symmetry of the vascular bundle of vegetative ultimate branches indicated different leaf sizes on opposing surfaces of the branch (Kenrick & Fairon-Demaret, 1991). Fairon Demaret and Leponce (2001) observed anisophylly, or bimodal leaf size, in attachment to opposing surfaces of vegetative ultimate branches of this species. Changing phyllotactic patterns along the vegetative ultimate branches of *A.* (*roemeriana*) *halliana*, were explained in light of Scheckler's anatomical studies indicating leaf insertion in an anomalous series of fractions outside of the Fibonacci series (Fairon-Demaret & Leponce, 2001).

The penultimate axis produces leaves and ultimate branches in the same ontogenetic spiral (Beck, 1971; Scheckler, 1978). Ultimate branches in *A. macilenta* are confined to two of the nine or more **orthostichies**, being borne in a distichous arrangement (Beck, 1971; Scheckler, 1978). Scheckler's thorough (1978) study noted variations to this arrangement, with larger lateral branch systems bearing three orthostichies of ultimate branches, and in addition suggesting that a degree of variability or randomness in the organotaxy is induced by variation in the sizes of primordia due to the production of different types of appendages in an orthostichy.

Study of a large sample of *Callixylon* wood from the lower Famennian of Morocco has identified three types of lateral appendages emerging from *Archaeopteris* trunks (Meyer-Berthaud *et al.*, 1999). In addition to apically derived smaller ephemeral appendages, and short-lived adventitious appendages interpreted as latent primordia, larger scaffold branches of adventitious and delayed development represent more permanent architectural structures on the tree. The latter organs were interpreted as being homologous to axillary branches of later seed plants, representing a major evolutionary breakthrough in *Archaeopteris* (Meyer-Berthaud *et al.*, 1999).

2.6 Early trees in southern Gondwana

Late Devonian forests were largely characterized by *Archaeopteris* (Meyer-Berthaud *et al.*, 1999; Algeo, Scheckler, & Maynard, 2001; Stein *et al.*, 2020), although the genus was not dominant, or even present, in some of the earliest known *in situ* forests (Berry & Marshall, 2015; Wang *et al.*, 2019; Stein *et al.*, 2020). With a worldwide distribution,

the genus has been considered a biostratigraphic indicator of the Late Devonian (Berry & Fairon-Demaret, 2001). New evidence of *in situ* roots has pushed the appearance of *Archaeopteris* further back in time, supporting arguments that the *Archaeopteris'* precursor *Svalbardia,* from the Middle Devonian, should be included in the genus (Stein *et al.*, 2020). This is also supported by widespread occurrence of *Callixylon* logs by the Givetian (Middle Devonian) (Cornet *et al.*, 2012).

Archaeopteris is considered to have been the first 'modern' tree, with wood architecture resembling that of later seed plants, giving it an unprecedented fitness advantage over other Late Devonian plants (Meyer-Berthaud *et al.*, 1999). Rooting innovations allowed the genus to pioneer new upland habitats that plants had previously been unable to thrive in (Algeo & Scheckler, 1998). This genus is suggested to have been deciduous, seasonally dropping its distal branches to form a dense leaf litter (Beck, 1971; Meyer-Berthaud *et al.*, 1999; Algeo *et al.*, 2001). Resultant suppression of the seedlings of other plants may have contributed to its dominance, exemplified by global *Archaeopteris* forests in the Famennian (Meyer-Berthaud *et al.*, 1999; Algeo *et al.*, 2001; Berry & Fairon-Demaret, 2001). *Archaeopteris*, however, disappeared at the end of the Devonian Period (Meyer-Berthaud *et al*., 1999; Algeo *et al*., 2001).

Leaves of this genus were identified at Waterloo Farm, from which a new species, *Archaeopteris notosaria* was described (Anderson *et al.*, 1995). Until research began at the Waterloo site it was not known that *Archaeopteris* forests had extended so far south of the equator. Unpublished portions of large tree stumps have also been found at Waterloo Farm, possibly corresponding to *Archaeopteris notosaria* (Figure 2.1). This species represents the most southerly known palaeo-occurrence of the worldwide *Archaeopteris* forests (Le Hir *et al.*, 2011).

Archaeopteris was not the only tree to have existed in the South African Devonian. Small trees like *Leptophloeum*, (and possibly *Kowieria*), suggest that precursors to giant arborescent lycopods were already present in the South African Famennian (Prestianni & Gess, 2014; Gess & Prestianni, 2018).

Figure 2.1: Portion of a coalified tree stump in sandstone at the Waterloo Farm locality, several metres northward of the 'main fish lens'. Hammer is roughly 30cm long. Photo: R. W. Gess, 1999.

2.7 Land plants, climate change and extinction

In the later stages of the Devonian Period, a major shift in Earth's atmospheric composition brought fundamental changes to the global climate. A drop in atmospheric carbon dioxide (CO_2) is evidenced by the stable isotope record ($\delta^{13}C$) of marine carbonates (Berner, 2001; Royer, 2006) and leaf stomatal pore density (Franks *et al.* 2014). By the mid Carboniferous, atmospheric CO_2 levels had dropped to around present-day levels, from an estimate of between 5- and 20-times present level at the beginning of the Devonian Period (Algeo *et al.*, 2001; Berner, 2001).

Widespread continental glaciation in Brazil (Caputo, 1985), and possibly in north (Algeo *et al.*, 2001) and southern Africa (Loock, 1967; Almond, Marshall, & Evans,

2002; Gess & Whitfield, 2020), are primary evidence for global cooling towards the end of the Devonian. A series of biotic crises lasting 20-25 million years brought the demise of Middle Devonian tropical reefs, whilst cold water adapted taxa thrived (Copper, 1986; Algeo *et al.*, 2001). The crisis involved 8-10 separate events (Caplan & Bustin, 1999), with the most intense extinctions recorded at the Frasnian/Famennian boundary (Kelwasser event, 372 Ma) and at the Devonian-Carboniferous boundary (Hangenberg event, ca. 358 Ma) (Sallan & Coates, 2010). Chronology and sequencing of these episodic biotic crises is increasingly well established across the Laurussian palaeocontinent (Caplan & Bustin, 1999; Kaiser, Aretz, & Becker, 2016). Collectively, they are known as the Late Devonian Extinctions, and are regarded as one of the 'big five' extinction events in Earth history, with 80% of marine invertebrate species disappearing, including one in four families (Algeo *et al.*, 2001). Vertebrate turnover at the end of the Devonian included the loss of most sarcopterygians and acanthodians, and the complete disappearance of placoderms (Sallan & Coates, 2010).

Early work considered five possible explanations for mass extinction towards the end of the Devonian; bolide impact, carbon dioxide venting at the sea floor, rapid sea-level fluctuations, climate change (cooling), and changes to oceanic circulation patterns as a result of the convergence of Laurussia and Gondwana (Copper, 1986).

Recent evidence suggests a unifying biological cause for the crises. In an inversion of the greenhouse effect, the removal of carbon from the atmosphere led to widespread glaciations in the Late Devonian, Mid- Carboniferous and Early Permian (Berner, 2001). Various studies have attributed this decrease in atmospheric carbon to the spread of land plants (Algeo *et al.*, 2001; Berner, 2001; Kenrick *et al.*, 2012; Morris *et al.*, 2015). Others have contested this hypothesis, stressing the complexity of feedback processes, including the reduction of albedo effect, and arguing that the spread of land plants may have had a negligible effect on global temperatures (Le Hir *et al.*, 2011). The reliability of correlations between atmospheric CO_2 and global temperatures has been challenged (Florides & Christodoulides, 2009), but the hypothesis is supported by studies on trends throughout the Phanerozoic (Royer, 2006), most noticeably on the Palaeocene-Eocene thermal maximum (Bowen *et al.*, 2015), and present-day global warming (Kidder & Worsley, 2012).

In brief, the Devonian plant hypothesis asserts that climate change and extinction were the result of drastic change to atmospheric composition and continental weathering rates due by land plants (Algeo & Scheckler, 1998). Extinctions are explained as resulting from the knock-on effects of the drawdown of carbon (in consequence of early forestation), including changes in atmospheric composition, climatic cooling and aquatic anoxia (Algeo *et al.*, 2001; Percival *et al.*, 2019). In the Mid–Late Devonian, deep rooted progymnosperms and seed plants appeared, and migrated into upland areas (Algeo *et al.*, 2001; Berner, 2001; Berry & Fairon-Demaret, 2001; Kenrick *et al.*, 2012). Forestation of the land brought widespread soil formation and increased organic effluent in river flow from the continents, leading to widespread eutrophication and black shale development in marine basins (Percival *et al.*, 2019). Burial of organic carbon, in turn, caused the intense drawdown of atmospheric CO_2 recorded through the mid Palaeozoic (Berner, 2001). Evolution of trees and seed plants therefore suggests a possible causal mechanism for the Late Devonian biotic crisis.

CHAPTER 3 – MATERIALS AND METHODS

3.1 Materials

3.1.1 Geological setting

Of the formerly undescribed material included in this study, all specimens are derived from two fossil localities in the Witpoort Formation (Witteberg Group), near Makhanda (formerly Grahamstown) in the Eastern Cape Province of South Africa. Their respective locations are shown in Figure 3.1. The localities Waterloo Farm and Coombs Hill both include concentrations of Late Devonian fossils preserved in carbonaceous black shale/mudstone, interbedded within thick packages of the resistant quartzites which characterize this formation. Due to their susceptibility to deep weathering, fine-grained layers are generally only exposed during quarrying and road cutting. Discovery of fossiliferous shale in the Witpoort Formation dates back to the 1840's with a road cutting at Howieson's Poort, south-west of Makhanda. A thin shale band near the base of the formation has provided fossil plant material comprising the holotypes of five, as yet enigmatic, species attributed to 'Psilophyta', Lycophyta and *Incertae sedis* (Anderson & Anderson, 1985). Prior to discovery of Waterloo Farm and Coombs Hill, known floras of this formation were limited to isolated occurrences of lycopod axes and the relatively fragmentary Howieson's Poort material (Anderson & Anderson, 1985). On the basis of apparent 'psilophyte' remains at Howieson's Poort, a Lower Devonian age was suggested for the Witpoort Formation (Rayner, 1988), however, this hypothesis has been falsified as more complete plant remains from Waterloo Farm have subsequently shown that the fructifications represented by '*Ðutoitia maraisia*' Plumstead 1967 are distal appendages of a relatively large plant (putative iridopteridalean, Prestianni and Gess, in prep), and are not closely related to the Early Devonian species *Dutoitia pulchra* Hoeg (Gess & Hiller, 1995a).

A Famennian age was ascribed to the Witpoort Formation on the basis of sequence stratigraphy (Cooper, 1986), and later supported by palynology (of overlying Lower Carboniferous-aged sediments) (Streel & Theron, 1999) and vertebrate biostratigraphy (Gess, 2016). Deposition and reworking of the texturally mature sand shoals characterising the Witpoort Formation may have been initiated by regressive eustatic shifts during the Famennian (Cooper, 1986). The Devonian-Carboniferous boundary is placed at the contact between the Witpoort Formation and the overlying Kweekvlei

Formation (Theron, 1994; Streel & Theron, 1999; Gess, 2016). Hence, the current understanding is that the upper and lower boundaries of this rock formation coincide with those of the final stage of the Devonian Period.

Facies analysis in the Makhanda area led to interpretation of the Witpoort Formation as having been deposited under marginal marine conditions including beach-barrier complex and high-energy shoreface settings (Hiller & Taylor, 1992). The textural maturity and paucity of fossils in sandy strata is suggested to be the result of extensive reworking of sediments (Hiller & Taylor, 1992). Subordinate argillaceous strata interbedded within the quartzitic package are derived from low energy sedimentation in back-barrier lagoonal or estuarine environments (Hiller & Taylor, 1992; Gess & Whitfield, 2020). Brackish water conditions for deposition of the fossiliferous shales have been supported by geochemical studies at both the Waterloo Farm and Coombs Hill localities (Hiller & Taylor, 1992; Hoosen, 2019).

The Witpoort Formation comprises stacked mature quartzites, totalling an estimated 350 m (Hiller & Taylor, 1992) to 800 m or more (Johnson, 1976) thickness in the Eastern Cape, although older estimates may have been inflated by structural duplication (Booth *et al.*, 1999). The Witpoort Formation is both under and overlain by more argillaceous strata of the Weltevrede Formation (Subgroup in the Western Cape), and the Lake Mentz Subgroup respectively (Figure 3.2). Together these comprise the Witteberg Group, which is the uppermost unit of the tripartite Cape Supergroup. Sediments comprising the Cambrian to Lower Carboniferous-aged Cape Supergroup accumulated along a passive margin tectonic setting to the south of Gondwana (Booth *et al.*, 1999). The Witteberg Group records firstly the progressive outbuilding of a sandy shoreline over the underlying shallow-offshore marine strata of the Bokkeveld Group, followed by a transgressive return to predominantly offshore sedimentation in the Upper Witteberg, in response to apparent eustacy (Cooper, 1986; Cotter, 2000).

Cape Supergroup strata were subjected to intensive structural deformation and low-grade metamorphism by regional compressional tectonics during the Late Palaeozoic (Shone & Booth, 2005; Thamm & Johnson, 2006). Northward directed compression was initiated by inferred subduction to the south, leading to uplift of the Gondwanide Orogen, spanning the length of Gondwana's southern-eastern margin (Miller *et al.*, 2016). Parallel NW-SE folds in the Makhanda region, form ridges where resistant

Witpoort Fm. quartzites are exposed, separated by valleys carved from argillaceous underlying and overlying formations. Waterloo Farm occurs on the less-deformed southwestern limb of the Grahamstown synclinorium, along a ridge known as Mountain Drive. The locality is considered to be stratigraphically near the top of the Witpoort Formation (Gess, 2016). Coombs Hill occurs on the corresponding northeastern limb, along Governor's Kop ridge. The relative position of the Coombs Hill succession within the Witpoort Formation is not yet well constrained. In accordance with the geological map (Figure 3.1), greater proximity to exposures of the underlying Weltevrede Formation than to the overlying Kweekvlei Formation (Lake Mentz Sub-Group) suggest that Coombs Hill is situated in the lower part of the Witpoort Formation. Sub-formational stratigraphic interpretation of this unit is hindered by its intense structural deformation, compounded by cover of vegetated recent alluvium. Furthermore, the Witpoort Formation has, as yet, yielded no stratigraphically useful microfossils.

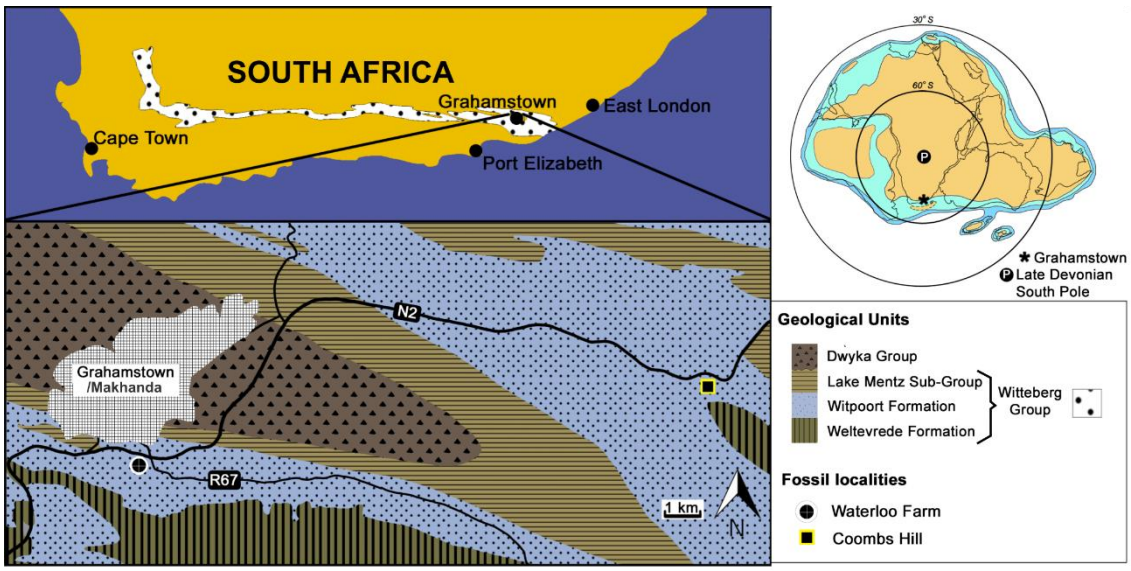

Figure 3.1: Geological map of the Grahamstown/Makhanda region (based on Council for Geoscience, sheet 3326 (1: 250 000), showing the positions of relevant fossil localities Coombs Hill (33°17'54.35"S 26°45'40.32"E) and Waterloo Farm (33°19'24.00"S 26°32'11.38"E). Stratigraphic units and their ages are provided at bottom right. Palaeogeographic reconstruction (top right) modified from Gess and Ahlberg (2018), based on projection of Domeier and Torsvik, (2014).

3.1.2 Provenance of fossil specimens

3.1.2.1 Coombs Hill locality

Coombs Hill is located on a north-facing ridge bordering the Coombs valley, around 30 km east of the town of Grahamstown/Makhanda, mapped geologically within the Witpoort Formation (Figure 3.1). The locality was discovered late in 2015 during road upgrades along the N2 national highway, where an enormous roadcutting intersected a hill of arenaceous quartzites (Figure 3.3). Interbedded, laterally extensive lenses of carbonaceous grey mudstone, bearing abundant remains of plants, were investigated by Dr. Rob Gess and myself.

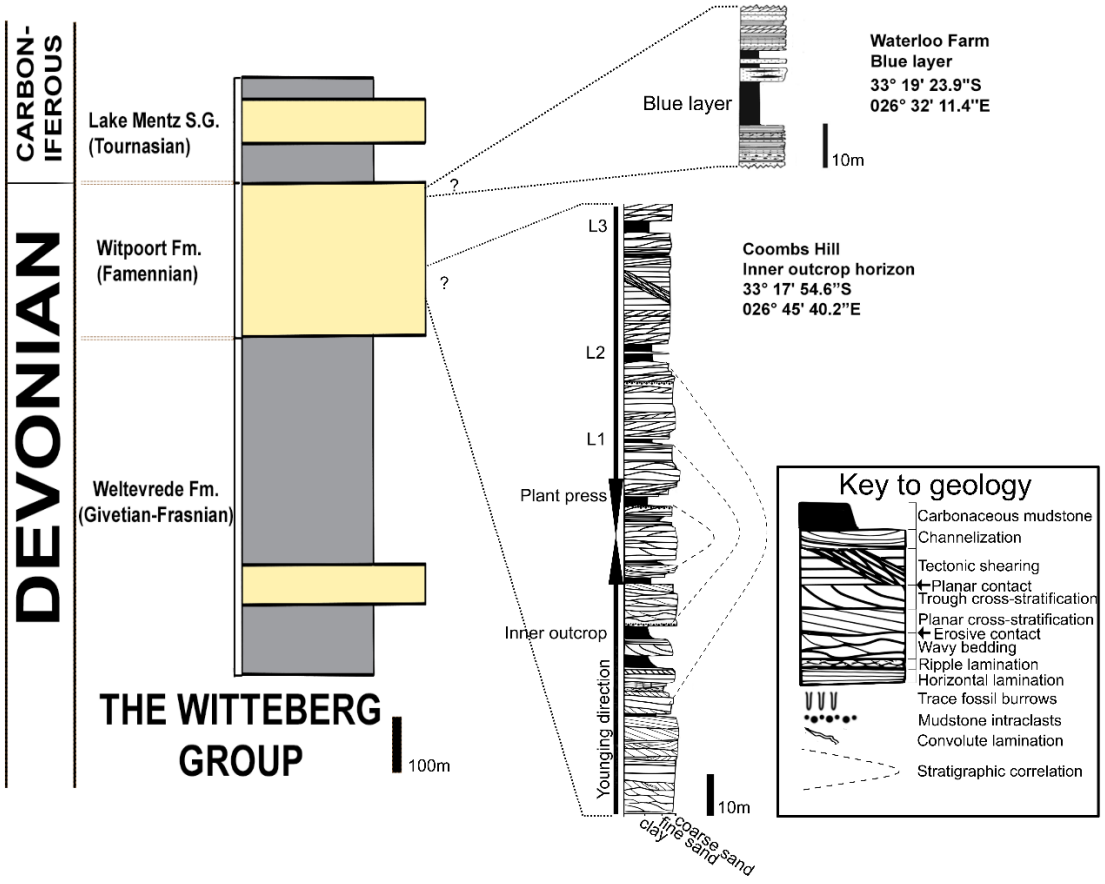

Figure 3.2: Metre-scale stratigraphic logs for Coombs Hill, modified from Harris (2017), and for Waterloo Farm, modified from Hiller and Taylor (1992). Note repetition of units at Coombs Hill due to structural folding. Stratigraphic units for the Witteberg Group redrawn to scale after (Theron, Thamm, & Minter, 1990).

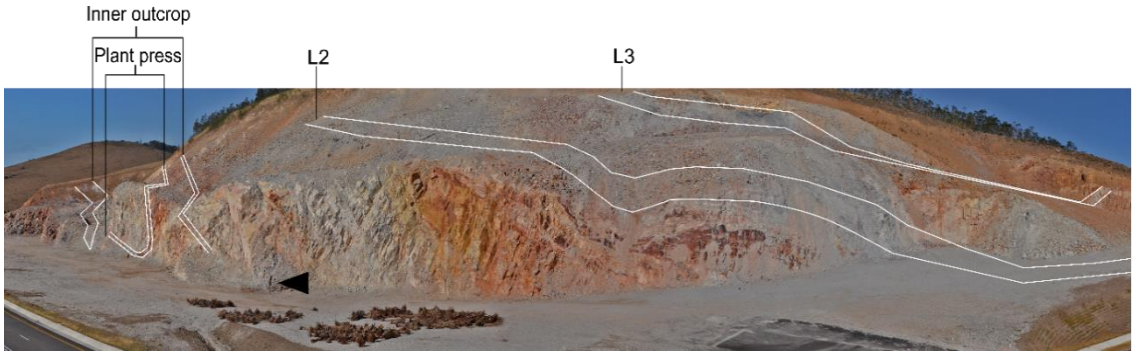

Figure 3.3: Knitted photograph of the road cutting at Coombs Hill, outlining the fossil bearing mudstone horizons. Person for scale is indicated by a black arrow. Vertical exaggeration: 1.5: 1. Photograph: C. R. Penn Clarke.

In 2017, whilst registered at the University of the Witwatersrand for Honours in Geology, I studied the sedimentology and stratigraphy of the Coombs Hill locality, recording its petrography, sedimentary structures and trace fossils (Harris, 2017).

Facies analysis indicated a similar depositional environment to that of Waterloo Farm, demonstrating deposits of high energy shoreface, beach and backshore channels and lagoons. Mudstones exhibited a far more massive structure than the 'Main Fish Lens' black shale layer at Waterloo Farm, splitting into far thicker, less sheet-like slabs. Structure of the mudstones suggest differences in local sedimentary conditions between the localities. Rapid deposition of mud at Coombs Hill, evidenced by cross-cutting, bedding-oblique emplacement of plant fossils, particularly at the Plant Press horizon (see below) may have contributed to the generally more massive mudstones (Harris, 2017).

Differences in preserved fauna and flora were also noted (Harris, 2017). For instance, although bivalve molluscs were common at both localities, they did not include the same genera. Habitat variance between the localities may explain differences in their preserved fauna. In addition, disparity in age between the localities of up to a few million years is hypothesised (Harris, 2017).

The Coombs Hill succession comprises a roughly 80 m thick stratigraphic sequence, partially duplicated around a synclinal fold axis (Figure 3.2). The upper limb of the syncline is overturned, so that the stratigraphically oldest beds occur at the topographically highest point of the cutting (Figure 3.3). Four mudstone marker beds

within the succession have aided the recognition of the duplication. The two stratigraphically uppermost mudstone horizons are duplicated about the fold axis at the topographically lower, eastern end of the cutting (Figure 3.3). Most of the strata in the cutting, including both right-way-up and overturned, dip at around 30° to the southwest, except for an increase in dip, up to 90° on the upper (southwestern) limb with proximity to the fold axis.

Abundant body and some trace fossils were recovered from the mudstones, whilst the quartzitic sandstones yielded only sparse trace fossils. The various mudstone horizons were individually named, and all fossil specimens were given field numbers specifying their stratigraphic origin. The fossil bearing mudstone layers are described below in stratigraphic order, from oldest to youngest.

The L3 horizon

This layer exhibits variable thickness and degrees of weathering. It occurs near the top of the cutting. At its westernmost extent the layer is less than a metre thick, and light grey in colour. Traced eastwards, the layer thickens to more than 2 m, becoming darker in colour where it has been less leached. The layer is around 30° from the horizontal and is upside-down, forming part of the overturned southwestern limb of the syncline. Fossil abundance varies throughout the layer. Near the stratigraphic base of the layer fossil remains are scarce, and are often disarticulated. Towards the middle-upper part of the layer, dense mats of vegetation occur, and these include plant remains attributed to *Archaeopteris* and iridopteridaleans. The uppermost part of the layer again preserves scarce plant remains.

After the road cutting had been completed, the L3 layer was benched in order to make the mudstone accessible for palaeontological excavation and remains exposed. During the roadworks, some of the mudstone was bulk excavated from the layer, and deposited at a nearby location for sampling. Most collected specimens were derived from this sample, and their distribution within the layer is therefore uncertain.

Flora collected includes very well preserved vegetative and fertile parts of *Archaeopteris notosaria* (described in Chapter 7) as well as remains tentatively compared with *cf.* Iridopteridales; *cf.* Cladoxylopsida; *cf. Palaeostigma robusta* Anderson and Anderson 1985; *cf.* Phaeophyta and indeterminable lycopod axes. Plant remains are associated with relatively rare bivalve molluscs.

The L2 horizon

A 2–3 m thick layer of poorly bedded mudstone, medium-grey in colour throughout, which produced a few plant fossils early in the excavation. Plant morphotypes include a lycopod axis, possibly *Colpodexylon*, but excluded from this study because of the lack of preserved leaves; and an isolated leaf of *Archaeopteris*. Disarticulated lycopod cortex was also found, as well as other unidentified plant remains. As the L2 layer consistently produced an abundance of grey mud with very little evidence of life it was not prioritised for excavation.

The L1 horizon

The L1 layer was initially identified by Dr Gess prior to the N2 road upgrade, as an approximately 30 cm thick, relatively gritty mudstone exposed in a pre-existing roadcutting. Dr. Gess sampled the layer for fossils in 2013, and found a poorly preserved and unidentifiable fossil fragment. During roadworks in 2015, not a single fossil was collected from the layer where it was exposed in the western part of the quarry. However, as excavations progressed, the layer was followed, and understood to be the lateral equivalent of the most productive horizon at the site, the Inner Outcrop horizon.

The Inner Outcrop horizon

This horizon was so named because during initial excavation of the layer, Inner Outcrop seemed a depositional site more proximal to the living environment of the plants than the underlying layers, preserving larger and more complete remains than had been discovered hitherto. The layer is thickest on the lower limb of the syncline where it retains the correct younging direction, with a roughly 30° dip. It attains a more than 6 m cumulative thickness, with the mudstone deposit being interrupted in the middle by around a metre of trough cross-stratified quartzite. Both the upper and lower parts of the layer thin rapidly towards the west, with the lower pinching out over a few tens of metres. The upper is sharply truncated by an erosively based trough cross-stratified sandstone unit. The upper part of the layer, 2–3 m at its thickest was the more palaeontologically productive. Both it and the lower portion exhibit laterally continuous alternating reddish and grey horizontal layers a few centimetres thick.

The Inner Outcrop is also expressed on the upper, overturned limb of the syncline, where it has thinned to less than a metre and is grittier in texture. It is correlated on the

basis of an equal distance from the fold axis. Thinning of the mudstone horizon and a coarser texture suggested a shallower setting closer to the lagoonal margins. This exposure produced only poorly preserved fragments of plants and trace fossils.

Large blocks from the upper part of the 'right-way-up' expression of Inner Outcrop, were excavated with the assistance of an excavator machine, transported on a flat-bed truck and stored out of the weather behind Albany Museum for future excavation.

Excavated from this layer were leafy lateral branches of *Archaeopteris* described in Chapter 7, lycopod axes initially attributed to '*Haplostigma'*, which are assigned to *Colpodexylon* in Chapter 4, and one lycopod specimen bearing terminal strobili which is provisionally attributed to 'lycopod D' in Chapter 6. Further plant remains (in order of abundance) are tentatively compared with *cf.* Iridopteridales; *cf.* '*Dutoitia' maraisia*; Zosterophyllopsida *cf. Serrulacaulis* Heuber and Banks; Algae *cf.* Phaeophyta; *cf.* Cladoxylopsida; *cf.* Gymnospermopsida; *cf.* '*Dutoitia' alfreda* Plumstead; *cf. Palaeostigma sewardi* Kräusel and Dolianti.

Plant remains are associated with bivalve molluscs, including thick-shelled and thin-shelled taxa. Trace fossils from within the layer included serially arranged *Lockeia* (probable bivalve locomotion traces), numerous small vertical and horizontal burrow traces and many round to spiral, granular structures interpreted as possible fish coprolites.

The Plant Press horizon

This horizon was exposed at a late stage of road construction and a relatively small sample was derived before much of its exposure was demolished. Like the underlying Inner Outcrop, it also preserves relatively intact plant remains. The mudstone is of variable thickness with a maximum of approximately 1 m, and dips at around 70° to the southwest. Its steepness of dip is due to proximity to the fold axis. The layer is duplicated around the syncline, and could be traced along its bend around the fold axis, thinning to less than half a metre on the lower fold limb where the dip is around 30°. Plant remains at this correlative horizon were, by contrast, very fragmentary.

The mudstone matrix of the Plant Press horizon is very light grey, probably as a result of leaching due to movement of groundwater along the fold axis. As with the Inner Outcrop layer, an excavator machine was utilised to rescue large blocks of the upper part of the layer which were transported to Albany Museum for future study.

At the upper fold limb, the layer preserves associated plants which crosscut each other on a vertical plane, such as, for example, the designated holotype of 'lycopod C' (*cf. Gilboaphyton*). This indicates that plant fossils were buried rapidly by mud. The layer preserves possibly the largest and most complete remains of plants from Coombs Hill, which include additional axes ascribed to 'lycopod C' in Chapter 5, and one, at least 6 cm thick, partial lycopod axis, described in Chapter 6. Further plant remains are compared with *cf.* Iridopteridales; Zosterophyllopsida *cf. Serrulacaulis* and *cf. Palaeostigma sewardi*.

Plant remains are associated with thick-shelled bivalves, in lower abundance than at Inner Outcrop, and serially arranged *Lockeia* traces.

3.1.2.2 Waterloo Farm locality

The Waterloo Farm locality is exposed in a road cutting to the south of Grahamstown/Makhanda. It was originally cut in 1985 during construction of a highway bypass around the town, and the exposed black shales were excavated by R.W. Gess *in situ* during the 1990s. The cutting was unstable due to the geological dip of strata, and was cut back twice; in 1999 and 2007. During the last two excavations by road engineers, R.W. Gess monitored exposure of fossiliferous strata, collected samples and rescued a large sample of blocks of shale for ongoing investigation.

Metre-scale stratigraphy of this locality was recorded by Hiller and Taylor (1992). Their sedimentological studies of the locality indicated a back-barrier, brackish water lagoonal system as the locus for deposition of the fossiliferous black shale (Hiller & Taylor, 1992). Subsequent palaeontological research is consistent with this interpretation as the assemblage includes both marine algae (Hiller & Gess, 1996) and non-marine charophyte algae (Gess & Hiller, 1995b), an estuarine fauna (Gess & Whitfield, 2020) and a terrestrial flora. Terrestrial plants include the heterosporous lycopods *Kowieria alveoformis* Gess and Prestianni 2018 and *Leptophloeum rhombicum* (Prestianni & Gess, 2014), *Archaeopteris notosaria* Anderson, Hiller et Gess 1995, a sphenophyte *Rinistachya hilleri* Prestianni and Gess 2018, a putative iridopteridalean (Gess and Prestianni in prep), and various undescribed material (Gess & Hiller, 1995a).

Two specimens here ascribed to 'lycopod B' (*Colpodexylon sp. nov.*) were recovered by RG during roadworks in 2007 from approximately 100 m westward along strike

from the Main Fish Lens (MFL). One (AM 7540) originated in a loose block of black shale derived from the Blue Layer (Figure 3.2) and the other (AM 7541) from sandier sediments immediately overlying the black shale.

3.1.3 Fossil material included in this study

3.1.3.1 Formerly undescribed material

Lycopsida

Lycopod fossils described here are attributed to three genera, including four new species.

Lycopod (*Colpodexylon*) *sp. nov.* A, includes five specimens (AM 7700–7704) from the Coombs Hill locality, Inner Outcrop horizon.

Lycopod (*Colpodexylon*) *sp. nov.* B, includes two specimens (AM 7540, 7541) from the Waterloo Farm locality, associated with the Blue Layer.

Lycopod *Gen. nov. sp. nov.* C (*cf. Gilboaphyton*) includes five specimens on three rock slabs (AM 7705–7707) from Coombs Hill, Plant Press horizon.

Lycopod *Gen. nov., sp. nov.* D. includes a single specimen (AM 7708) from Coombs Hill, Inner Outcrop horizon. A large lycopod axis (AM 7709) from the Plant Press horizon at Coombs Hill was included in the study to explore its possible relationship to 'lycopod D'.

Progymnospermopsida

Progymnosperm remains are attributed to *Archaeopteris notosaria*. The described specimens (AM 7710 – AM 7716) were all collected at Coombs Hill, from the L3 and Inner Outcrop horizons.

3.1.3.2 Formerly described and comparative material

For comparative purposes, three relevant holotype specimens were studied, as well as associated material from collections of the Albany Museum. Chapter 5 provides a description and re-illustration of the holotype of *Archaeosigillaria caespitosa* (Schwarz) Plumstead 1967 (AM 142).

Illustrations and brief description of lycopod specimens, including the holotype (AM 5297) and a formerly undescribed specimen (AM 5301), attributed to *Kowieria alveoformis*, are provided in Chapter 6 to augment the original description thereof.

The holotype of *Archaeopteris notosaria* Anderson *et al*. 1995 (AM 4918) is restudied for comparison with the Coombs Hill material in Chapter 7.

3.2 Methods

3.2.1 Collection and repository

The Coombs Hill collection was assembled in 2015 and 2016, during quarrying of around 1 million m^3 of rock by the South African National Roads Agency Limited (SANRAL). Regular sampling the fossiliferous mudstones during the roadworks gave an idea of the distribution of fossils throughout the exposed stratigraphy.

Large slabs of mudstone were opened using a builder's bolster and 4lb hammer. The rock tended to part on slickenside and shear surfaces, but careful targeting of bedding planes exposed plant fossils. These were collected where diagnostic features such as branching, leaves or fertile structures had been preserved and were accessioned into the Albany Museum collection. Together with field data, including stratigraphic origin, collector and date of collection, they are curated in the Devonian collection, housed at 87 Beaufort Street, Makhanda.

3.2.2 Preservation and taphonomy

Fossils from Coombs Hill and Waterloo Farm exhibit a very similar style of preservation. Organic matter was replaced by a metamorphic mica during the low-grade metamorphism characterizing this region of the Cape Fold Belt (Gess & Hiller, 1995a). This was subsequently altered to white kaolinite during uplift. They occur as flattened impressions in the carbonaceous grey to black clay-silt matrix.

Parting of the rock matrix usually favours the coarsest fossil material, which provides a plane of weakness. Plant fossils at these sites, are generally exposed at the level of the thickest axis. Further preparation is often required to expose appendages such as leaves, subsidiary branches and fertile organs that remain partially buried in the matrix.

3.2.3 Study and illustration of the specimens

Fossils were studied in detail with the aid of a Zeiss Stemi 408 binocular microscope. Microphotographs were attained with a fitted Zeiss Axiocam 105 colour camera. Photographs of specimens were attained with a Nikon DLSR camera, attached to a copy stand. Specimens too large to photograph on the copy stand (eg. AM 7707) were photographed by attaching the camera to a tripod.

Poor contrast between the rock matrix and fossil inhibits visibility of many of the Coombs Hill fossils, especially those from the Plant Press horizon. In addition, fossils have a directional mineral fabric which reflects light differentially according to the orientation of the specimen relative to the source of light. Rotating a fossil around a perpendicular axis causes it to alternately appear or disappear. To attain the best view of a specimen, either it or the light source are manipulated to obtain the most useful light angle.

A variety of methods were employed in order to better observe and illustrate the material. Low-angled sunlight was found to highlight the contrast between fossils and matrix for photographic purposes. For some of the material, cross-polarized light was utilised in conjunction with the Zeiss Stemi 408 in order to see millimetre scale details. Selected fossils were transported to Evolutionary Studies Institute (ESI) at the University of the Witwatersrand and studied with the Olympus S7X7 binocular microscope. Cross-polarized illumination was provided by a ring-light with rotating polarizer. Photographic contrast was enhanced using Adobe Photoshop CC 2019. Line drawings of fossils were produced in the same program, using a Wacom Intuos Pro-S graphics tablet to trace over photographs of the fossils. Drawings were made in continual reference to the fossil material.

Sporangia removed from *Archaeopteris notosaria* (AM 7710, AM 7714) and 'lycopod D' (AM 7708) during preparation of the fertile leaves were mounted on stubs and examined under the desktop Scanning Electron Microscope (PheNom) at ESI.

3.2.4 Preparation

Lycopod axes at Coombs Hill are commonly preserved as impressions of outer cortex filled internally by sediment. Compression has flattened stem and internal sediment to a thin wafer separating opposing surfaces of the axis. If leaves are attached, they are usually visible only along the margins of the stem. Elongate leaves such as those of *Colpodexylon* species, which are less than a millimetre wide, and have distal tips down to 0.1 mm wide, required delicate preparation (Figure 3.4). Preparation was performed under binocular microscopes at the Albany Museum Devonian lab and at ESI. Conventional techniques of *dégagement* include the use of sharp needles similar to those used for leather work, impacted with a light hammer (Fairon-Demaret, Hilton, & Berry, 1999). Modification of this technique was employed for preparation of the

Coombs Hill material. Because the rock matrix from Coombs Hill is very soft, particularly when weathered, it tended to smear rather than flake when sharp needles were used. For *Archaeopteris* fertile material manipulation of a needle by hand was sufficient to remove grains of matrix from sporophylls and sporangia. A rubber air blower was held in the other hand, to continuously remove flakes of clay that aggregated around the area of interest. For lycopod leaves it was more effective to use a small flat headed chisel, around 3 mm wide, and a light hammer, which resulted in flaking of the matrix, and caused minimal damage to the fossil.

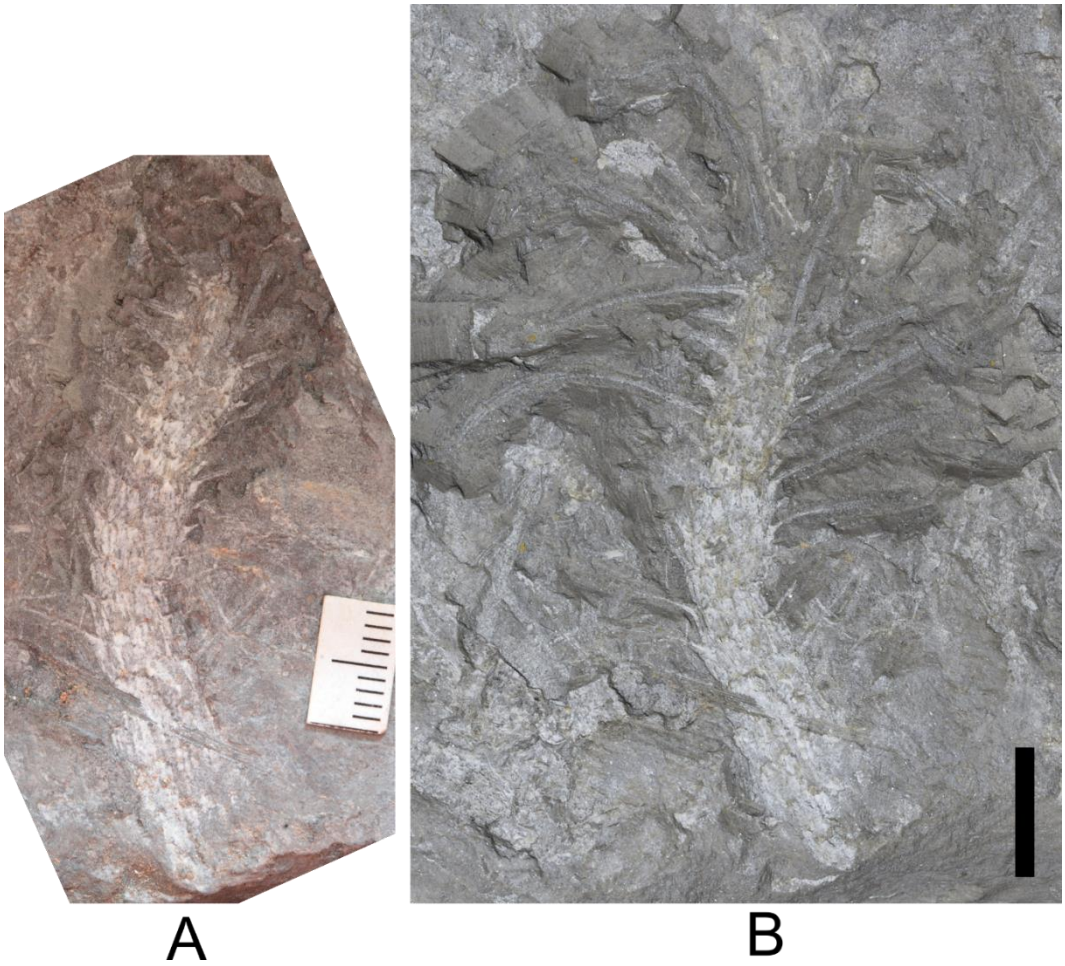

Figure 3.4: Leafy lycopod axis (AM 7700) described in Chapter 4, **A)** before and **B)** after preparation. Scale bars for both are 1cm.

3.2.5 Limitations

Clear illustration of specimens was hindered by the lack of polarizers on the Albany Museum Devonian lab binocular microscope, such that polarising film was used as a

substitute. Acquisition of polarizing filters for the Devonian Lab will greatly facilitate palaeobotanical research.

Furthermore, during initial fieldwork and preparation the author did not always collect all fragmentary counter specimens.

CHAPTER 4 – 'LYCOPODS A' AND 'B'

4.1 Introduction

Colpodexylon was first described by Banks (1944), who identified it as a herbaceous lycopod having three-tipped microphyllous leaves, with sporangia held on the upper surface of unmodified leaves, and a characteristic lobed xylem strand. He assigned it to Protolepidodendrales, a primitive lycopod order, which includes most of the herbaceous lycopod taxa known from the Middle Devonian (Bonamo *et al.*, 1988; Gensel & Berry, 2001). The genus formerly appeared to have disappeared near the boundary of the Middle–Upper Devonian, along with most, or all, other members of its order, to be replaced by a profusion of arborescent lycopods as well as 'trimerophyte' descendants (Berry & Fairon-Demaret, 2001).

Protolepidodendrales occurred worldwide in the Middle Devonian, and is represented in southern high-palaeolatitude regions by *Haskinsia* and '*Haplostigma'* (Cingolani *et al.*, 2002; Xu & Berry, 2008). The group may have been more diverse in southern Gondwana than is apparent as *'Haplostigma'* may include species from a variety of genera (Cingolani *et al.*, 2002). Without leaves preserved, attempting identification of protolepidodendralean axes is ill advised (Bonamo *et al.*, 1988). The possibility that *Colpodexylon* also extended into high latitudes was suggested by resemblance of a paratype of '*Haplostigma'* from the Upper Devonian of South Africa to *Colpodexylon,* although a positive identification is precluded by the specimen's incompletely preserved leaves (Cingolani *et al.*, 2002). Fossil material, here described, confirms the presence of *Colpodexylon* in South African Upper Devonian strata.

4.2 Systematic palaeobotany

Class – Lycopsida Pichi-Sermolli 1958

Order – Protolepidodendrales Pichi-Sermolli 1958

Family – Protolepidodendraceae Kräusel and Weyland 1949

Genus – *Colpodexylon* Banks, 1944 emend. Berry and Edwards, 1995

Type species – *C. deatsii* Banks 1944.

4.2.1 *Colpodexylon* species nova A

Figure 4.1, A–D; Figure 4.2, A–E; Figure 4.3, A–D; Figure 4.4, A–E

Holotype; AM 7700

Additional specimens; AM 7702, AM 7701 a + b, AM 7703 a + b, AM 7704 a + b

Locality; Coombs Hill

Horizon; Inner Outcrop

4.2.1.1 Diagnosis

Vegetative stems parallel sided, up to at least 31.6 cm long and 5–13 mm wide. Persistent vegetative leaves pseudowhorled, inserted in a low helix up to 20º from transverse, 10–12 leaves per **t**urn of the axis, alternating in successive pseudowhorls. Successive pseudowhorls occur at intervals of 4–6 mm down to 2 mm apically. Leaves microphyllous with emergent longitudinally elongate swollen bases 2–3 mm high and up to 1 mm wide, microphylls diverging from the stem at 60–90º, elongate, slender, at least 23–31.9 mm long, trifurcating at 2/3 to 3/5 of total length, up to 0.8 mm wide prior to division, distal segments around 0.25 mm wide each tapering to acuminate (?) tip, median segment longer than laterals, median segment 8.4–13.7 mm long (n=6), lateral segments 7.5-8.9 mm long (n=8). Fertile material unknown.

4.2.1.2 Description

Five specimens from the Inner Outcrop horizon at Coombs Hill are attributed to *Colpodexylon* sp. nov. A. Four of these (Figure 4.1, A–C, Figure 4.2A) are portions of axes with diagnostic leaves attached, and the fifth (Figure 4.1D) has incomplete leaves, but is attributed to the same species as it occurs at the same horizon as the others and is otherwise consistent with the diagnosis.

Stem morphology

Stems are 5–13 mm wide and 48–316 mm long, and are mostly very regular in width. None of the specimens are branched. The assigned holotype specimen, AM 7700, is a short segment of axis covered by leaves with swollen bases, tapers slightly toward the tip. A congruent decrease in the spacing of leaf base pseudowhorls, suggests that the tip of the specimen represents the apex, or near apex, of the plant (Figure 4.1A). Tentatively assuming that their full lengths are exposed, leaves on this specimen are shorter than those of the other specimens (see Figure 4.6 for comparison). AM 7704 a +

b (Figure 4.2, A–E), the longest axis by far, tapers from 12 mm wide, to about 5 mm wide distally, before being truncated by the edge of the rock. The tapering of AM 7704 may also indicate proximity to a growth apex. All other axes are truncated at both ends by rock breakage or taphonomic damage. Axes are ornamented by leaf bases, but appear otherwise smooth, except for AM 7704, which presents, towards its apical part, a pattern of continuous sinuous grooves that meander longitudinally between the leaf bases. These latter are mounted on corresponding ridges

Leaf arrangement and morphology

The attachments of leaves to the axis are marked by false leaf scars, where leaves have been broken off at the base, remaining in the matrix of the counterpart. Leaf bases are arranged in low helices, inclined at up to 20° from a transverse plane (Figure 4.3). The low helical angle creates the impression that leaves are inserted in whorls, and their arrangement is termed pseudowhorled. Each helical turn of the axis comprises 10–12 leaves, based on five or six consistently visible on one side of the axis. Leaf bases in successive pseudowhorls are not arranged in a vertical line, but alternate.

Bases of leaves are variable in morphology, ranging from swollen and elongate to shorter and arched. On the assigned holotype, each leaf is attached to a swollen base 2–3 mm long by up to 1 mm wide, with its long axis parallel to the stem. In profile along stem margins of the specimen, leaf bases appear to emerge from the stem surface (Figure 4.3A). Here, in sagittal view, they stand about 1 mm proud of the stem apically, and from there tapering downwards toward the stem. A narrow, elongate leaf emerges from the top of the swollen base. Counterpart specimens, representing the outer cortex on the side of the stem facing the matrix, show leaf bases as depressions of a similar morphology, being deepest adaxially, where a minute cylindrical cavity indicates the vascular trace of the leaf departing into the matrix (Figure 4.3C, D, arrows). The remaining cavity suggests that the vascular trace resisted decay long after burial and compaction. On AM 7703, leaf bases in face view are obovate or teardrop shaped depressions, rounded at the top, tapering and shallowing downwards (Figure 4.3C). These are very subtle, and only become visible under low-angled illumination. Leaf bases appear on AM 7704 as small arches around 1 mm wide and high at the point of leaf insertion. A leaf is observed extending upwards into the matrix overlying the stem from one of the bases (Figure 4.2D).

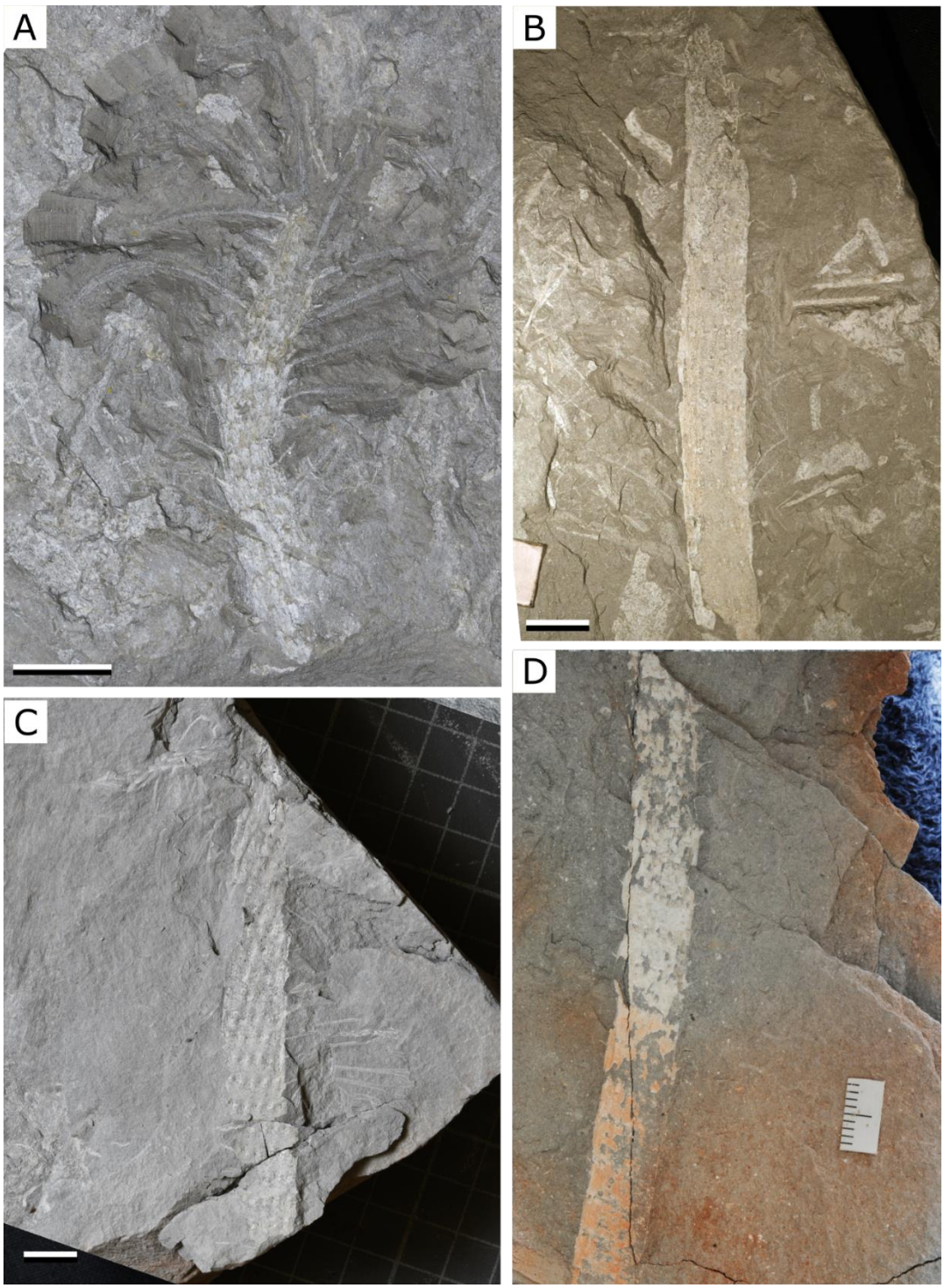

Figure 4.1: *Colpodexylon* sp. nov. A from Coombs Hill; **A)** holotype of the species, (AM 7700), **B)** partial axis with taphonomically damaged, typical leaves (AM 7702), **C)** axis with leaves attached (AM 7701a), and **D)** counterpart of axis (AM 7703b). All scale bars = 10 mm.

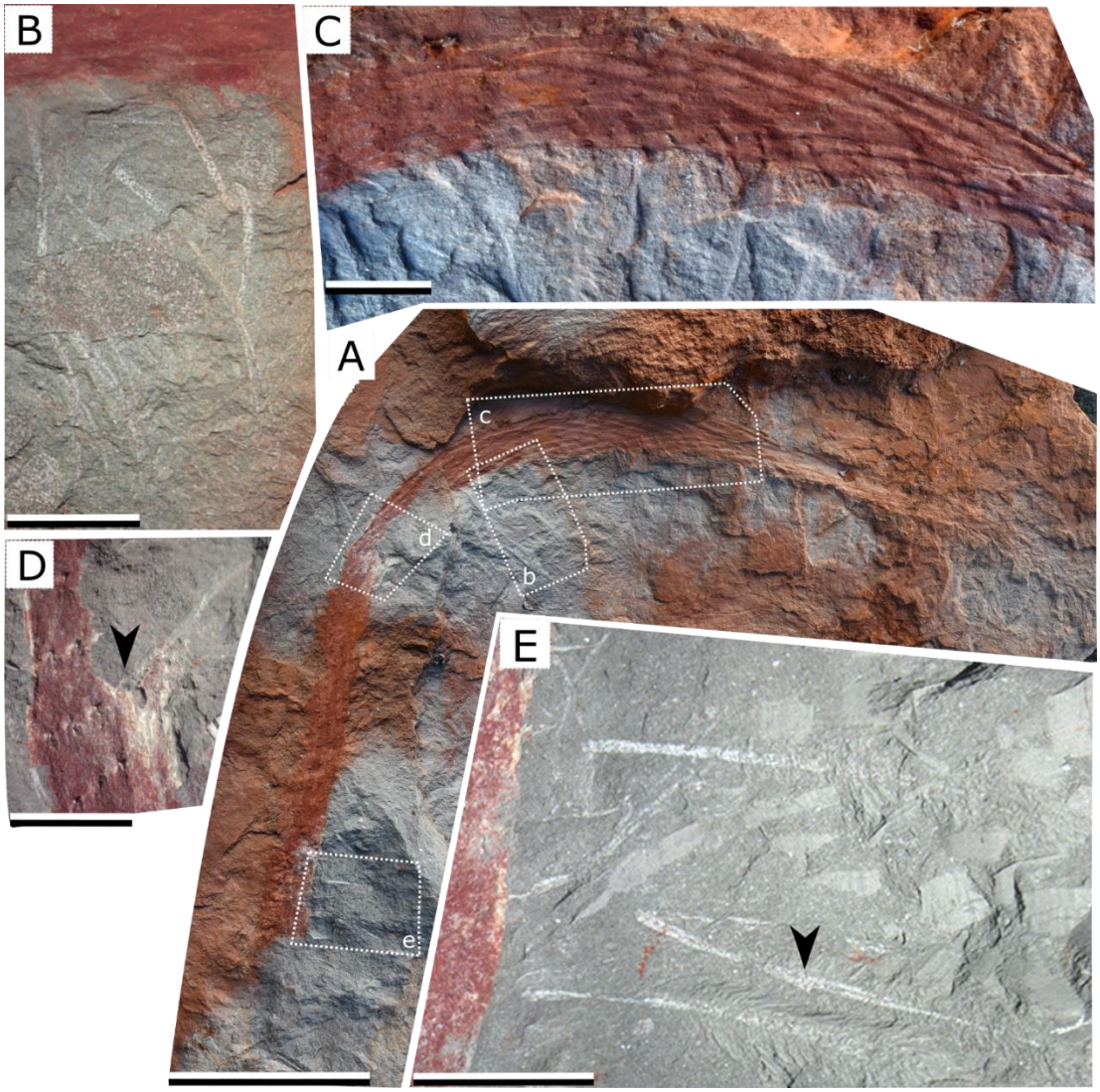

Figure 4.2: A) AM 7704 (scale bar = 5cm). B–E: Enlargements from (A), their positions on the specimen marked by stippled lines and indicated by small letters a–e (scale bars for B–E = 10 mm). **B)** Showing numerous overlapping trifurcate leaves, some of them attached to axis. **C)** Pattern of grooves and ridges ornamenting the axis. **D)** Showing a leaf at top right ascending into the matrix overlying the axis, from its attachment to a leaf base (arrowed). **E)** Partial leaves adjacent to the axis, one of which shows clearly the point of division (arrowed) from which the middle segment tapers gradually to an acuminate tip.

Pseudowhorls occur at 4–6 mm intervals, with smaller intervals (down to 2mm) measured from the compact area near to a putative growth tip (Figure 4.1A).

Leaves emerge from the top of the leaf base, and diverge at 60–90° from the stem. Near the base of leaves, where they depart from the stem, the leaf appears to have a furrow along the midline, which may continue for up to half of its length (Figure 4.4A, B). The leaf lamina is narrow and elongate, trifurcating at 2/3 to 3/5 of its entire length (Figure

4.4). Leaves are 23–31.9 mm long and up to 0.7–0.8 mm wide prior to division. The widest point on the leaf usually occurs immediately before division. Trifurcation produces three distal segments of equal width (around 0.25 mm) which taper evenly to an acute tip (Figure 4.2E). It is uncertain whether the true tips of leaves have been exposed during preparation. Distally the segments become so fine that they could no longer be prepared from the matrix, but an acuminate tip is suggested. In such cases, it is usually impossible to judge the full extent of leaf length, and recorded values are regarded as minima (Berry *et al.*, 2000). The preserved length of lateral segments is less (7.5–8.9 mm) than that of medial segments (8.4–13.7 mm). The lateral segments diverge from the medial by up to 10°. Leaves are abaxially curved to straight, and others are sharply bent adaxially (Figure 4.4E), or abaxially (Figure 4.4D). Variations in leaf posture clearly result from taphonomic damage. Leaves preserved on bedding planes will generally have been twisted perpendicularly to their orientation *in vivo*, and this may have produced a straightening effect. Note damage to the proximal regions of leaves on AM 7701, evidencing that they have been twisted (Figure 4.4D). Leaves in attachment to the holotype occur in three-dimensional space within the matrix. Extending from the axis margins, they are preserved side-on, as they would have been orientated in life. A relatively quick burial is suggested by the specimen. From this evidence, abaxial reflexing of leaves like that on the holotype was their most likely posture in life (Figure 4.4A, B).

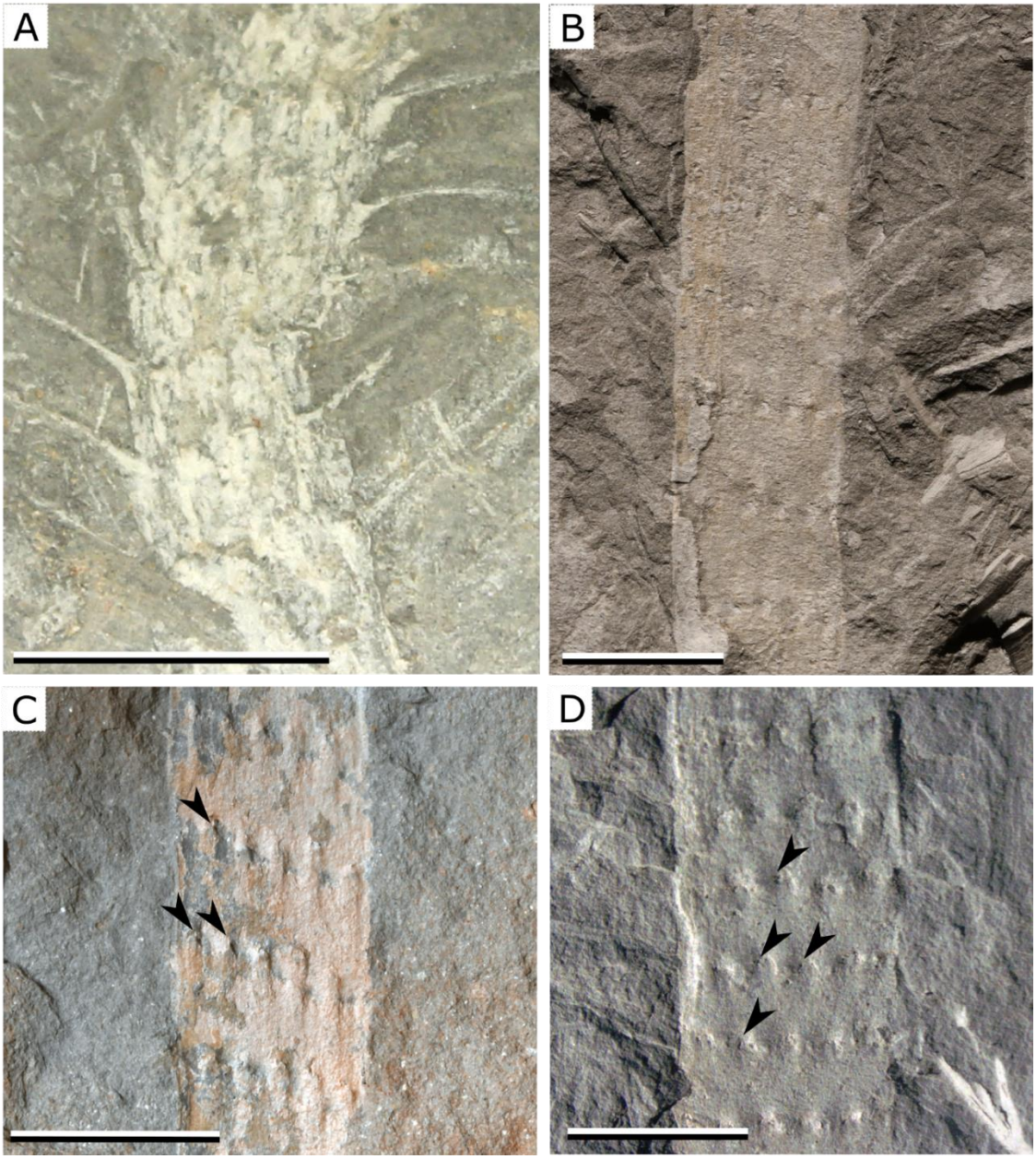

Figure 4.3: Axis and leaf base morphology of *Colpodexylon* sp. nov. A, showing enlargements of; **A)** the holotype, with emergent, swollen leaf bases (AM 7700), **B)** AM 7702b, showing a counterpart specimen with slightly depressed leaf bases, **C)** counterpart of axis (AM 7703b) showing leaf bases as depressions, under low-angled illumination from top left, **D)** counterpart of axis (AM 7701b), showing leaf bases as depressions under low-angled illumination from top left. Arrows on C and D indicate cavities representing leaf vascular traces. All scale bars represent 10 mm.

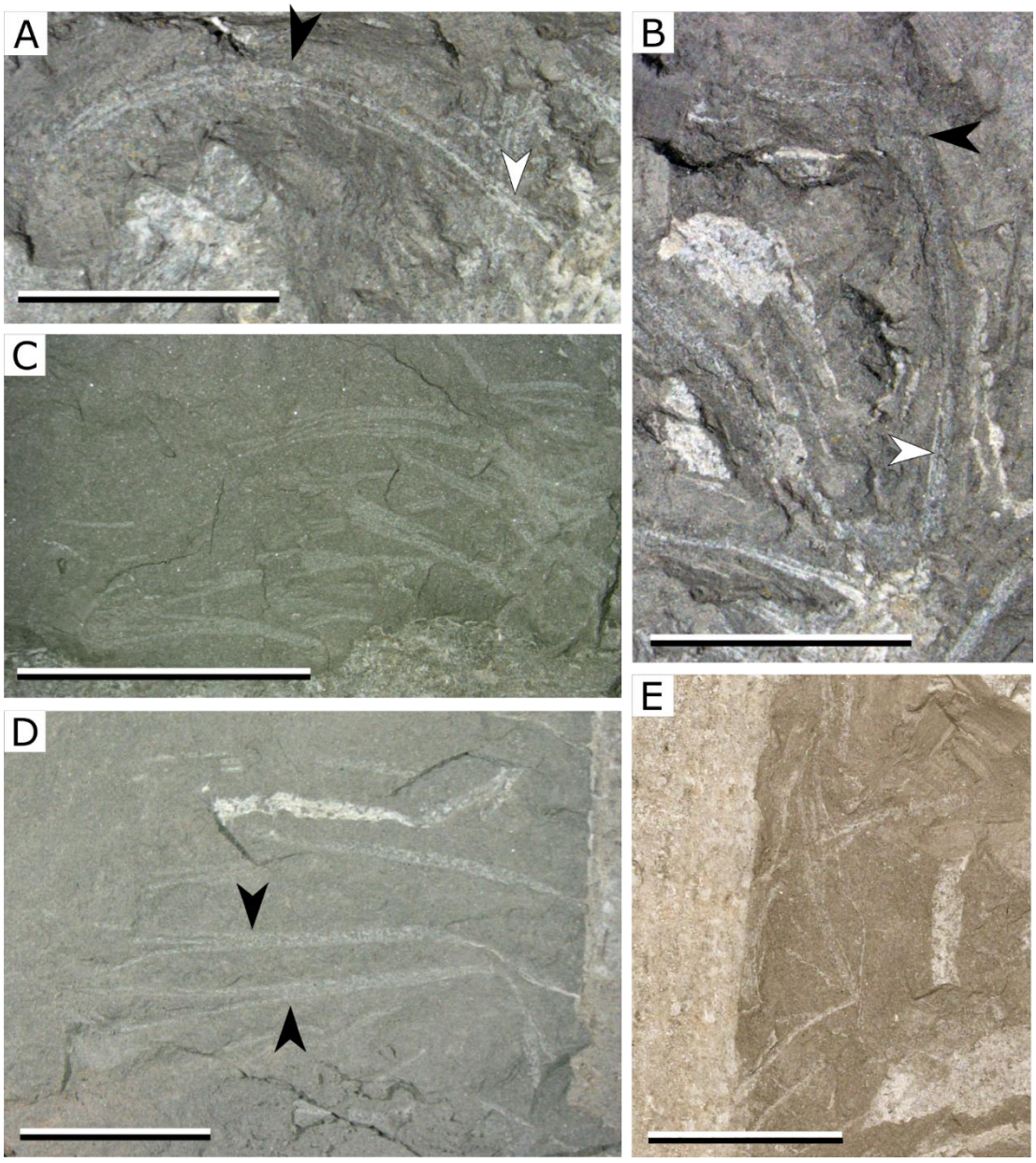

Figure 4.4: Leaves of *Colpodexylon* sp. nov. A from Coombs Hill; **A)** and **B)** enlargement of leaves from AM 7700 (Figure 4.1A), **C)** enlargement of several overlapping leaves on AM 7701a (Figure 4.1C), **D)** leaves attached to AM 7701b, **E)** enlargement of a leaf from AM 7702 (Figure 4.1B). Black arrows on A and D indicate estimated point of trifurcation, and white arrows on A and B indicate a medial furrow on the proximal region of the leaf. All scale bars = 10 mm.

4.2.2 *Colpodexylon* species nova B

Figure 4.5 (A–D)

Holotype: AM 7540

Additional specimens; AM 7541

Locality; Waterloo Farm

Horizon; Blue Layer (AM 7540) and sandier sediments immediately overlying the Blue Layer (AM 7541) approximately 100 m west of “MFL”.

4.2.2.1 Diagnosis

Vegetative stems up to at least 29.5 cm long and 6–9 mm wide (n=2), parallel–sided, with up to two isotomous dichotomies. Microphyllous leaves pseudowhorled, inserted in a low helix up to 20º from transverse, 10–12 leaves per turn of the axis, leaves alternating in successive pseudowhorls, which occur at intervals of 2.5–5 mm. Leaves with emergent longitudinally elongate swollen bases 1.5–4 mm high and 0.5–1.5 mm wide. Leaves persistent, elongate, slender, 17.5–21.9 mm long, trifurcating at around 7/8 of length, up to 0.9 mm wide prior to division, distal segments around 0.3 mm wide tapering to acute tips, median segment 3.3–3.9 mm long (n=3), lateral segments 2.3–3 mm long (n=8). Fertile parts unknown.

4.2.2.2 Description

Axes

The material ascribed to this species includes two slabs and counterslabs, each with a single specimen, both having leaves of a similar size and shape (Figure 4.5A, C). Axes are parallel sided and between 15.1 cm and 29.5 cm in preserved length, exhibiting two dichotomies spaced 189 mm apart on AM 7541 (Figure 4.5A). Axes are 6–9 mm wide and are very regular in width. Following dichotomy, daughter branches are equal to each other and to the parent axis in width. Daughter branches diverge at angles of 35°–45°. The two dichotomies of specimen AM 7541 produce daughter branches which enter the rock matrix at different angles. At the first dichotomy the right daughter branch descends into the matrix beneath the bedding plane of parting. At the second dichotomy the left axis does so. Preparation of the right-hand branch of the first dichotomy suggests that it was truncated prior to burial.

Leaf distribution and morphology

Stems are covered by leaves inserted in a low helix, at up to 20° from the transverse (Figure 4.5B, D). Pseudowhorls are well spaced, occurring in intervals of 2.5–5 mm. Five to six leaf bases are visible in a row, suggesting 10 to 12 leaves per turn of the axis (Figure 4.5D). Leaf bases are swollen, around 1.5–4 mm high and 0.5–1.5 mm wide and alternate in successive pseudowhorls. This base is oriented parallel to the stem, and

protrudes from the stem margin, before giving rise to a leaf. The emergent swollen leaf bases are most clearly seen on the assigned holotype, AM 7540 (Figure 4.5B).

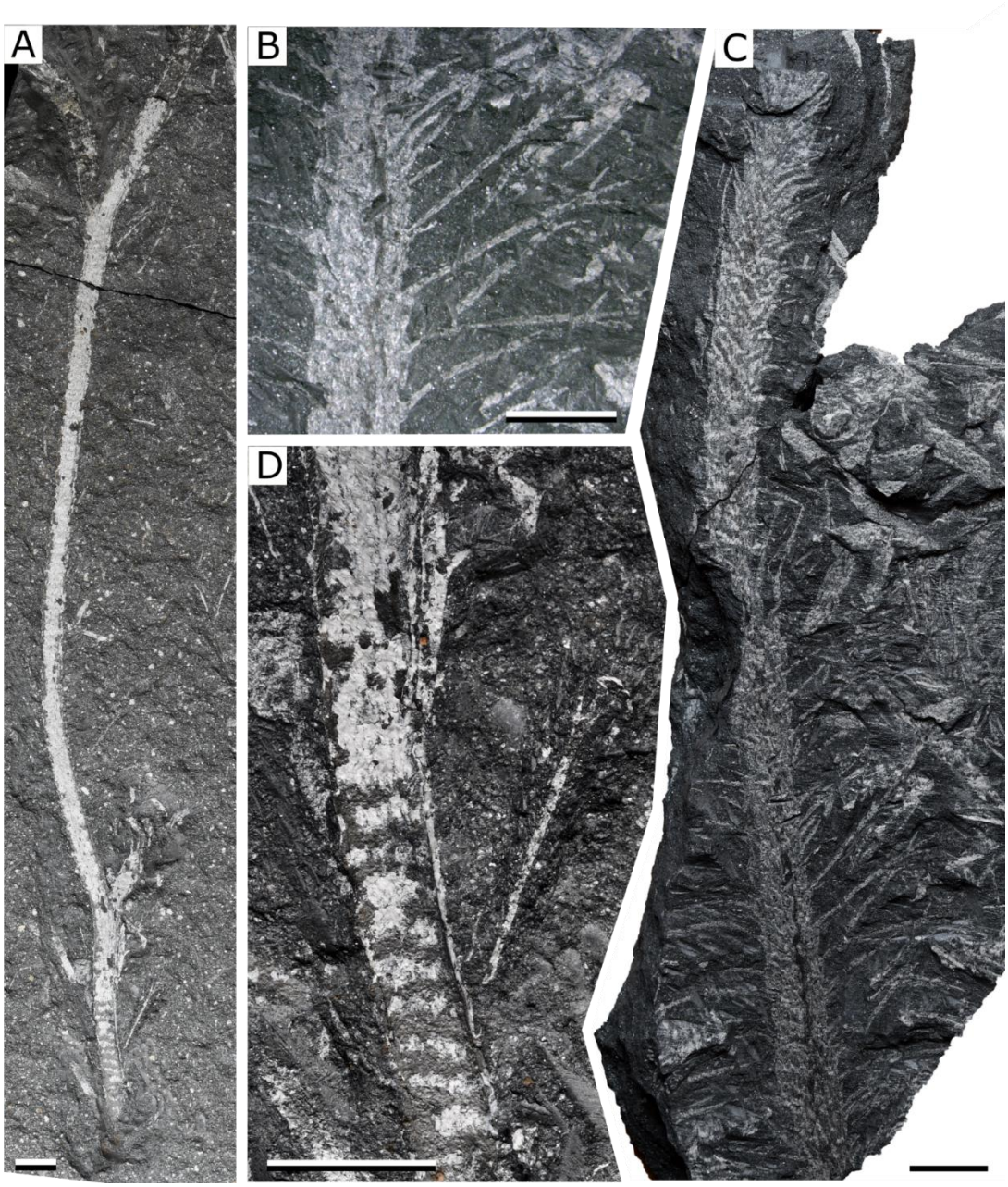

Figure 4.5: *Colpodexylon* sp. nov. B from Waterloo Farm; **A)** elongate axis showing two bifurcations (AM 7541), **B)** enlargement from (C) showing a leaf, **C)** the holotype (AM 7540), **D)** enlargement from (A) showing the leaves. All scale bars = 10 mm.

Four characteristic leaves, three of which remained visibly attached to stems, had previously been prepared from the matrix on the two specimens of this species by Dr. C Prestianni (Figure 4.5B, D). These are consistent in size and morphology. Numerous leaves attached to stems of the holotype diverge from the stem, typically at angles of

30°–70° but up to and exceeding 90°. The complete leaf (excluding the swollen base) is 17.5–21.9 mm in length (n=4), taken from where it emerges from the swollen base to the distal tip. The leaf lamina is narrow and elongate, trifurcating at around 7/8 of the total leaf length (Figure 4.5B, D, 4.6A). The leaf has very straight margins and widens slightly from the base up to the point of trifurcation, where it is maximum 0.7–0.9 mm wide. The three distal segments of the leaf are initially equal in width, around 0.3 mm wide, each tapering to an acute tip. The medial segment is the longest at 3.3–3.9 mm (n=3), and the lateral ones are 2.3–3 mm long (n=8). Lateral segments diverge from the medial one at between 15°–40°.

No sporangia were observed on either of the specimens.

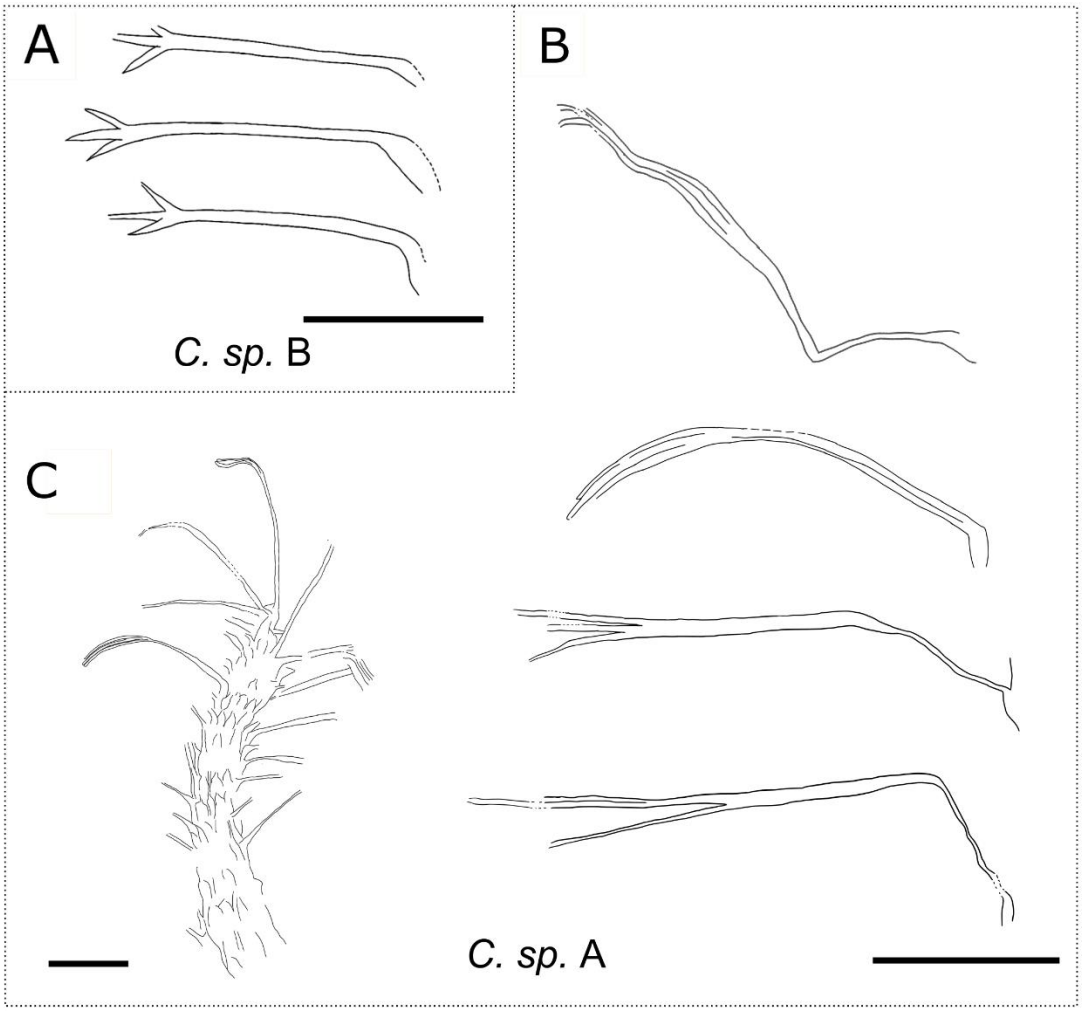

Figure 4.6: **A)** Line drawings of leaves of *Colpodexylon sp. nov*. B, specimen AM 7540, inverted from original orientation. **B)** Line drawings of leaves of *Colpodexylon sp. nov*. A, the lower two from AM 7701, the upper from AM 7702 (inverted), and the remaining leaf from AM 7700. **C)** Line drawing of specimen AM 7700 (*Colpodexylon sp. nov.* A). Stippled lines are interpretive on all drawings, all scale bars = 10 mm.

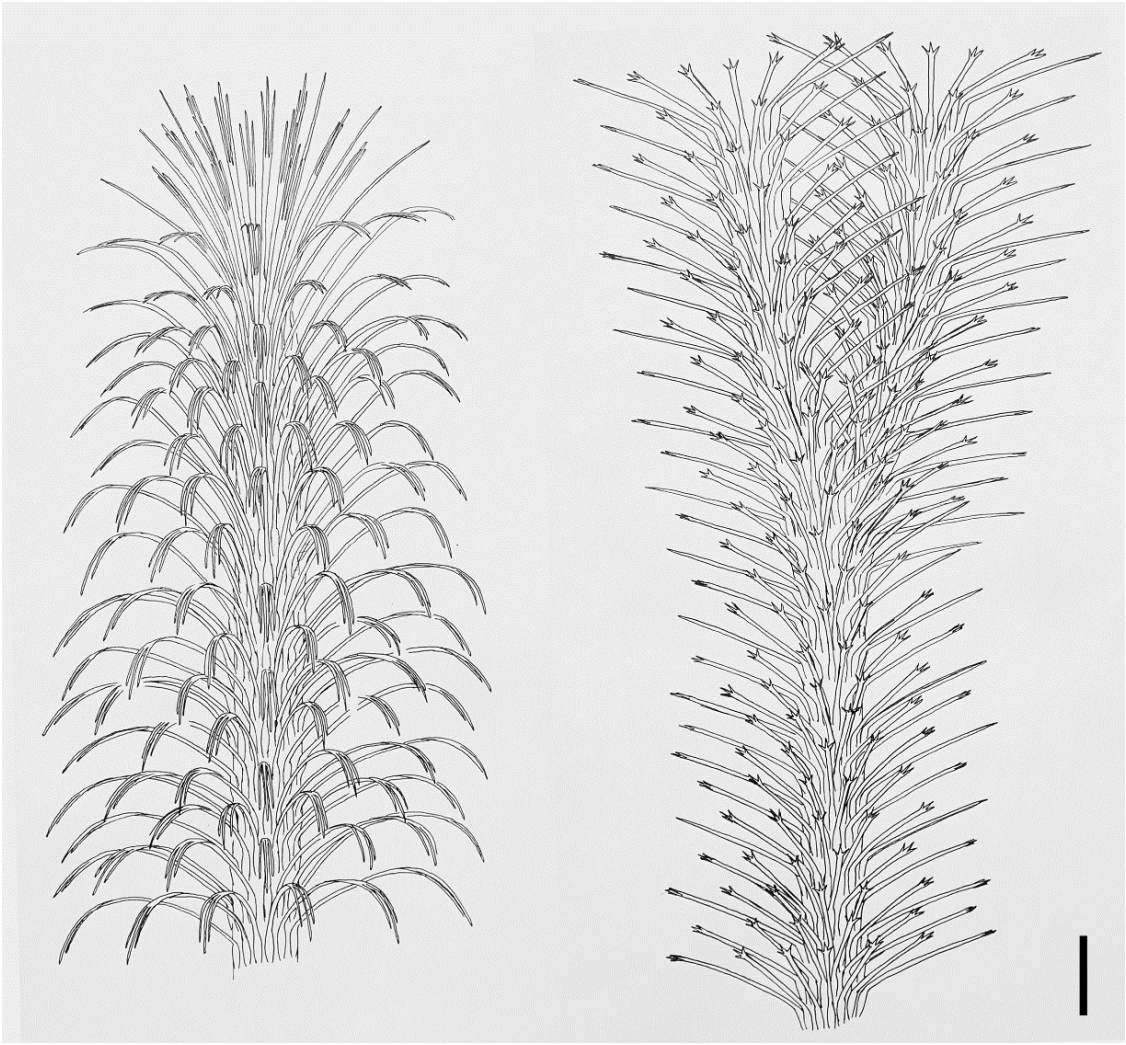

Figure 4.7: Suggested reconstructions of 'lycopod A' (left) and 'lycopod B' (right), scale bar = 10 mm.

Table 4.1: Table of characters for *Colpodexylon* species, modified from Berry and Edwards (1995)

Species	Stem Width (mm)	Swollen leaf base (mm)	Leaves/ Pseudo-whorl	Length X Width (mm)	Central Segment (mm)	Lateral Segments (mm)	Sporangia (mm)	Authors
C. deatsii	12–15	?preserv. 3.5 X 1	16–20	20–30 X 0.5–0.8	12–15	4–8	1.8–3.8 X 0.5–1.6	Banks 1944, Grierson & Banks 1963
C. trifurcatum	10–25	?preserv. 3–4 X 2	8–12	15–30 X 1.4–2	7.5–15	3–5	4.3–6 X 1.5–2.8	Banks 1944
C. cachiriense	5.3–9.5	-	7–9	> 14.7 X 0.6–1	+- 7	+- 3	-	Edwards & Benedetto 1985
C. camptophyllum	12–30	-	16–20	18–19 X 0.6–1.2	3.3–8.6	1.4–3.5	2.4–4.3 X 0.8–1.8	Berry & Edwards 1995
C. coloradense	10–20	-	5–8	5–8.7 X 0.9–1.9	1.2–2.0	0.5–1.6	2.4–4.3 X 0.8–1.6	Berry & Edwards 1995
?C. variable	14–18	1.3–1.7 X 0.8–1.5	15–16	5.3–7.7 X 0.4–0.7	2.0–2.5	0.9–1.1	1.1–1.2 x 1.0	(Schweitzer & Cai 1987) Ma & Xu 2017
C. gracilentum	3.3–15	1.5–2 x 0.5–0.7	7–8	6.5–7.8 X 0.9–1	1.5–2.1	1.5–2.1	2.9–3 x 2–2.2	(Dou & Sun 1983) Xu & Wang 2011
C. sp. nov. A	6–13	2–3 x 1	10–12	23–31.9 X 0.7–0.8	8.4–13.7	7.5–8.9	-	This study
C. sp. nov. B	6–9	2–4 X 0.5–1.5	10–12	17.5–22 X 0.7–0.9	3.3–3.9	2.3–3	-	This study

4.3 Comments

4.3.1 Taphonomy

Leaf bases on the assigned holotypes of both species (AM 7700 and AM 7540) appear to be swollen and emergent from the stem surface. Other specimens of *C. species nova* A (‘lycopod A’), however, have leaves with bases that are less distinctly swollen. In the less swollen state, there is usually some damage, twisting or bending to the remainder of the leaf. On AM 7704 (Figure 4.2), leaf bases are preserved as small arches. Following Banks (1944), we interpret this form as indicating a cross section of the leaf beyond the leaf base. This is supported by a leaf emerging from one such base, extending upwards into the matrix (Figure 4.2D). Visible attachment of a leaf implies that the stem surface is represented, and it appears smooth, with no evidence of

emergent swollen bases. Non swollen bases on AM 7704 may have been reduced by decay or desiccation. Banks (1944) described swollen leaf bases for the type species of *Colpodexylon*, similar in size, or slightly larger, than those observed here, but considered them to have been submerged beneath the stem surface. Berry and Edwards (1995) suggested that the supposed swollen leaf bases of Banks were taphonomic rather than anatomical, and regarded swollen leaf bases as a character uniting the short-tipped *Colpodexylon* species (Berry & Edwards, 1995). The holotype of 'lycopod A', however, suggests swollen bases on a long-tipped species. Since the leaves on this specimen appear relatively undamaged, emergence of leaf bases from the axis implies that this was their form in life. This hypothesis is supported by similarly emerging swollen bases on the holotype of *C. species nova* B ('lycopod B').

The pattern of ridges and grooves observed distally on the axis of AM 7704, is the only evidence for this pattern in the sample. They may represent a decay state of the axis involving the superimposition of inverted, originally thickened areas of outer cortex, as suggested for Venezuelan *Colpodexylon* (Berry & Edwards, 1995). Banks (1944) remarked a similar pattern on *Colpodexylon* axes, suggesting that the lobed xylem strand of the genus has been superimposed on the stem surface after decay of the inner cortical tissues. Characteristic sinuous ridges and grooves occur on axes of most protolepidodendralean species (Bonamo *et al.*, 1988). It is therefore unlikely that the feature is due to the characteristic lobate xylem of *Colpodexylon*. Indeed, Grierson and Banks (1983), identified thickened areas of outer cortical cells directly beneath similar grooves on the surfaces of permineralized *Haskinsia* stems. Berry and Edwards (1995) invoked a detailed taphonomic explanation of the preservation of originally thickened outer cortex as grooves on *Colpodexylon* axes. To what extent swollen leaf bases noted on some of the specimens are related to thickened areas outer cortex is uncertain, given the small number of specimens studied and their advanced degree of compression and remineralization.

4.3.2 Taxonomy

The possession of helically inserted leaves which trifurcate on a single plane indicate that the two species described here belong to the Lycopsid Order Protolepidodendrales, genus *Colpodexylon* Banks 1944, according to the revised generic diagnosis of Berry and Edwards (1995). *Colpodexylon* was a Middle to early Late Devonian herbaceous lycopod (Berry & Edwards, 1995; Berry *et al.*, 2000; Gensel & Berry, 2001). Seven

species are recognized prior to this study (Table 4.1), which include two from the Upper Emsian to Lower Frasnian of New York (see 4.3.3 below), three from the (?) Givetian of Venezuela, and two species from the Middle Devonian of North and South China respectively. Material comparable to the younger New York species, *C. deatsii*, has also been reported from the (?) Lower Frasnian of Columbia (Berry *et al.*, 2000). Equivocal reports of *Colpodexylon* include a stratigraphically poorly constrained example from Vietnam on which trifurcate leaves were not clearly demonstrated (Janvier, Thanh, & Gerrienne, 1989), and a species described from the Famennian of Ukraine, '*C. schopfii'* Lemoigne and Itschenko, 1980. The latter was tentatively assigned to the genus, however Berry and Edwards (1995) doubted this assignment as leaves were smaller than any known *Colpodexylon* species, and were not proven to have been trifurcate. Furthermore, the given reconstruction of a leaf by Lemoigne and Itschenko (1980) shows the leaf to divide three-dimensionally, which is inconsistent with the revised generic diagnosis.

Species of *Colpodexylon* were informally characterized by Berry and Edwards (1995) as either long-tipped or short-tipped species. Long-tipped *Colpodexylon* have leaves which trifurcate at around half of the length of the leaf, whilst leaves of short-tipped species divide distally to produces proportionally short tips (Berry & Edwards, 1995). The two new species, which originate at separate localities, share a number of characteristics such as swollen leaf bases arranged in well-spaced pseudowhorls and a similar number of leaves per helical turn of the axis which would make them difficult to distinguish on the basis of isolated axes. They are however clearly distinguished by having long-tipped ('lycopod A') and short-tipped ('lycopod B') leaves.

'Lycopod A' from Coombs Hill is very comparable in leaf morphology to the New York State long-tipped species, *C. deatsii* Banks 1944 and *C. trifurcatum* Banks 1944. There is significant overlap in the range of leaf sizes recorded in 'lycopod A' and *C. deatsii*, although the former includes slightly longer leaves and has fewer leaves per turn of the axis (Table 4.1). 'Lycopod A' also has longer lateral segments relative to medial segments than *C. deatsii*. *C. deatsii* was recorded in earliest Frasnian-aged deposits in New York and possibly Columbia (Berry *et al.*, 2000). *C. trifurcatum* is older (lower Middle Devonian), and it shares with 'lycopod A' a lower number of leaves per turn of the axis than *C. deatsii* (Table 4.1). 'Lycopod A' differs from both *C. deatsii* and *C. trifurcatum* in exhibiting a greater degree of spacing between successive

pseudowhorls and between leaf bases, which do not contact one another. The well-spaced pseudowhorls are similar to those of *C. camptophyllum* Berry and Edwards 1995, a Venezuelan short-tipped species, but leaves of the latter are far smaller. Though the leaves of the Coombs Hill species are similar to those of *C. deatsii* they are distinguished on the basis of differences in leaf distribution and morphology. Its significant difference in age and palaeogeographical occurrence furthermore support delineation of a separate taxon.

'Lycopod B' has planate leaves up to 22 mm in length that divide distally at around 7/8 of their length to produce proportionally short tips. This distinguishes it from 'lycopod A' and likewise the two New York species. Described short-tipped species of *Colpodexylon* include one from Venezuela, *C. coloradense* Berry and Edwards 1995, and three from China, the validity of which have been disputed. Two of these, *C. gracilentum* Dou and Sun 1983 emend. Xu and Wang 2011 and *C. laminatum* Dou and Sun, 1983 have been synonymized (Xu & Wang, 2011). Prior to this their assignment to *Colpodexylon* had been challenged and suggestion made that preparation of the leaves might reveal them to be more similar to *Leclercqia* or perhaps *Minarodendron* (Berry & Edwards, 1995). Inclusion of the remaining Chinese species, *C. variable* Schweitzer and Cai 1987 emend. Ma and Xu, 2017 within *Colpodexylon* has also been challenged on the basis that this species lacks a characteristic lobed xylem strand (Wang and Berry pers. comm. in Xu *et al*. 2018). Devonian lycopod species with three-tipped leaves described from China also include *Minarodendron* (Schweitzer and Cai) Li 1990 and *Tiamophyton* Xu *et al.* 2018. The former has leaves which trifurcate three-dimensionally, distinguishing it from *Colpodexylon* (Liu *et al.*, 2013). *Tiamophyton* has small three-tipped leaves, bearing an abaxial keel (Xu *et al.*, 2018). We note that all Chinese protolepidodendraleans with trifurcate leaves, have leaves less than 10 mm in length. With their proportionally short leaf tips, the leaves of 'lycopod B' most closely resemble *C. coloradense* from Venezuela though they too were much shorter than those of 'lycopod B' (5–8.7 mm as opposed to 17.5–22 mm long).

'Lycopods A' and 'B' resemble 'short-tipped *Colpodexylon*' in having emergent swollen leaf bases, but both present leaf lengths overlapping with the overall ranges reported for the long-tipped group, and share a number of leaves per pseudowhorl that is intermediate between the lower number generally suggested for short-tipped variety and the higher number proposed for the long-tipped variety (see Table 4.1 for

comparison). Overall the two species present a suite of characters intermediate between the known species of *Colpodexylon*, confirming the prediction of Berry and Edwards (1995) that intermediaries would be found with further searching. It is plausible that 'lycopod B' is derived from 'lycopod A' by reduction in the lengths of the leaf tips, and the possibility of a sister relationship is not excluded.

4.3.3 Range of the genus

Occurrences of *Colpodexylon* in New York, according to Banks (1944), suggest a stratigraphic range of lower Middle to lower Upper Devonian. This age range probably encompasses the ages of those from Venezuela and Columbia, although the latter two occurrences are to some extent correlated on the basis of floral comparisons to New York (Berry & Edwards, 1995; Berry *et al.*, 2000). Berry and Edwards (1995) considered the genus to range from Late-Eifelian to Early Frasnian, a period of less than ten million years (ICS, 2019 (Cohen *et al.*, 2013)). Prior to the present study, the stratigraphically uppermost occurrence of the genus was the type locality of *C. deatsii*; locality 1 of Banks (1944), which he reported as occurring at a quarry along the Delaware River, about one mile southeast of Pond Eddy, New York. Banks included the locality within the Delaware River Flags, considering it to fall within the lower Upper Devonian. The locality, according to Ver Straeten has more recently been mapped within the upper part of the Oneonta Formation (=middle Delaware River Formation of Rickard, L. V., (1975)) confirming a probable Lower Frasnian age (Ver Straeten pers. commun. 2019). Hence, previous evidence suggested the last appearance of *Colpodexylon* to be around 380 Ma.

Material herein diagnosed not only represents the first unequivocal record of *Colpodexylon* in southern Gondwana but also its first known record from the Famennian. These younger occurrences extend the range of the genus by between 10 and 20 million years (Cohen *et al.*, 2013).

CHAPTER 5 – 'LYCOPOD C'

5.1 Introduction

During my honours project (Harris, 2017), lycopod stems from Coombs Hill with closely packed leaf bases displaying a 'checkerboard' arrangement, and bearing small, spine-like leaves along the stem margins, were compared with published records of *Archaeosigillaria caespitosa* (Plumstead, 1967; Anderson & Anderson, 1985). This species includes material from historical collections in the Witteberg Group. The holotype was formerly described as *Bothrodendron caespitosa* by Schwarz (1903), and re-described and assigned to *A. caespitosa* by Plumstead (1967). She identified the specimens as *Archaeosigillaria* based on morphology and distribution of the leaf bases, but was unable to recover leaves on any of the specimens. Additional specimens from stratigraphically higher (Upper Witteberg Group) and lower (Bokkeveld Group) strata were added to the species by Anderson and Anderson (1985), including material formerly assigned to *Drepanophycus, Protolepidodendron, A. devriesii* and *Haplostigma*, some of which had spine-like leaves preserved along the stem margins. Subsequently Berry and Edwards (1997) removed *caespitosa* from *Archaeosigillaria* according to their revised diagnosis of the genus. They however suggested that some of the material illustrated by Plumstead deserved re-investigation with potential for re-inclusion in the genus (Berry & Edwards, 1997).

Archaeosigillaria is a significant name, as it has been reported from Devonian and/or Carboniferous strata on all continents, except Australia (Plumstead, 1967; McLoughlin & Long, 1994; Berry & Edwards, 1997; Carrizo & Azcuy, 2006). The genus exhibits a sigillarian **phyllotaxy** comprising distinct orthostichies (Thomas & Meyen, 1984) and has been considered to resemble a small prototype for the giant sigillarian lycopods that were widespread in the Carboniferous coal swamps, with possible implications of ancestry (Berry and Edwards, 1997).

Archaeosigillaria is characterized by hexagonal patterns on the stem formed from sedimentary infill of swollen leaf bases (Berry and Edwards, 1997). Reviewing published reports of material assigned to the genus, Berry and Edwards (1997) excluded all species lacking clear evidence of **leaf base sediment bodies**, since hexagonal patterns of the stem are a convergent character in fossil lycopods. They retained only the type species, *A. vanuxemi* (Göppert) Kidston 1901, including the

leafless holotype specimen, and material that could be shown to have the characteristic leaf base structure. *Archaeosigillaria*-like stems with leaves were transferred to the genus *Gilboaphyton*. The family Archaeosigillariaceae was resurrected to include these two genera.

Fertile structures of *Archaeosigillaria* and *Gilboaphyton* are unknown, which inhibits understanding of the family's relationships at the ordinal level. Affinity to Protolepidodendrales has been tentatively suggested on the basis of a herbaceous habit and divided leaves (Gensel and Berry, 2001), however, Archaeosigillariaceae is currently referred to as Order *Incertae sedis* (Berry and Edwards, 1997; Carrizo and Ascuy, 2006).

Here, new specimens from Coombs Hill are described in detail and attributed to Archaeosigillariaceae on the basis of leaf and leaf base morphology. The specimens are assigned to a new genus and species, the holotype of which, uniquely for the family, is fertile. This study confirms the presence of an archaeosigillariid in the South African Devonian, and suggests the need for a broad study on other South African material previously attributed to this group. Comparison with the holotype specimen of *Archaeosigillaria caespitosa* suggests a plausible conspecificity, but the lack of leaves preserved on the specimen precludes their synonymy.

5.2 Systematic palaeobotany

Class – Lycopsida Pichi-Sermolli 1958

Order – Protolepidodendrales Pichi-Sermolli 1958

Family – Archaeosigillariaceae Kräusel and Weyland 1949

Genus novum

Species nova

Holotype; AM 7705 (axis I)

Additional specimens; AM 7705 a + b (axis II), AM 7706, AM 7707

Locality; Coombs Hill

Horizon; Plant Press

5.2.1 Generic diagnosis

Lycopodiaceous plant with isotomous branching. Axes ornamented by swollen leaf bases which vary from nearly contiguous, laterally elongate hexagonal, to well-spaced, longitudinally elongate and elliptical. Leaf bases sometimes with internal sediment filled cavities. Leaf bases in helical pseudowhorls, and aligned in longitudinal orthostichies delimited by narrow grooves, and diagonal parastichies. Persistent leaves laminar, adaxially curved, trifurcate at around 2/3 of length, with lateral segments smaller than medial segment. Sporophylls isomorphic to vegetative leaves, occurring near to apex. Sporangia ellipsoid, sessile (?), and borne proximally on adaxial surface of sporophyll.

5.2.2 Specific diagnosis

Axes up to at least 270 mm in length, 5–17 mm in width (n=5), parallel sided, dichotomous with daughter branches equal in width, diverging at 20–30°. Stem surface bearing isotropically distributed swollen leaf bases. Leaf bases occur as protrusive, contiguous hexagons (on larger axes?), or well-spaced ellipses (on smaller axes?), sometimes with an internal sediment-filled cavity around 1 mm long and 0.5 mm wide and deep. Swollen bases up to 3 mm wide and 2.5 mm long, arranged in orthostichies delimited by narrow grooves and diagonal parastichies. Persistent leaves inserted in a low helix, alternating in successive pseudowhorls. Leaves laminate, adaxially curved, up to 5.2 mm in length, around 1mm wide above swollen base, narrowing slightly before trifurcating at around 2/3 of length. Distal segments sub-parallel to axis, acuminate, middle segment around 0.4 mm wide at base and up to 2.2 mm long, lateral segments around 0.3 mm wide at base and up to 1.8 mm long, diverging from the middle at 10–40°. Sporophylls isomorphic to vegetative leaves, occurring near the apex of axis, bearing sessile (?) sporangia on the proximal adaxial surface. Sporangia ellipsoid, elongated parallel to subtending leaf, on average 2 mm long and 1.2 mm high.

5.2.3 Description

Lycopod genus nov., sp. nov. C (hereafter, ‘lycopod C’) is typified by a well-preserved specimen, AM 7705 (Figure 5.1A, B, axis I) and its counterpart (Figure 5.3A), a lycopodiaceous axis having two dichotomies and covered by leaves. Another cross cutting axis of the same species occurs on the same slab (Figure 5.1B, axis II)

Originating at the same horizon were two other slabs, AM 7706 a + b (Figure 5.2B, C) and AM 7707 (Figure 5.2F), bearing specimens also attributed to this species on the basis of axis and leaf morphology.

5.2.3.1 Axes

The holotype specimen (AM 7705, axis I, Figure 5.1) is 288 mm long and proximally 14 mm wide. Two levels of dichotomy are preserved along the axis. The terminal dichotomy is isotomous with daughter branches that appear to be unequal in length. The shorter left-hand terminal segment, however, seems to have suffered damage prior to burial, and it may well originally have been equal in length to its sister branch. A more proximal dichotomy is also observed on the specimen. The fossil has been deposited in such a way that this dichotomy occurs perpendicular to bedding with only the upper daughter branch visibly attached to the parent axis. It was deemed unnecessary to destroy the upper in order to prove the connection between the lower and the parent axis. In width the daughter branches of both dichotomies are between half and two thirds of the parent axis, but roughly equal to each other, and diverge at 20º–30º. The right-hand (underlying) daughter branch of the first dichotomy is distally reflexed towards, and disappears beneath its overlying sister branch. This was revealed by further preparation after the photograph in Figure 5.1A was taken (stippled lines on Figure 5.1B, axis I).

A branch of the same species (axis II, Figure 5.1B) passes beneath axis I near the assumed first dichotomy. At a bedding horizon 8 mm lower down, axis II was unlikely to have been connected directly to the upper specimen prior to burial. The proximal part of axis II was not located but it may remain buried in the matrix (stippled lines on axis II, Figure 5.1B). This underlain, cross-cutting branch is proximally similar in width (9–11 mm) to the daughter branches of the first dichotomy of the overlying specimen. Distally it widens to 17 mm before narrowing again prior to being terminated by the rock edge at a higher bedding horizon than axis I. It is uncertain whether the distal broadening of axis II is related to dichotomy. The final 50 mm of this stem is only visible on the counter-part specimen (Figure 5.3A). Figure 5.1B shows an outline drawing of the counterpart, inverted and aligned to the correct position.

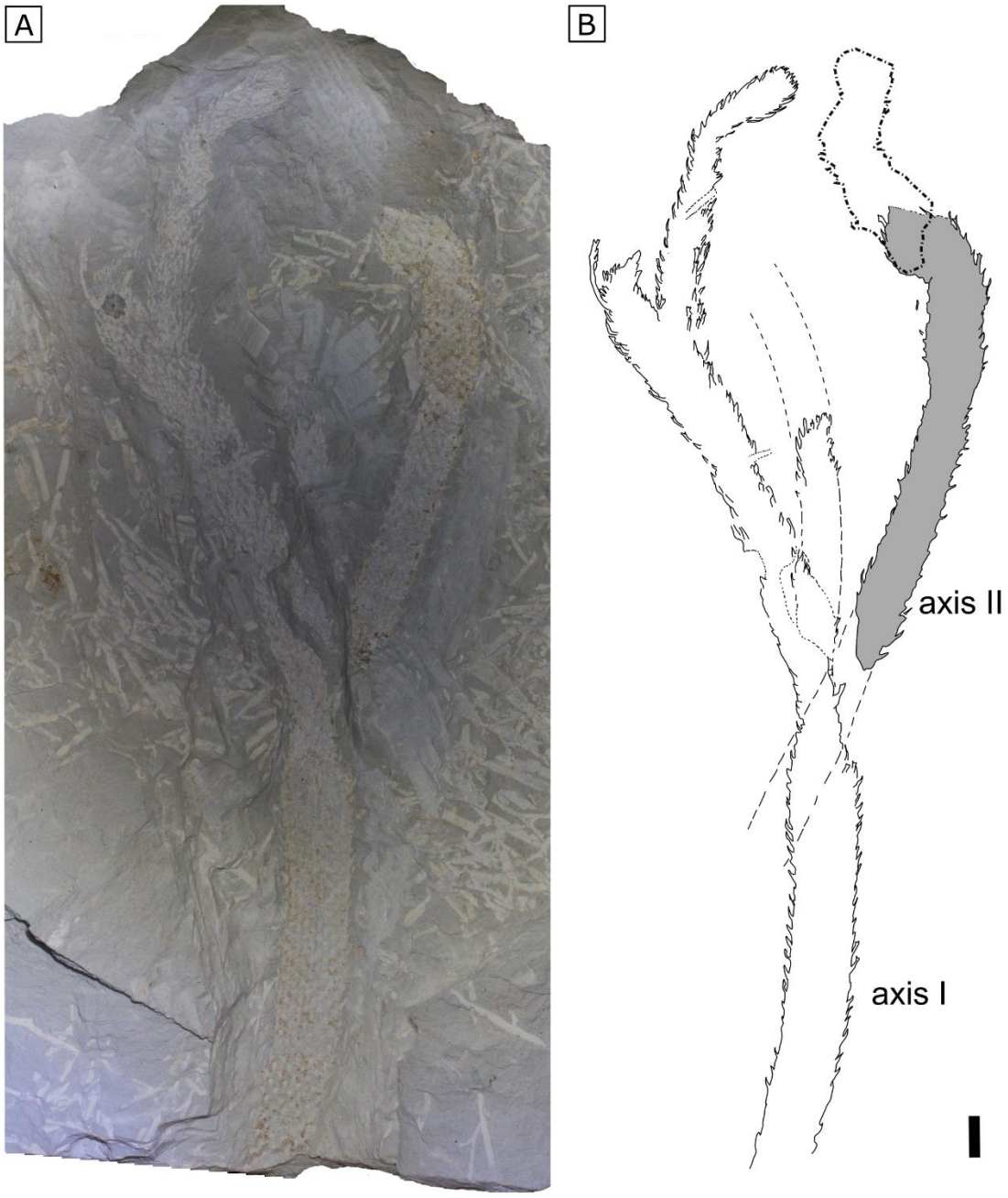

Figure 5.1: **A)** Holotype of 'lycopod C' (AM 7705a). **B)** Line drawing of the specimens in (A), long stipples are interpretive lines, and short stipples represent broken surfaces on the fossil, alternating long and short stipples indicate the approximate original position of the counterpart specimen (illustrated in Fig. 5.3A), which has been inverted and aligned to the correct position. Stippled lines on axis I are informed by preparation of the specimen subsequent to capture of the photograph in A. The visible part of axis II is shaded grey. (A) and (B) to same scale, scale bar = 1cm.

AM 7706 a + b (Figure 5.2B, C) is a branched fragment of axis in part and counterpart, with characteristic leaves attached (see below). The left branch (on the counterpart) is truncated near its base and it adds no information about the nature of branching. The

stem impression shows sinuous grooves between the longitudinal rows of leaf bases. This pattern is not visible over the whole specimen, but it is particularly clear on the proximal region of the counterpart (Figure 5.3C). The part shows corresponding ridges on the underlying side of the axis (Figure 5.3B) Other stem surface impressions in this study are less obviously grooved, to smooth between the leaf bases.

AM 7707 is a large slab with two axes, one around 25 cm long and 9–10.5 mm in width, and the other 18.2 cm long and 10.5–12.3 mm wide (Figure 5.3E, F). They present a slightly convex profile. The axes lie on the same bedding plane, perpendicular to each other. Both terminate in ruptured ends (pre-burial damage), and their origins are lost to rock breakage. Both stems are very regular in width. They differ from AM 7705 in that both are filled internally by sediment, which has been compressed into a thin wafer separating opposing cortical surfaces. Like AM 7706, the axes are also ornamented by sinuous longitudinal grooves (internally ridges) meandering between the leaf bases, although they are much less distinct than on the former.

5.2.3.2 Leaf base arrangement and morphology

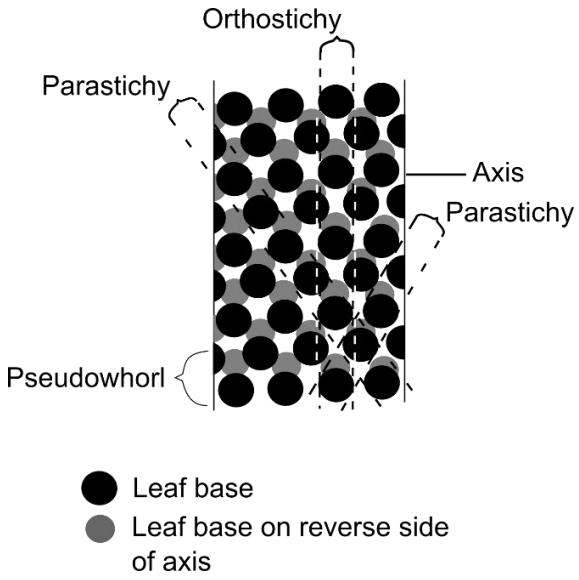

Figure 5.2: Schematic diagram illustrating the geometric arrangement of helically inserted leaf bases on axes of ‘lycopod C’.

Visible stem surfaces are covered by false leaf scars where the splitting plane of the rock matrix has broken through the swollen bases of leaves. Leaf bases show the precise arrangement of leaf insertion on the stem.

On all axes, leaf bases are aligned in orthostichies comprising leaf bases of alternating pseudowhorls aligned in longitudinal rows delimited by parallel sinuous grooves and **parastichies** going both ways at around 45º to the perpendicular (Figures 5.3–5.4). The geometries characterizing leaf bases on the axes are illustrated in Figure 5.2. Their roughly isotropic distribution produces a checkerboard pattern. The true pattern of insertion of leaves appears to be helical pseudowhorls with 4–5 leaf bases visible on one side of thicker stems, and 2–4 on thinner stems suggesting that each pseudowhorl would have had 5–10 leaves in total (Figure 5.3). The number of leaves per pseudowhorl is precisely half the number of orthostichies surrounding the axis. Leaf bases of successive pseudowhorls alternate, and the spacing between pseudowhorls varies from 1 mm to negligible such that successive leaf bases may interlock much like the teeth of a zip.

Leaf bases on the assigned holotype specimen, AM 7705, are not very clearly preserved and vary in size and shape. Axis I is exposed at various preservational levels along its length; proximally exposing the level of swollen leaf bases, and distally revealing leaves underlying the axis. Along the proximal region of the axis, leaf bases are represented by small longitudinally elongate ellipses of fossil tissue up to 2 mm high and twice high as wide (Figure 5.4C). Immediately prior to the first dichotomy, the axis is ornamented by larger, contiguous leaf bases up to 2.5 mm long and up to 3 mm wide, which are roughly hexagonal to rhombic in shape, and are delimited by a pattern of narrow grooves or ridges. This type of leaf base is also expressed on the counterpart specimen, which represents the distal expression of axis II. The topography of the bases on the specimen is only visible under low-angled illumination (Figures 5.3D, 5.4A). There appears to be some interference between structures of opposing surfaces of the stem (Figure 5.4A). This may be a result of the absence of sedimentary infill of the axis. Evidently the axis was rapidly interred whilst in a very complete state, preventing infill of the axis by sediment following decay of inner cortical tissues, which has permitted superimposition of external cortical surfaces from either side of the axis. The axis was subsequently compressed until essentially flat. Other less complete specimens

from the same horizon, differ in having internal sedimentary infill, resulting in preservation of more distinctive surface topography of the leaf bases.

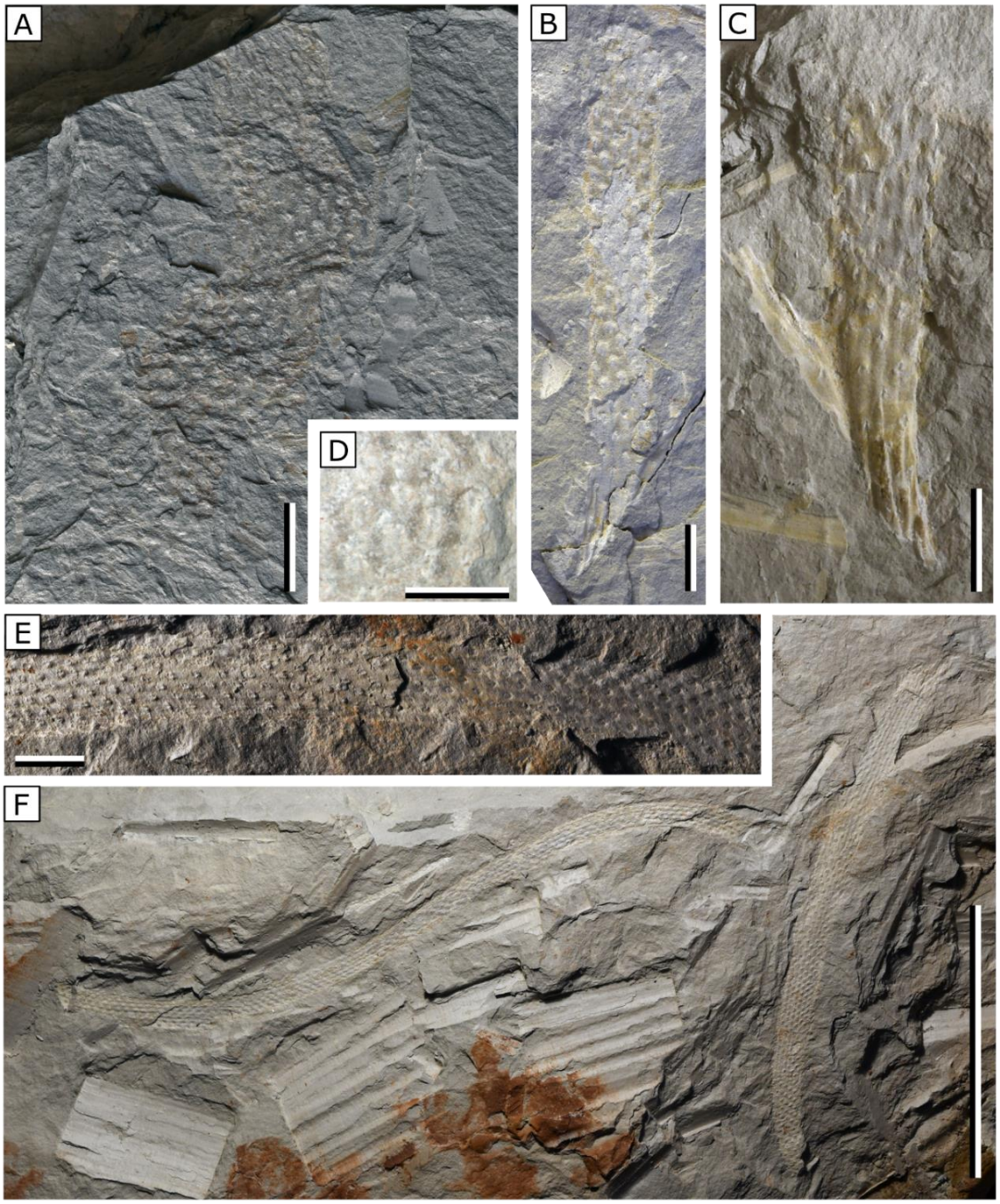

Figure 5.3: **A)** Counterpart to the holotype (AM 7705b) showing the distal section of axis II. (scale bar = 1cm). **B)** Portion of an axis (AM 7706a, scale bar = 1cm). **C)** Counterpart to axis shown in (B) (AM 7706b, scale bar = 1cm). **D)** Enlargement from (A), showing contiguous hexagonal leaf bases, under low angled illumination from top left (scale bar = 2mm). **E)** Enlargement from the right-hand axis shown in (F), under low-angled illumination from the top left, showing opposing cortical surfaces separated by a thin wedge of sediment (middle of photograph) (scale bar = 1cm). **F)** Two partial axes (AM 7707, scale bar = 10cm).

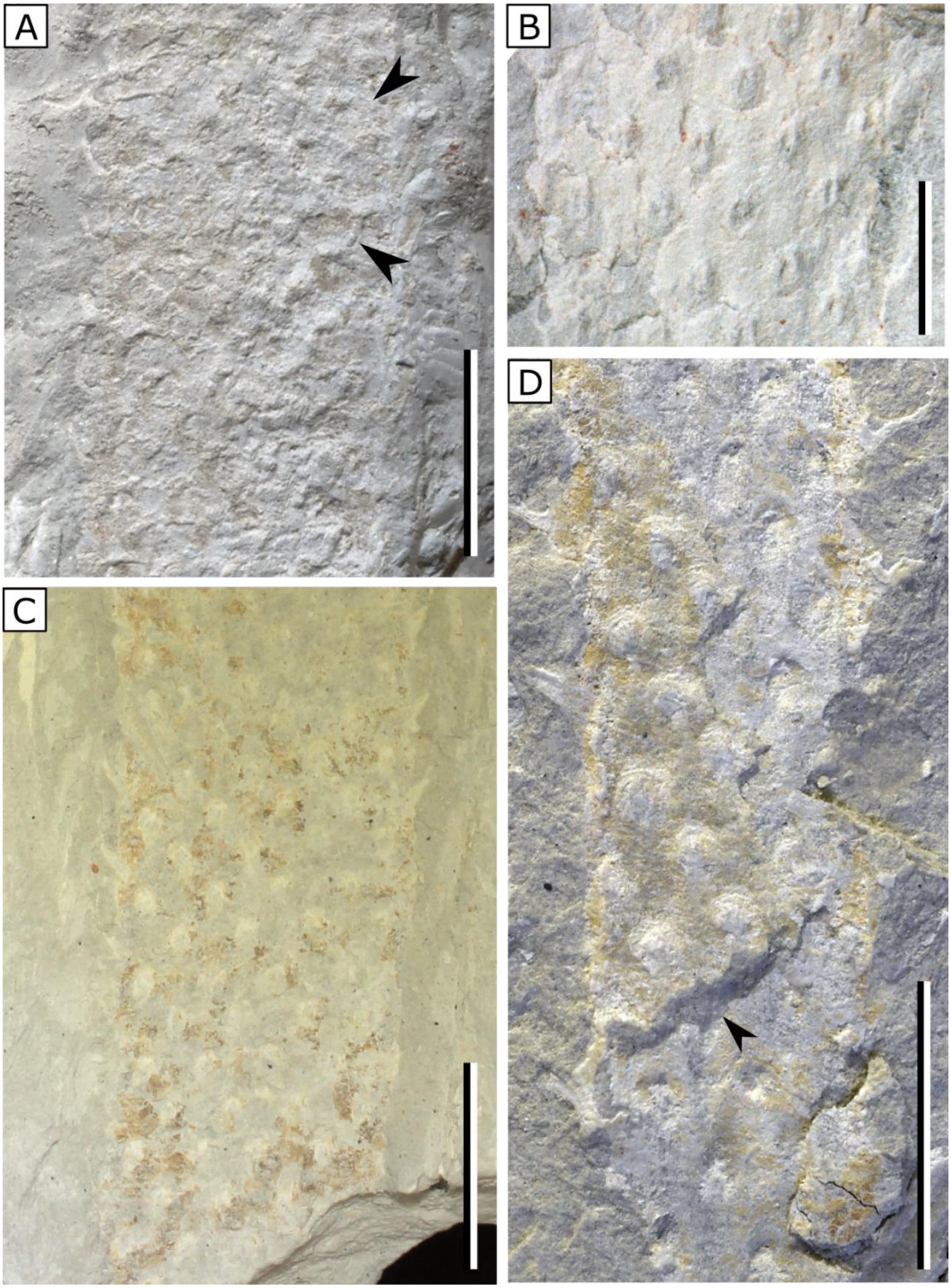

Figure 5.4: **A)** Close up of AM 7705a, photographed under low angled illumination from the top left. Arrows delimit region of the stem where contiguous hexagonal leaf bases are most clearly expressed. **B)** Close up of AM 7707, showing small, elliptical leaf bases, note the sediment visible in the centre of some of the bases. **C)** Enlargement of the proximal section of the holotype (AM 7705a), showing small, elliptical leaf bases. **D)** Close up of AM 7706b. Arrow indicates thin wafer of sediment inside the axis. Note the larger round bases on the overlying fossil surface, and narrower, elliptical bases on the opposing surface underlying the sedimentary wafer. All scale bars = 1cm, except B (5mm).

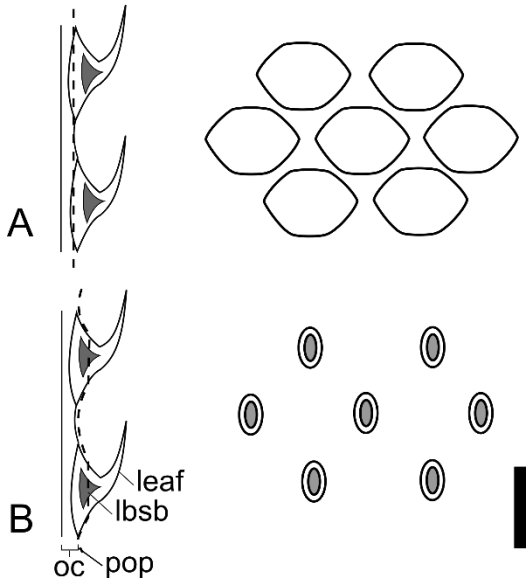

Figure 5.5: Diagram illustrating hypothesis for variation in leaf base morphology as a result of minor differences in plane of parting. **A)** shows on the left a sagittal view of the leaves and leaf bases, with internal lbsb's shaded grey. A stippled line indicates the plane of parting of the rock matrix. Resulting leaf bases in plan view are shown on the right. **B)** Illustrates the same structures shown in (A), with a slightly different level of parting of the rock matrix. Note that parting on B favours the interface between the surface of the axis and matrix. The resulting leaf bases in plan view shown on the right. Abbreviations: pop= plane of parting; lbsb = leaf base sediment body; oc= outer cortex. A and B to same scale, scale bar = 3mm.

Both axes on AM 7707 present leaf bases of a consistent size and shape, conforming to the smaller, elliptical type observed proximally on the holotype. Leaf bases have a similar distribution to that on the holotype, as illustrated in Figure 5.2. That these axes belong to the same species as the holotype is confirmed by leaf morphology (see below). Leaf bases on AM 7707 are well-spaced, longitudinally elongate ellipses, up to 1.5 mm high, and half to two-thirds as wide (Figure 5.4B), which emerge in positive relief from the axis. Leaf bases preserved on the opposing surface (facing the rock matrix) of the stem produce an inverse morphology, being depressed rather than raised (Figure 5.3E). Each elliptical leaf base comprises a raised ring of fossil tissue with a central crater of sediment. Grey mudstone is visible in the centre of many of the leaf bases, comprising leaf base sediment bodies in plan view (Figure 5.4B). Central to most leaf bases on the specimen, overlying the sediment-filled cavity, a longitudinally elongate organic trace 0.4–0.8 mm long and 0.2–0.4 mm wide, is visible, indicating emergence of the leaf external to the sediment-filled cavity. The stem surface is smooth in texture between the leaf bases, and along certain sections of the axes, the leaf base orthostichies occur on ridges, separated by shallow grooves. This subtle topography is

only evident under low-angled illumination (Figure 5.3E). Leaves are adpressed onto the surface of the axes (Figure 5.6F), and this indicates that the true surface of the axis is represented in between the leaf bases. Along axis margins, leaf bases are preserved in sagittal view, each presenting a round protrusion up to 3 mm long and up to 1.5 mm deep (Figure 5.6F, G. I). Where parting of the matrix has intersected the midline of the leaf base, a sediment filled cavity is sometimes visible, representing a leaf base sediment body in profile view (arrows on Figure 5.6E, G). This cavity is up to 1 mm high and up to 0.5 mm deep. It is subtriangular to rhomboidal in shape, with a concave medial margin(s), and convex lateral margins. The walls of the leaf base surrounding the cavity are as little as a quarter of a millimetre thick.

AM 7706 (Figure 5.3B, C) preserves a short section of axis in part and counterpart. In addition to bearing characteristic leaves, as well as leaf base sediment bodies (Figure 5.6E), the specimen provides a link between the distinct leaf base types observed on AM 7705 and AM 7707. The part is ornamented with a pattern of round, nearly-contiguous leaf bases, each of which is 2.5–3 mm in height and width. They suggest a similar form and arrangement to those of the holotype, although their margins are more rounded. The leaf bases are slightly raised, and are separated by shallow depressions. A section of the axis where the thin wedge of endocortical sediment (arrow, Figure 5.4D) has pulled away reveals a different leaf base morphology on the opposing surface of the compressed axis. Here, leaf bases are represented by small, well-spaced ellipses, up to 2 mm high and around twice higher than wide. These bases seen on the corresponding section of the counterpart (Figure 5.3C), appear almost identical to the leaf base types observed on AM 7707. Between the smaller leaf bases, the cortical surface is smooth in texture, by contrast with the coarser texture surrounding the larger round bases on the opposing surface. It is most likely that variation in leaf base morphology and apparent surface texture are the result of different levels at which parting of the matrix has intersected the leaf bases. This hypothesis is demonstrated in Figure 5.5. Smaller, well-spaced, protrusive leaf bases are interpreted as representing intersection higher up on the leaf base, external to the stem surface, where leaf base margins converge to form the leaf. The surrounding smooth surface, like on AM 7707, is the true surface of the stem. Larger, nearly contiguous bases are intersected more proximally, at a level just beneath the stem surface.

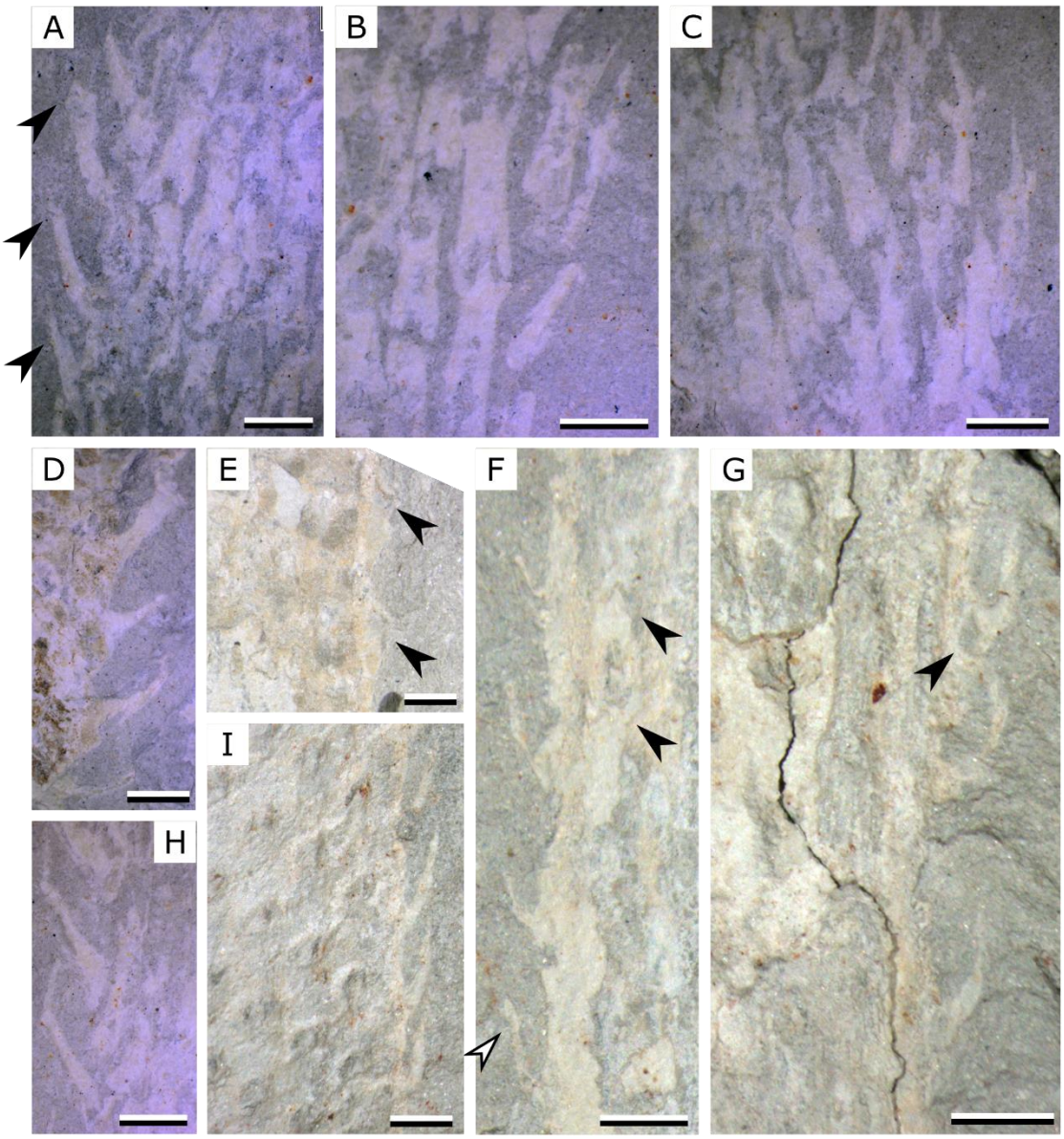

Figure 5.6: Microphotographs of leaves, photographed under cross-polarized, unilateral light; **A–D, H)**, enlargements from the holotype (AM 7705a), with arrows on (A) indicating the point of leaf trifurcation, **E)** enlargement from AM 7706a, arrows indicate leaf base sediment bodies exposed in profile at axis margins, **F, G, I**) enlargements from AM 7707, black arrows on (F) show leaves adpressed onto the axis, white arrow indicates trifurcation of the leaf, arrow on (G) indicates leaf base sediment body. All scale bars = 2mm.

5.2.3.3 Leaf morphology

Leaves are visible in profile all along the margins of the stem on all five of the axes ascribed to the new genus and species (Figures 5.1, 5.3), where they usually appear spine-like; curving adaxially, and tapering from the swollen base to a distal point. Careful study of leaves in face view, however, shows them to be laminate and

consistently trifurcate (Figure 5.6). These are most clearly preserved on the holotype. It was with great difficulty that trifurcation was demonstrated on the other specimens. Attempts at preparing leaves presumed to extend into the sediment below the axes on AM 7707 failed, and it was later discovered that the leaves have been adpressed against the stem. A few of these are very faintly visible and trifurcate in a similar manner as on the holotype (arrows on Figure 5.6F).

Leaves on the holotype (AM 7705, axis I), observed in plan view on the underside of the axis (Figure 5.6A–C), are the best preserved in this sample. The leaves show most of the length of the laminae, truncated slightly above the swollen bases. The latter have been lost along with most of the counterpart during preparation of the specimen. This distal region of the part offers a rare internal view of leaves. The cross-section of the leaf near the base, where it curves towards the viewer, is arched, implying that the abaxial surface of the basal part of the leaf is convex (Figure 5.6A–C).

Leaves are 3.7–5.22 mm in length, measured along the adaxial margin from insertion on the stem to the distal tip. Above the enlarged base, the leaf is up to 1.1 mm wide in face view. From this relatively wide base, leaves narrow slightly before trifurcating at around 2/3 of the total length, producing three distally pointed segments (Figure 5.6A–C, F). The terminal segments each taper evenly to a point. The middle segment is usually slightly wider (ave. width 0.4 mm, n=6) and longer (up to 2.2 mm, ave. length 1.6 mm, n=11) than the lateral ones (ave. width 0.3 mm, n=5; and up to 1.8 mm in length, ave. 1.3 mm, n=4). Lateral segments diverge at 10–40° from the middle one.

Observed in profile (side view) at stem margins, leaves diverge from the stem at 25–50° and are adaxially curved. Distal tips of leaves are subparallel to the stem margin. Some leaves have a sharp adaxial bend around the level of trifurcation (Figure 5.6H), and others are gradually curved (Figure 5.6G). Preserved in profile some of the leaves appear thickest immediately above the swollen base, up to 1 mm wide, and others appear no wider near the base than over the rest of the leaf. The leaves along the margins have been preserved side-on, and laterally compressed, so that their apparent sagittal thickness is likely increased by varying degrees of bending and crushing during burial and lithification. Attempts at preparing out whole leaves preserved in this manner have been futile, probably as a result of the damage sustained by lateral compression. Hence, it is rare that more than one distal segment is visible on leaves preserved in

profile. Where visible, the lateral segments point towards the stem slightly and the middle segment is more sub-parallel to the stem (Figure 5.6A, G).

5.2.3.4 Fertile organs

Towards the distal part of the holotype specimen, AM 7705, several elliptical structures interpreted as sporangia are borne about the stem, apparently in attachment to the adaxial surfaces of leaves (Figure 5.7B–E). Their margins are indistinct, but their consistent size and appearance indicates a repeated structure. Sporangia are 1.4 mm–2.7 mm long (mean = 1.97 mm, n=8) and 1 mm—1.7 mm wide or high (mean = 1.22 mm, n=8). At least six leaves along the margins of the stem have these structures, positioned on the proximal upper surface of the leaf, prior to its adaxial curve. The structures are oriented with the long axis in parallel to the subtending leaf. The means of attachment cannot be discerned, but no evidence of a pedicel is observed. More of them can be distinguished in superimposition on leaves preserved in face view, but in most cases their boundaries are obscure due to dense mineralization (Figure 5.7E, arrows). Leaves associated with these structures are measured up to 6 mm long (marginally longer than vegetative leaves), but are otherwise no different in shape or proportion from the typical vegetative leaves.

The sporangia are not well preserved, and no ornament or in situ spores were observed. Their fine mineralization suggests that sporangia were more delicate than the subtending leaves. Sporangia are only observed in attachment to leaves along the distal 3 cm of the right-hand terminal branch of axis I on the holotype (AM 7705a).

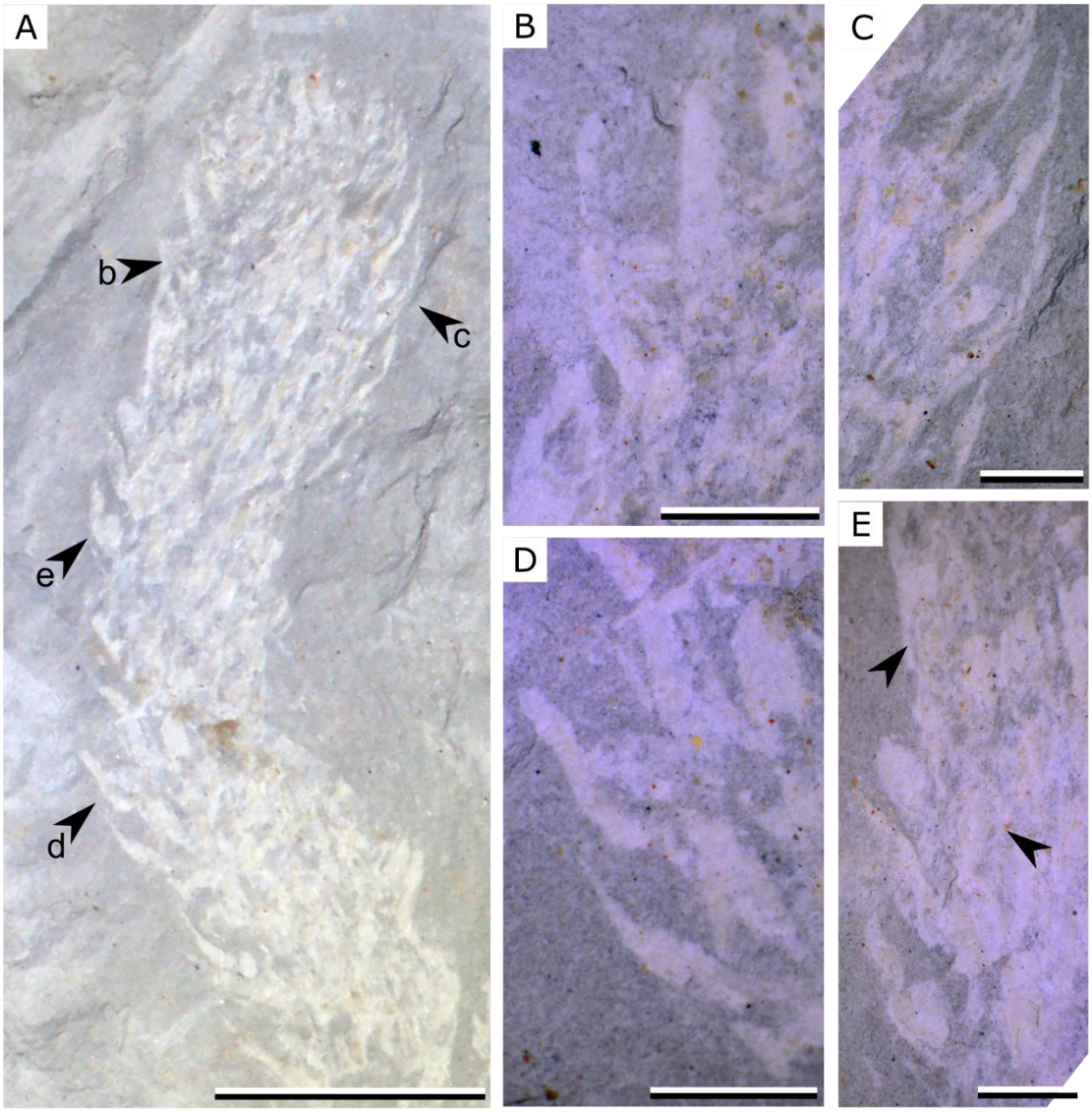

Figure 5.7: Fertile leaves and sporangia of 'lycopod C'; **A)** enlargement of the distal part of axis I on the holotype (Figure 5.1A, scale bar = 1cm), arrows labelled b–e indicate the position of microphotographs B–E on the specimen, **B–E)** enlargements of sporophylls and sporangia, arrows on (E) indicate elliptical structures adpressed onto leaves. Note that the sporophyll in (B) was prepared further after the photograph (A) was taken. Scale bars for B–E = 2mm.

5.3 *Archaeosigillaria caespitosa* (Schwartz) Plumstead 1967

(Holotype figured by Plumstead, 1967, plate XI, no. 6; Anderson et Anderson 1985, Plate 8, no. 13)

The holotype (AM 142) comprises a cylindrical sandstone cast, 45 mm long and 15 mm in maximum diameter, truncated at both ends (Figure 5.8A). The specimen was

collected in 1853 by A. G. Bain in the Cold Bokkeveld of the Ceres District. Its museum call card places it stratigraphically in the Lower Witteberg Group.

The specimen is preserved as a dark, fine-grained ferruginous oxide, and is uniformly dark in colour where broken. The surface of the specimen is ornamented by prominent elliptical mounds, representing leaf bases. A veneer of beige coloured, coarser-grained sediment covers the specimen between the leaf bases, presumably comprising remnants of the matrix. Leaf bases are isotropically distributed on the stem surface. These are only clearly apparent on one side of the cast as the other is damaged. Leaf bases are arranged helically, in pseudowhorls, and alternate in successive turns of the axis. Six leaf bases are visible in each pseudowhorl on the well-preserved face of the specimen, indicating around 12 leaves per pseudowhorl. As on ‘lycopod C’, leaf bases are aligned in longitudinal orthostichies and parastichies at 35–40° from the perpendicular.

Leaf bases are 1–1.5 mm wide and high, and usually slightly higher than wide, and the spacing between adjacent leaf bases is between 0.5 to 1 mm. Bases vary in size, and those that are truncated closer to the apparent stem surface are larger, with more angular sides, tending towards a hexagonal shape. The perimeter of the leaf base forms a raised rim surrounding a central depression, which on some bases is expressed as a cylindrical cavity, roughly 0.5 mm in diameter (black arrows on Figure 5.8B). The cavity is filled with sediment of a similar colour and texture to that remaining between the leaf bases. It is interpreted as representing a leaf base sediment body. Other leaf bases are smaller, elliptical in shape and more protrusive. Some of the latter present a small triangular protuberance emerging from the centre of the base and extending adaxially (white arrows on Figure 5.8B). These appear to be emergent leaves which are truncated shortly above the base.

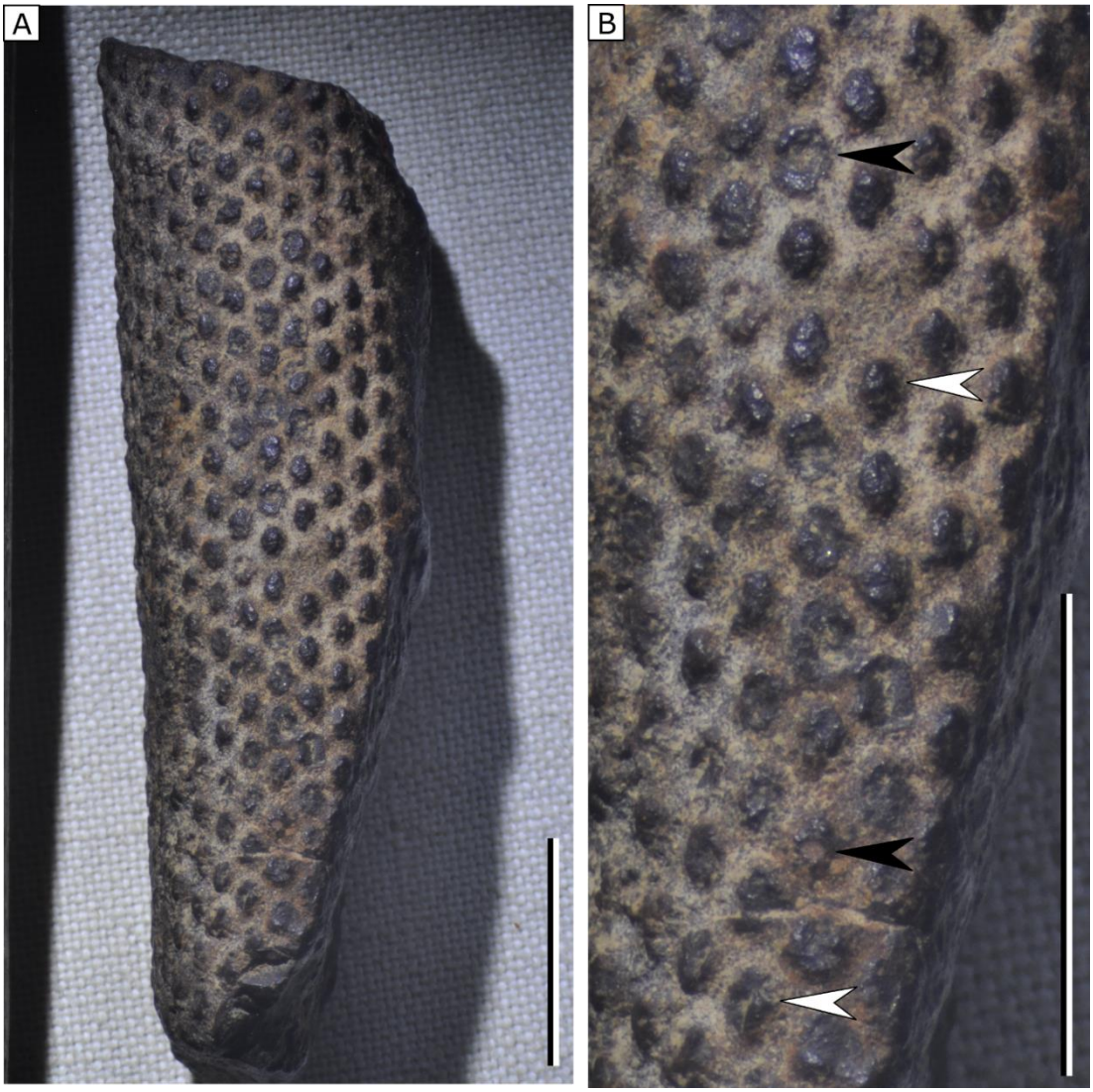

Figure 5.8: **A)** Holotype of *Archaeosigillaria caespitosa* (AM 142). **B)** Enlargement from the proximal part of the specimen in (A) showing morphology of the leaf bases, black arrows indicate leaf bases having a central sediment-filled cavity, and white arrows indicate leaf bases with an emergent triangular protuberance. Scale bars for A and B = 1cm.

5.4 Summary and comments

A new genus and species (‘lycopod C’) of Devonian lycopod is here described. It is characterized by helically arranged laminate leaves up to 5.2 mm in length, which trifurcate at around two-thirds of the leaf length to produce three distally pointed, acuminate tips, the lateral of which are marginally shorter and thinner than the middle. A sporangium is borne adaxially on the proximal surface of the distal leaves. Subtending sporophylls are isomorphic to vegetative leaves, and only occur within a few centimetres of the apex of the plant. Leaves are attached to swollen bases. A

sediment-filled cavity within leaf bases occurs where taphonomy has facilitated replacement of decay prone inner tissues of the stem with sediment – though the holotype was preserved prior to this level of decay. The leaf bases range in preserved morphology from nearly contiguous, laterally elongate hexagons, to longitudinally elongate, well-spaced ellipses, arranged in longitudinal rows delimited by narrow grooves. Leaf bases are roughly isotropically distributed about the surface of the axis.

The two successive dichotomies of axis I on the holotype (AM 7705) are orientated at 90° to each other. This may be related to branching geometry of the plant, or to partial twisting of the axis. Burial of the first dichotomy perpendicular to bedding was facilitated by rapid burial characterizing this mudstone horizon. Twisting of the axis to remain in this unbalanced state would require attachment to a proximal vegetative structure. A more proximal dichotomy giving rise to axes I and II is plausible given their cross-cutting relationship, and complete state of preservation. Available evidence is however equivocal.

5.4.1 Taxonomic affiliation

The new species is assigned to Lycopsida on the basis of helically arranged, apparently microphyllous leaves, and sporangia borne adaxially on the leaves. Divided leaves and sporophylls that are isomorphic to the vegetative leaves are characters that unite the protolepidodendralean lycopods, and on this basis the new species is assigned to Protolepidodendrales (Berry & Fairon-Demaret, 2001). Among protolepidodendraleans, several taxa have three tipped leaves. *Colpodexylon* has leaves which trifurcate in a planate manner, *Minarodendron* has leaves that trifurcate three-dimensionally, producing perpendicularly oriented tips, *Tiamophyton* has leaves that trifurcate in a similar manner to *Colpodexylon*, but was differentiated from them by the presence of an abaxial keel on the leaf, *Gilboaphyton* is a possible protolepidodendralean (Berry & Edwards, 1997), and has laminate leaves which produce two relatively small lateral teeth at around midway along the leaf.

Leaves of the new species are superficially similar to those of short-tipped *Colpodexylon* species. '*C. variable*', for example, has leaves that are 5–7 mm in length, which trifurcate at around two-thirds of the leaf length. '*C. variable*' has swollen leaf bases that are round to rhombic where broken open on the surface of stem impressions (Ma & Xu, 2017). Bases are nearly contiguous, and are arranged in a similar manner to

those of ‘lycopod C’. As noted in the previous chapter, it has been recommended that ‘*C. variable*’ should be removed from *Colpodexylon* (Wang and Berry pers. comm. in Xu *et al*. 2018) . Since the generic identity of the Chinese species is unresolved, its relationship to the present material is a matter for further investigation in China. *C. coloradense* from Venezuela has leaves up to 8.7 mm long, trifurcating at around 4/5 of the total length. Unlike ‘lycopod C’, the leaves recurve away from the stem. It has swollen leaf bases, which have an arrangement somewhat resembling that in ‘lycopod C’. In no species of *Colpodexylon* have archaeosigillarian-type sediment-filled swollen leaf base cavities been reported. Despite superficial similarities, ‘lycopod C’ cannot, therefore, be assigned to *Colpodexylon*.

Gilboaphyton is the only three-tipped-leaf lycopod genus with swollen leaf bases, filled internally by sediment (leaf base sediment bodies) (Berry & Edwards, 1997). Overall similarity of the laminate, three-tipped leaves with swollen bases and possession of leaf base sediment bodies indicate that the new species is most comparable to *Gilboaphyton*. *Gilboaphyton* often presents leaf bases as hexagons or ellipses defined by a pattern of grooves on the stem surface (Arnold, 1937; Berry & Edwards, 1997). The genus currently includes three species. *G. goldringiae* Arnold 1937 from the Givetian of New York State, has leaves up to 6 mm long, which broaden from a relatively narrow base to produce two small, distally oriented lateral teeth (0.5–0.8 mm long) from its widest point, approximately midway along the leaf (Fairon-Demaret & Banks, 1978; Berry & Edwards, 1997). *G. griersonii* Berry and Edwards 1997 from the Eifelian of Venezuela and the Givetian of New York State, is similar to *G. goldringiae* in having leaves that produce small distally oriented lateral teeth, but differs in having leaves that are widest at the base, and its leaves are slightly longer and more slender (Berry & Edwards, 1997). In profile the distal part of the leaf lamina of *G. griersonii* curves away from the axis (Berry & Edwards, 1997). *G. argentinum* Carrizo and Azcuy 2006, from the Lower Carboniferous of Argentina, has leaves up to 4.5 mm in length, which are recurved toward the axis, and produce lateral teeth that are transversely orientated. The leaf bases of the Argentinian species are of roughly equal dimensions, in contrast to the longitudinally elongate leaf bases of the American and Venezuelan species (Carrizo & Azcuy, 2006).

Leaves of ‘lycopod C’ share with *G. griersonii* and *G. argentinum* a relatively wide base, from which the leaf narrows. Leaves are very similar in overall size to

Gilboaphyton species. The point of trifurcation is, however, positioned more distally on the leaf in the South African species. Swollen leaf bases are slightly wider than long, or equidimensional, and in this respect are most similar to those of *G. argentinum*. Unfortunately, no fertile material is known for *Gilboaphyton*, and so no comparisons can be made in this regard.

As leaves are known to be somewhat variable amongst lycopods, including the extant genus *Huperzia*, the disparity between 'lycopod C' and *Gilboaphyton* may not exceed the known variability within lycopod genera (Berry & Edwards, 1995). It is tempting, therefore, to include 'lycopod C' in *Gilboaphyton*. This would require emendment of its generic diagnosis, because the new species does not have leaves that are 'divided into a large medial segment and two *substantially* smaller and shorter distal-pointing opposite lateral segments about *midway* along the total leaf length' (my italics) (Berry and Edwards, 1997, p. 63). The lack of information on sporophyll and sporangia morphology in *Gilboaphyton*, however, inhibits unequivocal allocation of 'lycopod C', because we cannot confidently say that its fertile organs characterize the genus. Rather, a new genus is erected, and included within the family Archaeosigillariaceae. Discovery of fertile *Gilboaphyton* may yet suggest 'lycopod C' to be congeneric.

The new genus and species presents a unique record of fertile structures amongst Archaeosigillariaceae. Grierson (1962) reports that one *putative* fertile example was hitherto described within the Archaeosigillariaceae by Senkevitsch (1956), suggesting sporangia borne adaxially on sporophylls. However, more recent research considers the absence of confirmed fertile organs to inhibit ordinal classification of the family (Berry & Fairon-Demaret, 2001; Gensel & Berry, 2001). As a result, the family is placed in *incertae sedis* (Berry & Edwards, 1997; Carrizo & Azcuy, 2006). Fertile structures of 'lycopod C' support of the notion that Archaeosigillariaceae belongs within the Order Protolepidodendrales (Gensel & Berry, 2001).

5.4.2 Variation in 'lycopod C' and comparison with *A. caespitosa*

'Lycopod C' presents a variety of apparent leaf base morphologies. This wide disparity in appearance amongst lycopod stems of a single species from a common stratigraphic horizon, demonstrates the well-known problem of lycopod taxonomy based on stem varieties (Chaloner *et al.*, 1980; Bonamo *et al.*, 1988; Berry & Edwards, 1995; Gensel & Pigg, 2010). Lacking leaves, the various types of apparent leaf bases in 'lycopod C'

specimens might be attributed to more than one ‘form’ species. Differences in taphonomy between specimens used to define *Gilboaphyton* and material from Coombs Hill present a challenge for comparison between the former and ‘lycopod C’. Coombs Hill specimens have been subjected to extreme compression and partial metamorphism which have eliminated some of the surface topography normally observed on lycopod stems. Furthermore, the holotype of ‘lycopod C’ was rapidly buried prior to decay of internal tissues and infiltration of resultant cavities by sediment, precluding development of ‘leaf base sediment bodies’.

Variation in preserved leaf base morphology are, in part, attributed to differences in the level of parting in ‘lycopod C’. This serves to explain the variation between smaller elliptical and larger contiguous round to hexagonal bases on the described specimens. The holotype of *Archaeosigillaria caespitosa* likewise exhibits larger, nearly contiguous leaf bases where they have been truncated at or near the surface of the axis, but where more complete, the bases appear as smaller, well-spaced ellipses that each give rise to a leaf.

Hexagonal stem patterns occur variably in *Gilboaphyton goldringiae*. Studying a large sample of the species, which included hundreds of specimens, Grierson, (1962) concluded that the occurrence of hexagonal leaf bases was related to the size of stems, suggesting that the bases of smaller (possibly younger) stems were more elliptical. The small sample of ‘lycopod C’, here studied, is consistent with his observations, since the holotype specimen is the only axis presenting contiguous hexagonal leaf bases, and is also the largest axis in the sample.

The occurrence of apparent leaf base sediment bodies on the holotype of *A. caespitosa* provides an argument for retention of the species for South African stems of the described morphology. ‘Lycopod C’ cannot be synonymized with *A. caespitosa* due to the lack of leaves on the latter, although with similarities in leaf base morphology and arrangement, potential conspecificity is not excluded. Following examples whereby *A. vanuxemi* and *A. conferta* have been retained for leafless archaeosigillariid axes (Berry & Edwards, 1997; Carrizo & Azcuy, 2006), *A. caespitosa* should be retained as such.

A careful review of specimens assigned to *A. caespitosa*, and their stratigraphic horizons is required for a clear understanding of the range and diversity of archaeosigillariids in the Witteberg Group. *A. caespitosa* has been reported from the

Lower to Upper Witteberg Group, suggesting a range from the Frasnian to Early Carboniferous (Plumstead, 1967; Anderson & Anderson, 1985; Evans, 1999). In light of Berry and Edward's (1997) study, the hypothesis that *Archaeosigillaria* in South Africa crosses the Devonian-Carboniferous boundary, will need to be tested by review of the specimens and their localities of origin. *A.* cf. *piconensis* reported from Middle Devonian strata of the Bokkeveld Group, suggests the possible earlier appearance of the genus in the Cape Supergroup (Chaloner *et al.*, 1980). The Bokkeveld specimens were suggested by Anderson and Anderson (1985) to be synonymous with *A. caespitosa*, however, this is equivocal. Current evidence does not allow for extrapolation of the true range and diversity of archaeosigillariids in the Cape Supergroup.

CHAPTER 6 – 'LYCOPOD D'

6.1 Introduction

Two specimens from Coombs Hill present evidence of a putative rhizomorphic lycopod, including a fertile distal branch, and a trunk with isoëtalean-like leaf bases, which may represent separate organs of a tree. This material is compared with the known diversity of Devonian lycopods, and its likely affinities are discussed. The fertile branches are diagnosed as a new genus and species, which combines with *Kowieria* and *Leptophloeum*, to indicate that a diversity of heterosporous lycopods was present at high latitudes during the Famennian.

6.2 Systematic palaeobotany

Lycopsida – Pichi-Sermolli 1958

Order – *Incertae sedis*

Family – *Incertae sedis*

Genus novum

Species nova

Holotype; AM 7708 (a + b)

Locality; Coombs Hill

Horizon; Inner Outcrop

6.2.1 Combined diagnosis

Fertile axes up to 205 mm in preserved length, with at least 2 successive isotomous dichotomies. Daughter branches diverge at 45–60°. Axes entirely covered in persistent vegetative leaves proximally and anisomorphic sporophylls distally. Vegetative leaves entire, linear, up to, at least, 16 mm long and up to 0.3 mm wide, widest at the base and tapering therefrom. Sporophylls entire, linear, 18–28 mm long, with short, narrow pedicel giving rise to enlarged, spoon-like region up to 2.7 mm long and 0.8 mm wide, above which leaf is up to 0.3 mm wide tapering to acuminate tip. Proximal sporophylls

may lack sporangia. Sporophylls in terminal, dichotomizing strobili. A single round to elliptical sessile sporangium adaxially attached to widened portion of sporophyll, with long axis parallel to sporophyll, 1–2.1 mm long and 0.8–1.5 mm high.

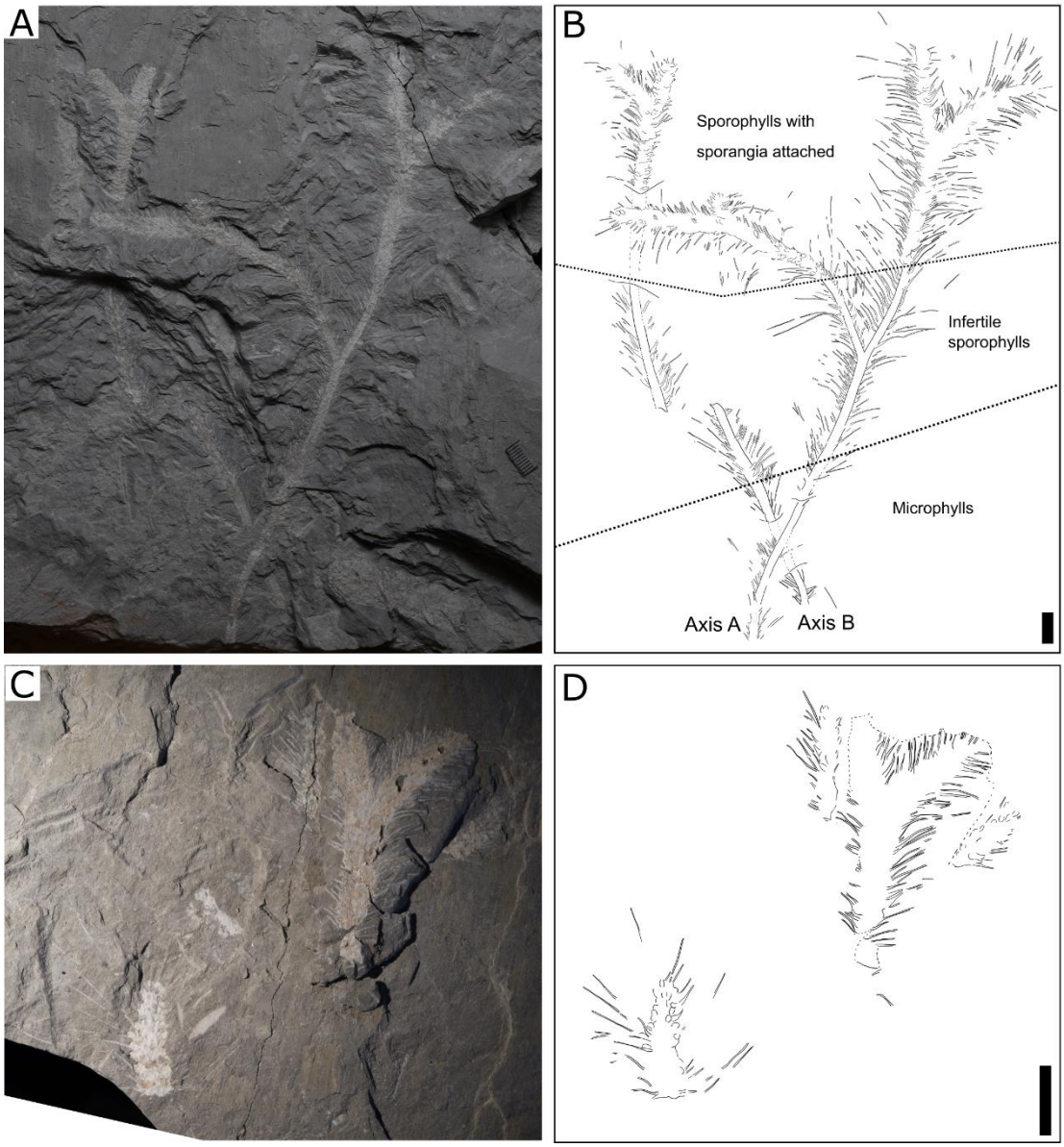

Figure 6.1: Holotype of 'lycopod D' (AM 7708); **A)** part (AM 7708a), **B)** line drawing of part, stippled lines separate areas on the axes bearing different leaf types as labelled. A and B to same scale, scale bar = 1 cm. **C)** Counterpart (AM 7708b) to the upper left area of the slab in (A), **D)** Line drawing of counterpart. C and D to same scale, scale bar = 1 cm.

6.2.2 Description

6.2.2.1 General observations

This description is based on specimens from a single rock slab and counterpart (AM 7708 a and b), which include two similar axes (axes A and B, Figure 6.1B) preserved as

overlapping impressions. Both are terminated proximally by the edge of the rock. The axes are covered by leaves (microphylls and sporophylls) and both have distal apices at approximately the same distance from their preserved origination.

6.2.2.2 Branching

Axis A is the better preserved of the two. It is 201 mm in total preserved length, and exhibits two successive, equal dichotomies. Prior to the first bifurcation, the axis is 93.7 mm long and uniformly 2.8 mm wide. Bifurcation of this axis produces two narrower daughter branches that diverge at 45° and are both 2.3 mm wide. The right-hand branch extends 72 mm before bifurcating at 55° to produce near equal terminal axes, 36 mm and 33.8 mm in length. The left-hand branch of the first dichotomy extends 66 mm before it similarly bifurcates to produce a pair of terminal axes. Only the left of these is entirely preserved on the part specimen and is 34.5 mm long, whereas the right is truncated by a slickenside fault. The remainder of the right-hand terminal segment is preserved on the counterpart where only the distal 17.3 mm are visible (Figure 6.1C). The width of the axes after the first dichotomy is only apparent for the first 25 mm, after which they are obscured by a dense covering of sporangia that extends to the distal tips.

Axis B is 70 mm long and initially 2.3 mm wide. Proximally, near the edge of the slab it crosses underneath axis A, and thereafter widens to 3.8 mm before narrowing again to 2.4 mm where it has been broken off prior to burial. The remainder of this axis has been displaced 15 mm to the left, where immediately above the breakage it is 2.8 mm wide, and extends a further 98.7 mm before dichotomizing terminally. Terminal segments diverge at 60° and are interrupted on the part specimen where they are intersected by a slickenside surface.

6.2.2.3 Notes on structural deformation of the fossil

The specimen has suffered dislocation and displacement of one of the four distal tips on axis A and both on axis B, due to intersection by a slickenside surface. All three apices are preserved on the counterpart (Figure 6.1C). These appear to have been displaced proximally by movement along the slickenside.

To reverse the displacement detailed drawings of both part and counterpart were overlain to scale (Figure 6.2). It was established that both the truncated tips of axis B, as well as the right-hand terminal segment of the left-hand branch of axis A (also

truncated at the slickenside), were displaced by an equal amount (20–25 mm) and in the same direction, parallel to lineations on the slickenside surface. The missing terminal portions of axes a and b were thereby restored to their correct position by reversing the displacement (Figure 6.2B).

Restoration of the original position of the part and counterpart indicates the lengths of the two terminal segments of axis B to be 30–35 mm. Altogether a length of around 205 mm for axis B is estimated.

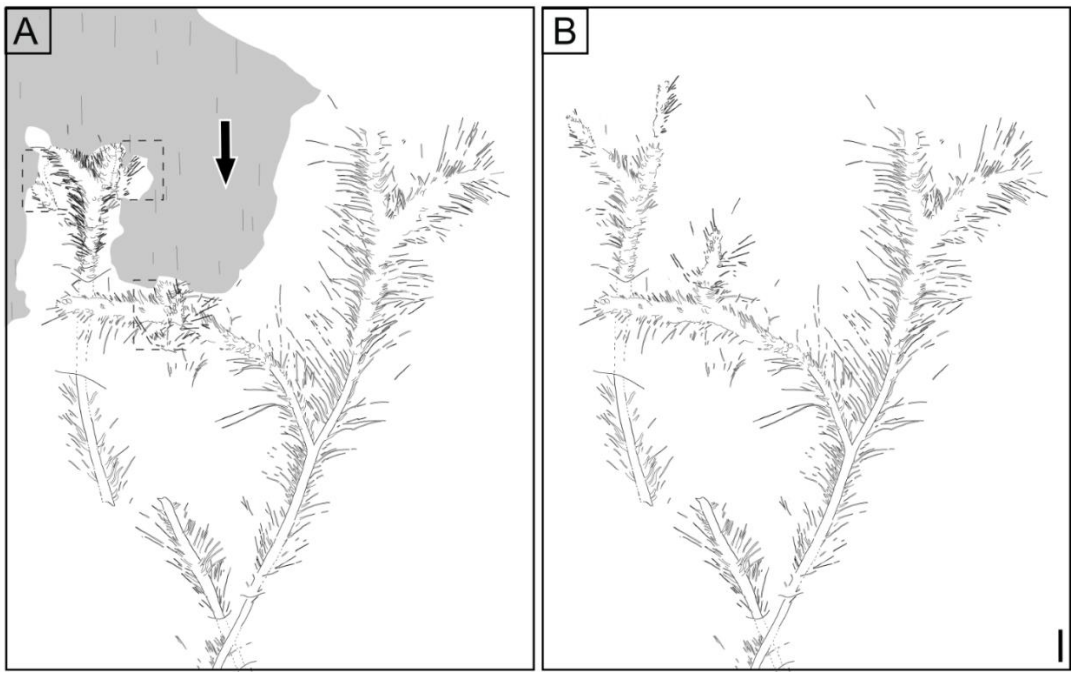

Figure 6.2: **A)** Line drawings of AM7708a and b (Figure 6.1B, D) are overlain to same scale. Drawing of counterpart has been inverted to match that of the part. The grey area shows the extent of exposure of the slickenside surface on the rock slab surface, with parallel slickenlines traced. Dashed lines indicate the distance between the truncated tips of axes on the part specimen, and bases of the corresponding tips on the counterpart. Arrow indicates the extrapolated direction of movement along the slickenside surface. **B)** Restoration of the specimen by shifting the counterpart drawing to reverse displacement caused by the slickenside. (A) and (B) to same scale, scale bar = 1cm.

6.2.2.4 Vegetative leaves

The proximal portions of both axes A and B are entirely covered by microphyllous leaves, which appear densely spaced where seen in profile along their margins (Figure 6.1A, B, 6.3A). No marks of insertion are visible on the axis, and their exact arrangement is not apparent. Vegetative leaves diverge at angles of 15–33° from the axis and the remainder of the leaf is straight to slightly abaxially curved. They are

elongate and needle-like with entire margins. Proximally the microphyll is around 0.3 mm, where it is widest, tapering evenly to 0.1 mm or less distally. Microphylls are at least 16 mm long, but it was not possible to degage their extremely fine ultimate tips. A clear transition occurs between vegetative leaves and the more robust fertile leaves, as seen on axis B (black arrow on Figure 6.3A).

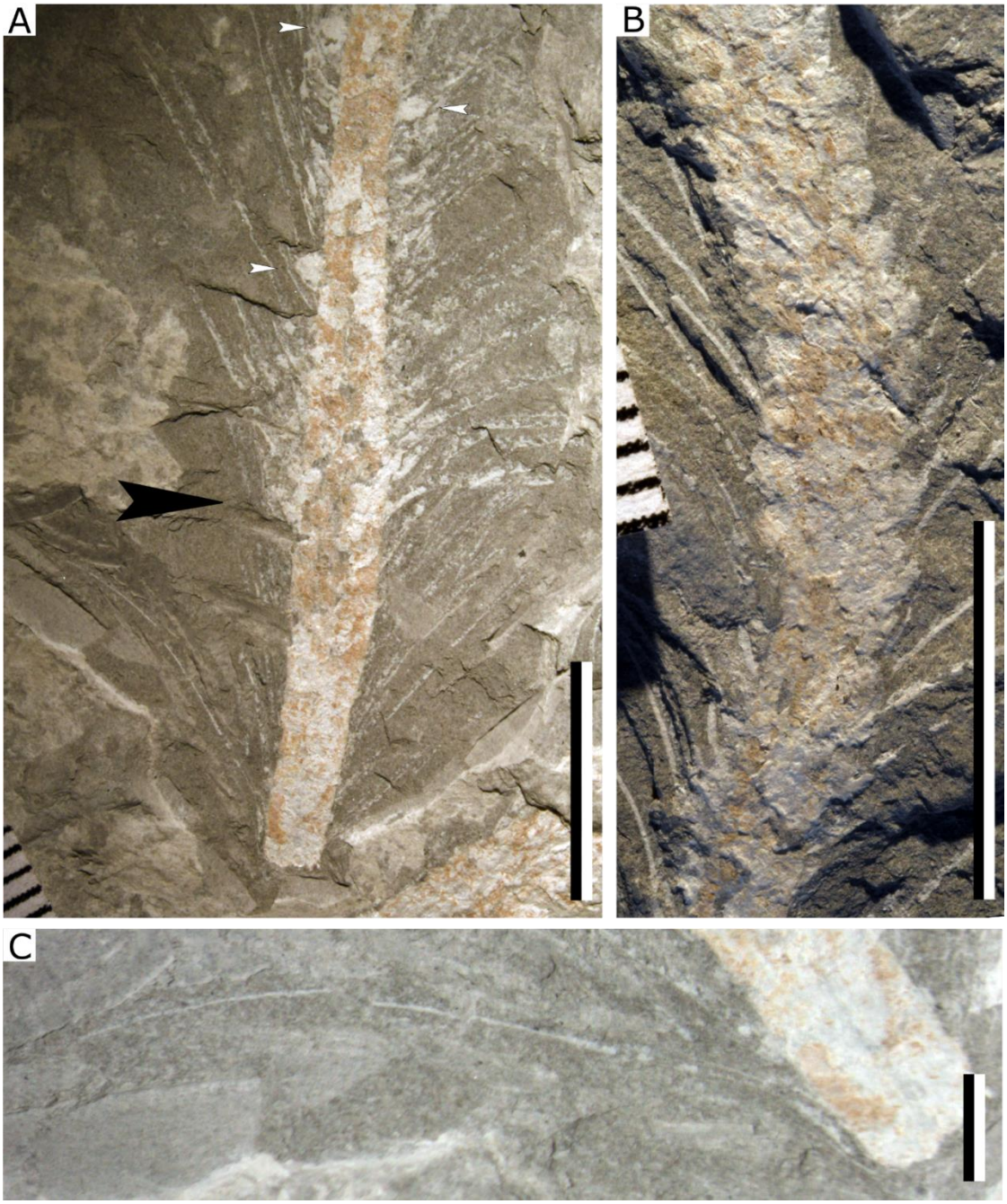

Figure 6.3: Enlargements of AM 7708a; **A)** showing transition from microphylls to sporophylls (largely lacking sporangia) on Axis B (indicated by black arrow), remains of sporangia are indicated by white arrows (scale bar = 1cm), **B)** transition from sporophylls lacking sporangia, to fertile sporophylls on Axis A (scale bar = 1cm), **C)** enlargement of a microphyll from (A) (scale bar = 2mm).

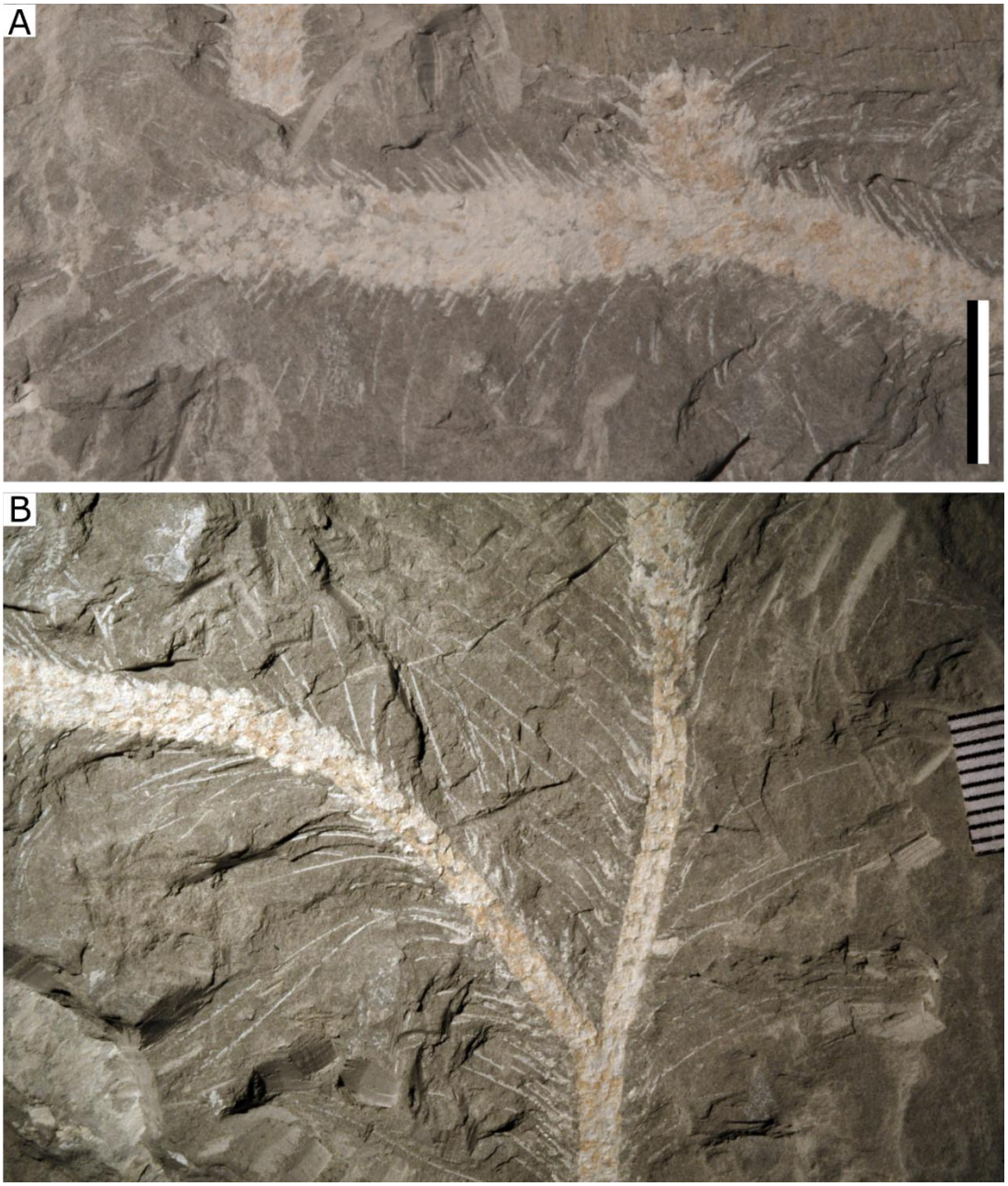

Figure 6.4: Enlargements of AM 7708a (Figure 6.1A, B), **A)** showing left distal bifurcation of Axis A (scale bar = 1cm), and **B)** first bifurcation of Axis A (scale in mm).

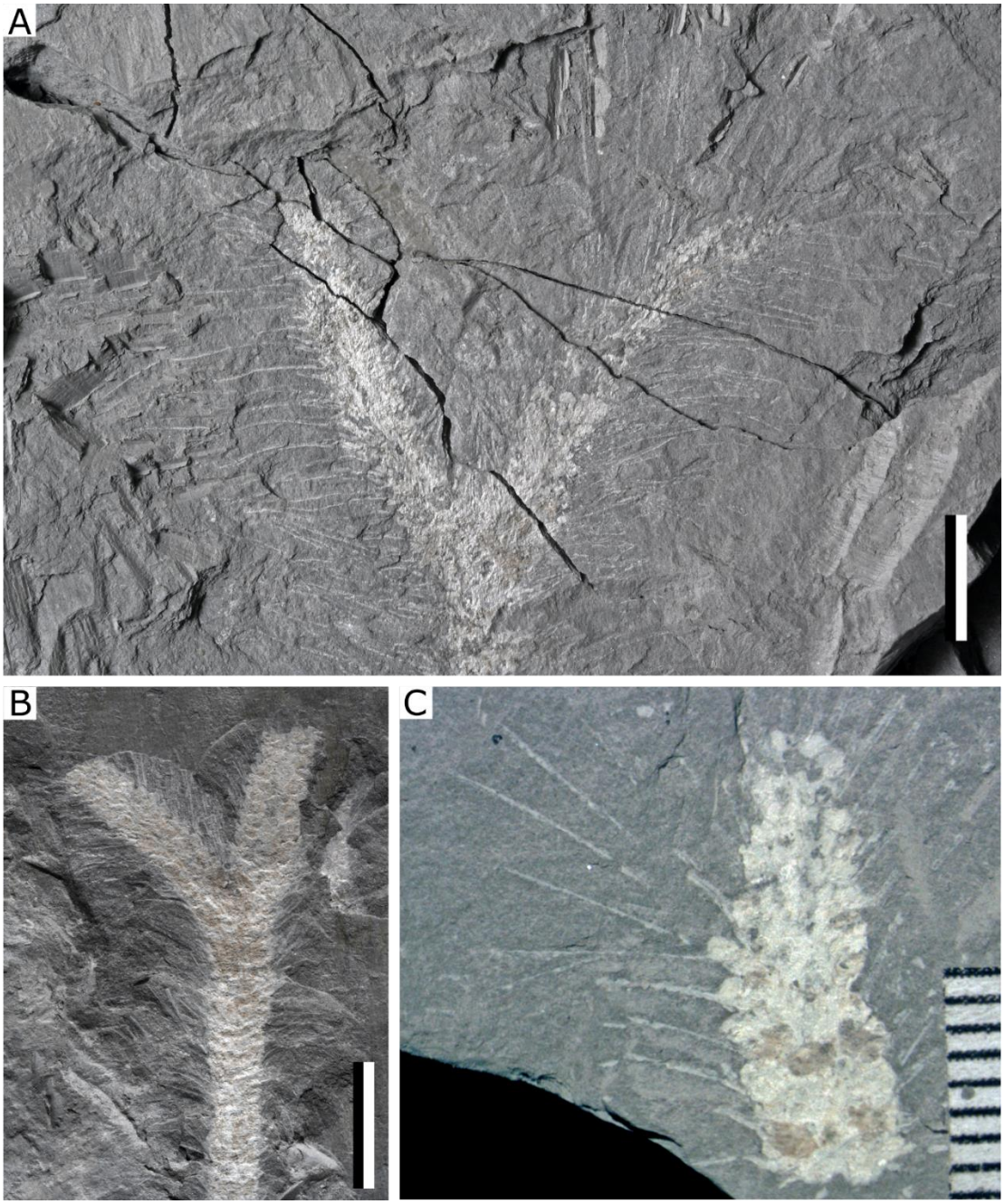

Figure 6.5: Enlargements of AM 7708, **A)** showing the right distal bifurcation of Axis A (scale bar = 1cm), **B)** showing the distal bifurcation of axis B, note that the tips have been truncated by a slickenside surface. (scale bar = 1cm), **C)** enlargement from the counterpart specimen (Figure 6.2C, D) showing the right-hand tip of the left-hand distal bifurcation of Axis A, which was truncated on the part by a slickenside surface (scale in mm).

6.2.2.5 Fertile leaves

Modified leaves bearing sporangia are densely arranged in dichotomizing terminal strobili 70–82 mm long and 4–6 mm wide (Figure 6.4A, 6.5A, B). This terminal fertile

region encompasses the second preserved level of bifurcation on axis A, as well as the distal bifurcation of axis B (Figure 6.1B). Fertile sporophylls are attached from around midway between the first and second successive dichotomies to the apices of axis A. More proximally on the axis is a zone bearing apparent sporophylls, most of which lack sporangia. Infertile sporophylls are attached to axis A from 5 cm above its preserved origin, extending beyond the first dichotomy until a clear transition to the fertile region at the same level on both daughter branches (Figure 6.1B, 6.4B). Although corresponding zones of both fertile and infertile sporophylls occur on axis B, the transition is obscured by matrix where axis B passes underneath axis A. The more proximal sporophylls are interpreted as sporophylls from which the sporangia have abscised, although a few of them do appear to retain weathered-looking sporangia (Figure 6.3A). A spoon-like widened base is evident on all sporophylls, and where present, sporangia appear to be borne within this expansion of the leaf (Figures 6.3B, 6.5C).

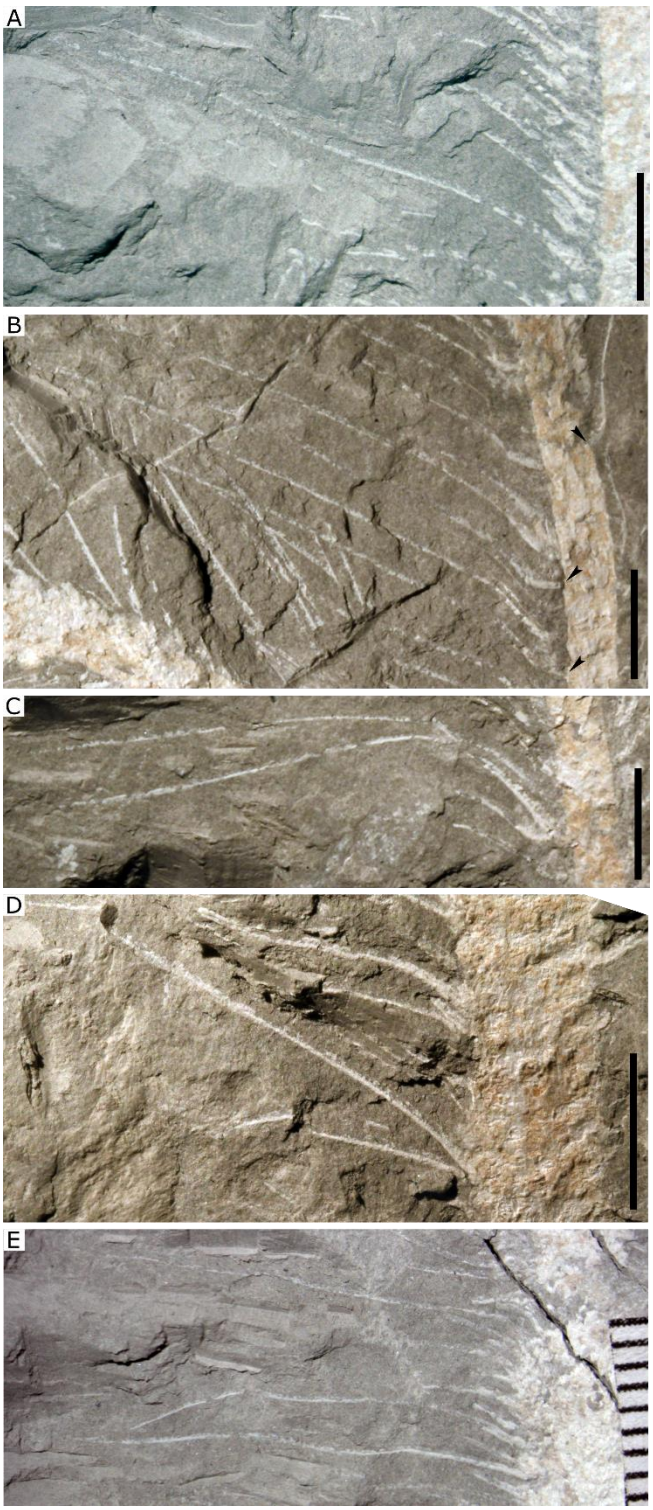

Figure 6.6: Sporophylls of 'lycopod D'; A–C) sporophylls lacking sporangia (black arrows in (B) indicate the narrow pedicel), D–E) fertile sporophylls. Scale bars for A–D = 5mm, scale for E in mm.

Sporophylls are erect and linear, 18–28.1 mm long. Their description is derived from sagittal views along the stem margins, as no plan view of a full leaf was observed. Evidently the leaves were rigid, and strongly attached to the axis, as despite their elongate, narrow form, they have remained relatively undistorted. They have a narrow pedicel 0.4–0.8 mm long and 0.1–0.2 mm wide, which gives rise to a broad adaxially curved portion 2.4–2.7 mm long and 0.6–0.8 mm wide, forming a spoon-like base. The remainder of the leaf is needle-like, 0.3 mm in average maximum width, tapering evenly to an acute distal point. Sporophylls are mostly straight but some are slightly curved abaxially. They differ morphologically from the vegetative leaves in being wider and longer, having a widened, adaxially curved region near the base (Figure 6.3A, 6.6A–E). The margins of sporophylls lack crenulation. Occasional slight apparent unevenness along sporophyll margins is attributed to uneven parting of the mineral fabric that comprises the fossil. No evidence of a ligule was observed on any of the leaves.

Some complete sporophylls were prepared from the matrix. Proximal sporophylls lacking sporangia are 24–28.1 mm in total length (n=6), whereas distal, fertile sporophylls are 18–22 mm long (n=4).

The angle of divergence of sporophylls is higher than that of vegetative microphylls. The pedicel, visible only on sporophylls lacking sporangia, diverges from the stem at an angle of between 68 and 90° (Figure 6.6B, black arrows). Above the spoon-like base, proximal sporophylls lacking sporangia (Figure 6.6A–C), generally diverge at an angle of 30–50° from the stem. Distal sporophylls bearing sporangia (Figure 6.6D–E) diverge from the axis at an angle of 45–90°, except for those at the very tips, which extend from the axis at a low angle approaching parallel.

Low-angled rows of 3–4 round to elliptical sporangia are visible in plan view (Figure 6.3B), suggesting a helical, pseudowhorled distribution with around 6–8 sporophylls in a single turn of the axis.

6.2.2.6 Sporangia

Sporangia are attached to all sporophylls on axis A from 25–30 mm beyond the first bifurcation until the distal tips. For much of this length sporangia are so densely packed and heavily mineralized that their margins are impossible to define. In this region the

axis is entirely hidden beneath a sleeve of sporangia. Proximally and distally on the strobili the sporangia can be individually determined (Figure 6.4A, B). They are round to elliptical, of fairly uniform size (1–2.1 mm long and 0.8–1.5 mm high (n=8)), with the long axis parallel to the subtending leaf. There is no clear difference in size between proximal and distal sporangia. Each sporangium is attached to the adaxial surface of the laterally expanded portion of a sporophyll, the margins of which partially enfold it to form a sporangial cup (Figure 6.3B, 6.5C).

Figure 6.7: **A)** Enlargement of proximal sporangia on Axis A, with arrows indicating round structures representing possible megaspores. **B)** Enlargement of proximal sporangium on Axis A, with arrows indicating a possible tetrad of megaspores. **C)** Enlargement of the distal region of Axis B, prior to terminal bifurcation, with arrows indicating sporangia with a granular ornament indicating possible microspores. All scale bars = 2mm.

6.2.2.7 Spores

Some sporangia display feint apparent internal structures. In proximal sporangia near the base of the strobilus on axis A these comprise round shapes approximately 300–500 μm in diameter some of which appear to be arranged in tetrads (Figure 6.7A, B). They are tentatively interpreted as poorly preserved megaspores. Microscopic examination provided no further resolution as the reflective phyllosilicate mineral fabric obscures detail, and boundaries between the putative structures are unclear. Along the distal part of axis B, prior to the terminal dichotomy, some of the sporangia present a fine granular texture, suggesting possible presence of microspores (Figure 6.7C). Examination under SEM, however, revealed no details of these structures.

6.2.3 Comments on 'lycopod D'

Proximal inflection of axes A and B, where they are broken off at the edge of the rock, as well as their terminations at roughly the same distance from there, indicate that these two axes were probably attached at a more proximal unseen dichotomy, and belong to the same individual plant. Axis B does not visibly dichotomize at the same level as the first preserved dichotomy on axis A. Since the axis has been broken and displaced at around that level, it is possible that the axis did originally dichotomize, and that the sister branch to the remaining terminal portion of axis B, was lost prior to burial.

The axes on AM 7708 are dissimilar to lycopod axes described in Chapters 4 and 5, in being narrower, more densely mineralized and lacking internal sedimentary infill. No leaf bases are recorded on the axes, probably because parting of the rock matrix has favoured the weakness corresponding to the centre of the densely mineralized axis, whereas on protolepidodendralean axes, parting seems to favour the level of outer cortex.

Leaves with the sporophyll-like morphology, but lacking sporangia, and situated between the vegetative leaves and the terminal strobili, are suggestive of sporophylls which have shed their sporangia. Though some shaggy-looking sporangia remain in attachment to sporophylls in this region, these are possibly older sporangia remaining on the plant from a previous season of fertile growth. Seasonal growth is compatible with the possibility that these axes derive from a large perennial plant.

There appear to be spores preserved within some of the sporangia, suggesting a possible bisporangiate cone with megaspores borne proximally and microspores

distally, though their preservation precludes confident discernment of their morphology, numbers or dimensions. As a result, they have not been considered in the diagnosis.

Table 6.1 (continued over page): Characters for heterosporous lycopods in the Devonian. Taxa with bisporangiate strobili are indicated by green shading, those with monosporangiate strobili in red, and those lacking strobili, or with uncertain distribution of spore types, are marked with orange (abbreviations; lig. – ligule; sp. – sporophyll; mod. – modifications; refs. – references; inc. – incomplete; Fam. – Famennian; Frasn. – Frasnian; Givet. – Givetian; Carb. – Carboniferous; strob. – strobilar; arr. – arrangement; term. – terminal; mono. – monosporangiate; bi-sp. – bisporangiate; interv. – intervals; s.l. – *sensu lato*)

Taxon	**Order; Family**	**Age**	**Sp. margin**	**Sp. mod.**	**Sp. length (mm)**	**Lig?**	**Strob. arr.**	**Refs.**
Kossoviella	*Incertae sedis*; Kossoviellaceae	Frasn.	crenulate	none	8–18	No	Bi-sp., term.	Orlova *et al*., 2019
Kowieria	*Incertae sedis*	Fam.	entire	none	≤20	No	Bi-sp., term.	Gess and Prestianni, 2018
Mixostrobus	*Incertae sedis*	Givet.	entire (?)	none	7–10	No	Bi-sp., term.	Senkevitsch *et al*., 1993
Yuguangia	*Incertae sedis*	Givet.	dentate	heel	8–10	Yes	Bi-sp., term.	Hao *et al*., 2007
Bisporangio-strobus	Lepidocarpales; Cyclostigmaceae	Frasn./ Fam.	?	heel	2.5 ?inc.	No	Bi-sp. term.	Chitaley and McGregor, 1988
Cymatostrobus	Isoëtales s.l.	Fam.	?	heel and keel	?	? No	Bi-sp. term.	Evreïnoff *et al*., 2017
Cyclostigma	? Isoëtales s.l.; Cyclostigmaceae	Frasn./ Fam.	ciliate	none	up to 80	? No	Bi-sp. term.	Chaloner, 1968
Changxingia	Isoëtales s.l; *Incertae sedis*	Frasn./ Fam.	entire	alations and heel	22	Yes	Mono. term.	Wang *et al*., 2014

Lepidostrobus	Isoëtales s.l; *Incertae sedis*	Frasn./ Fam. – Lower Carb.	entire	alations, heel and keel	9.5–10.5	Yes	Mono. term.	Meng *et al*., 2013
Minostrobus	Isoëtales s.l.; *Incertae sedis*	Fam.	entire	alations, heel and keel	6–7 plus pedicel	Yes	Mono. term.	Meng *et al*., 2013, 2015
Sublepidoden-dron grabaui	Isoëtales s.l.; Sublepidoden-draceae	Fam.	entire	keel	≥20	No	Mono. term.	Meng *et al*., 2016
S. songziense	Isoëtales s.l.; Sublepidoden-draceae	Fam.	entire	alations and keel	10–15	? No	Mono. term.	Wang *et al*., 2003
Wuxia	*Incertae sedis*	Fam.	spiny	none	≤96	No	Mono. non-term.	Berry *et al*., 2003
Monilistrobus	*Incertae sedis*	Fam.	spiny	none	≤18	No	Interv. along axis	Wang and Berry, 2003
Chamaedendron	*Incertae sedis*; Chamaedend-raceae	Frasn.	dentate	none	≤30	No	N/A	Schweitzer and Li, 1996
Longostachys	? Isoëtales s.l.; Longostachy-aceae	Givet.	spiny	none	15–30	No	Term.	Cai and Chen, 1996
Barsostrobus	*Incertae sedis*	Fam.	dentate	none	15–17	No	N/A	Fairon-Demaret, 1991
'Lycopod D'	*Incertae sedis*	Fam.	entire	none	18–28	No	Term.	This study

6.3 Comparisons with Devonian lycopods

A review of a large part of the published Devonian heterosporous lycopod diversity, summarized in Table 6.1, provides some indication of the likely affinities of ‘lycopod D’. The simple elongate sporophylls with modified, spoon-like bases, and their terminal strobilar arrangement, place this lycopod in all likelihood amongst the heterosporous forms. The species can be decisively excluded from Protolepidodendrales, as it has none of the characteristic features thereof.

A homosporous arborescent lycopod from the Givetian of China, *Hoxtolgaya* Xu *et al*., 2012, has been suggested to occupy a phylogenetic position intermediate between the Protolepidodendrales and the heterosporous lycopods (Taylor *et al.*, 2009; Xu, Wang, & Wang, 2012). It has sporophylls which have toothed margins, but are otherwise similar to those of ’lycopod D’, though it differs in that sporophylls of *Hoxtolgaya* are not arranged in terminal strobili.

The earliest heterosporous lycopods are *Longostachys latisporophylla* Zhu *et al.* emend. Cai and Chen, 1996 and *Yuguangia ordinata* Hao *et al*. 2007 from the Givetian of China and *Mixostrobus givetensis* Senkevitsch *et al*. 1993 from the Givetian of Kazakhstan. The latter two have terminal bisporangiate strobili, but only megaspores have been recovered from the strobilus of *Longostachys* (Berry *et al.*, 2003; Hao *et al.*, 2007; Taylor *et al.*, 2009). The Chinese Givetian forms both have dentate sporophylls (Cai & Chen, 1996; Hao *et al.*, 2007); in *Longostachys* much longer (20–70 mm long), and in *Yuguangia* much shorter (8–10 mm) than the entire sporophylls of ’lycopod D’. *Mixostrobus* is described from a petrified strobilus, which is much shorter and wider than that of ‘Lycopod D’ (Senkevitsch *et al.*, 1993).

6.3.1 Comparison to Late Devonian bisporangiate lycopods

Cyclostigma kiltorkense Haughton 1855 differs from the present material in having sporophylls that are far larger (80–200 mm or more in length), and which have delicate fimbriation along the margins. *Clevelandodendron* Chitaley and Pigg, 1996 is a small, unbranched lycopod which bears a single compact terminal bisporangiate strobilus, 90 mm long and 60 mm wide, and hence its overall organization is very different to ’lycopod D’. *Bisporangiostrobus harrisi* Chitaley and McGregor 1988 has short, cigar shaped strobili, differing from the elongate, narrow, dichotomizing strobili of the Coombs Hill specimen. *Cymatostrobus irvingii* Evreïnoff *et al*. 2017 is represented by a

permineralized strobilus, and its sporophylls are modified with a heel and keel, neither of which are observed on ‘lycopod D’.

Among reviewed Devonian heterosporous lycopods, the only taxon with dichotomizing terminal strobili is *Kossoviella timanica* Petrosjan emend. Orlova *et al.* 2018 from the Frasnian (Upper Devonian) of Russia. The strobilus of this species bears megaspores proximally and microspores distally. It has an elongate, linear sporophyll with a spoon-like base, strongly resembling that of ’lycopod D’. However, sporophylls of *Kossoviella* have a subtle crenulation along the proximal margins, which provides the only clear difference between the two. In addition, sporangia are slightly smaller in the Coombs Hill species, and the leaves and sporophylls are longer. The lack of clear spore morphology in the new species inhibits confirmation of a close relationship between them. As a result, to prevent creating an erroneous grouping, the new species is not included in *Kossoviella*.

Another bisporangiate lycopod with some similarity to the new taxon is *Kowieria alveoformis* Gess and Prestianni 2018. It has terminal strobili which are, however, not known to bifurcate. Sporophylls of both *Kowieria* and ‘lycopod D’ have entire margins but differ in relative dimensions. The sporangial cup of *Kowieria* sporophylls is longer, and the total sporophyll is shorter than in ‘lycopod D’, with sporangia of *Kowieria* (3 – 4.5 mm in length) being distinctly larger than those of ‘Lycopod D’ (1 – 2.1 mm in length). A striking difference between ‘lycopod D’ and *Kowieria* is that the latter has consistently falciform microphylls and sporophylls, whereas in the former they are straight. In addition, the apparent regular shedding of sporophylls in the Waterloo Farm species is not evidenced in ‘lycopod D’. Naked axes of *Kowieria* are not rare, and shed microphylls are commonly found dispersed on bedding planes bearing the same characteristic falciform shape. ‘Lycopod D’ rather appears to shed its sporangia, retaining sporophylls on the axis. The clear differences between the two species, and a lack of intermediate forms therefore permits conspecificity to be confidently discounted.

6.3.2 Comparison to heterosporous lycopods with terminal monosporangiate strobili

The most derived members of the heterosporous clade bear monosporangiate strobili (DiMichele & Bateman, 1996). Most, if not all, Devonian members of this group present modifications to the sporophyll such as an abaxial keel, heel and alations (Table

6.1), and the lack thereof separates ‘lycopod D’ from the group. In addition to such modifications, *Sublepidodendron* (Nathorst) Hirmer 1927, *Changxingia* Wang *et al*. 2014 and *Lepidostrobus* Brongniart 1828 have short, cigar-shaped strobili, very different from the narrow dichotomizing strobili of ‘lycopod D’ (Qi Wang *et al*. 2003; D. Wang *et al*. 2014). *Minostrobus* Wang has an elongate, slender strobilus, but its sporophylls are short and triangular. Monosporangiate strobili of the above-mentioned genera, except for *Changxingia* tend towards having strongly pedicellate sporophylls with upturned laminae forming a protective sheath covering sporangia. Furthermore, all of the monosporangiate forms reviewed here, except *Sublepidodendron* have been described as ligulate. These derived characters are not observed in ‘lycopod D’.

A number of disparate heterosporous taxa present features that distinguish them from bisporangiate and monosporangiate groups discussed above. ‘Lycopod D’ is readily excluded from comparison with Devonian heterosporous genera that lack terminal strobili, including *Barsostrobus famennensis* Fairon-Demaret 1977, *Chamaedendron* Schweitzer and Li 1996 and *Monilistrobus yixingensis* Wang and Berry 2003. *Wuxia bistrobilata* Berry *et al.* 2003 has terminal microsporangiate strobili, and megasporangiate strobili borne at dichotomies of the axis. Its sporophylls are enormous and spiny and non-comparable to those of Lycopod D. *Lobodendron fanwanense* Liu *et al*, 2015 and *Otzinachsonia beerboweri* Cressler and Pfefferkorn 2005 do not present leaves or fertile structures for comparison. *Leptophloeum rhombicum* Dawson 1862 is an arborescent, rarely branched lycopod presenting contiguous rhombic leaf abscission scars along its axis (Wang, Geng, & Dilcher, 2005; Prestianni & Gess, 2014). Its sporophylls have been described as peltate in shape, possibly arranged in strobili (Wang *et al.*, 2005). The known morphology of this plant shows little overlap with ‘lycopod D’.

6.3.3 Possible affinities of ‘lycopod D’

Based on currently available character sets, ‘lycopod D’ cannot be ascribed to any known species. Although superficially very similar to *Kossoviella timanica*, ‘lycopod D’ may be distinguished by presence of entire margins to the sporophylls. ‘Lycopod D’ bears a somewhat less marked resemblance to *Kowieria alveoformis* with which it shares a similar palaeogeographic region (though it is likely not precisely contemporaneous). It is however distinguished on the basis of differences in sporophyll size and posture, size of sporangia, bifurcated strobili and persistence of leaves and

sporophylls in Lycopod D. Lack of well-preserved spores of ‘lycopod D’ furthermore adds uncertainty to understanding of its relationships with *Kossoviella* and *Kowieria*.

Kowieria, like *Kossoviella*, has terminal bisporangiate strobili. Apart from lesser differences, such as clear lack of bifurcating strobili and crenulate sporophyll margins in *Kowieria*, these latter two genera display significant differences in their megaspores. The megaspores of *Kowieria* are spiny (see 6.6), being ascribed to the *Lagenicula* spore type, whereas those of *Kossoviella* are laevigate. On this basis, despite superficial similarities, these taxa may belong to different families. By extension, similarities between the Coombs Hill species, and either *Kossoviella* or *Kowieria*, must be treated with caution, and a plausible generic relationship to one or the other cannot be explored further without a clear understanding of the megaspores.

‘Lycopod D’, represents a possible distal ramification of a rhizomorphic lycopod. Review of Devonian lycopod diversity indicates its likely affinities to lycopods with bisporangiate strobili, which are considered to be basal and paraphyletic amongst the heterosporous lycopods (DiMichele & Bateman, 1996; Xue, 2011). Poorly preserved megaspore- and microspore-like structures in its strobilus tentatively support its affiliation to the group. Though lack of information on the spores, internal anatomy, and roots of ‘lycopod D’ preclude its definite assignment to any lycopod family, it can confidently be assumed to form part of basal rhizomorphic lycopod diversity. ‘Lycopod D’ contributes to a growing body of disparate Late Devonian heterosporous lycopods known from partial material, and resolution of their relationships will become increasingly possible with description of newly discovered material and reconstruction of more taxa as whole organisms. Several Devonian lycopods exhibiting heterospory are considered arborescent, although absolute confirmation of this is often precluded by the limitations of preserved material. (eg. Gess and Prestianni 2018; Orlova *et al*. 2019). Well-preserved remains of Devonian arborescent genera *Longostachys, Clevelandodendron, Chamaedendron, Leptophloeum, Cyclostigma* and *Sublepidodendron*, indicate that they were already widespread by the Famennian. The possibility of arborescence in Lycopod D gains some support from presence of a large lycopod axis recovered from the Coombs Hill locality (below).

6.4 Large lycopod axis

A large axis bearing fusiform leaf bases from Coombs Hill (AM 7709), albeit from a slightly higher stratigraphic horizon (Plant Press), confirms the temporal presence of arborescent lycopods in this palaeogeographic setting and possible conspecificity with ‘lycopod D’ is not excluded.

6.4.1 Description of AM 7709

The specimen comprises a fragmentary portion of a bedding surface, around 10 cm x 6 cm, entirely covered by evenly spaced impressions of lycopod leaf bases (Figure 6.8A). The specimen largely comprises a counterpart which lacks a part, although a partial compression remains on the specimen.

The stem compression is near two dimensional. On the layer furthest from the viewer, leaf bases are represented by slight bulges on the surface, whereas the overlying surface to the left of the specimen (white arrow on Figure 6.8A), shows leaf bases as grooves. Inverse topography observed on different surfaces of the specimen indicates opposing cortical surfaces. It is unlikely that the surfaces represent different levels of decortication of the same side of the axis because their respective leaf bases are not in phase.

Leaf bases are elliptical to fusiform, elongated parallel to the presumed long axis of the stem. On the underlying cortical surface, they are represented by slightly thickened areas of mineralized tissue, 4–6 mm long, and 1.5–2.5 mm wide (Figure 6.8B). The upper margin is rounded, while the lateral margins taper downward to a point. On better preserved scars the midline exhibits a linear ridge or groove (about one third of a millimetre wide) extending for most of the length. This ridge is intersected by a transverse arch around 1 mm from the top of the leaf base, forming a T-shape or cross (arrows on Figure 6.8B). The slightly overlying surface, seen to the left of Figure 6.8A, presents scars as depressions. Here they are smaller, 2.5–4 mm in length, and 1–2 mm wide also showing a central ridge.

Bases are arranged in diagonal parastichies at around 45° to their long axis. Up to twelve scars can be counted in a diagonal line, with adjacent scars around 2 mm apart. The lateral margins of the axis are not preserved, however, it is at least 61 mm wide.

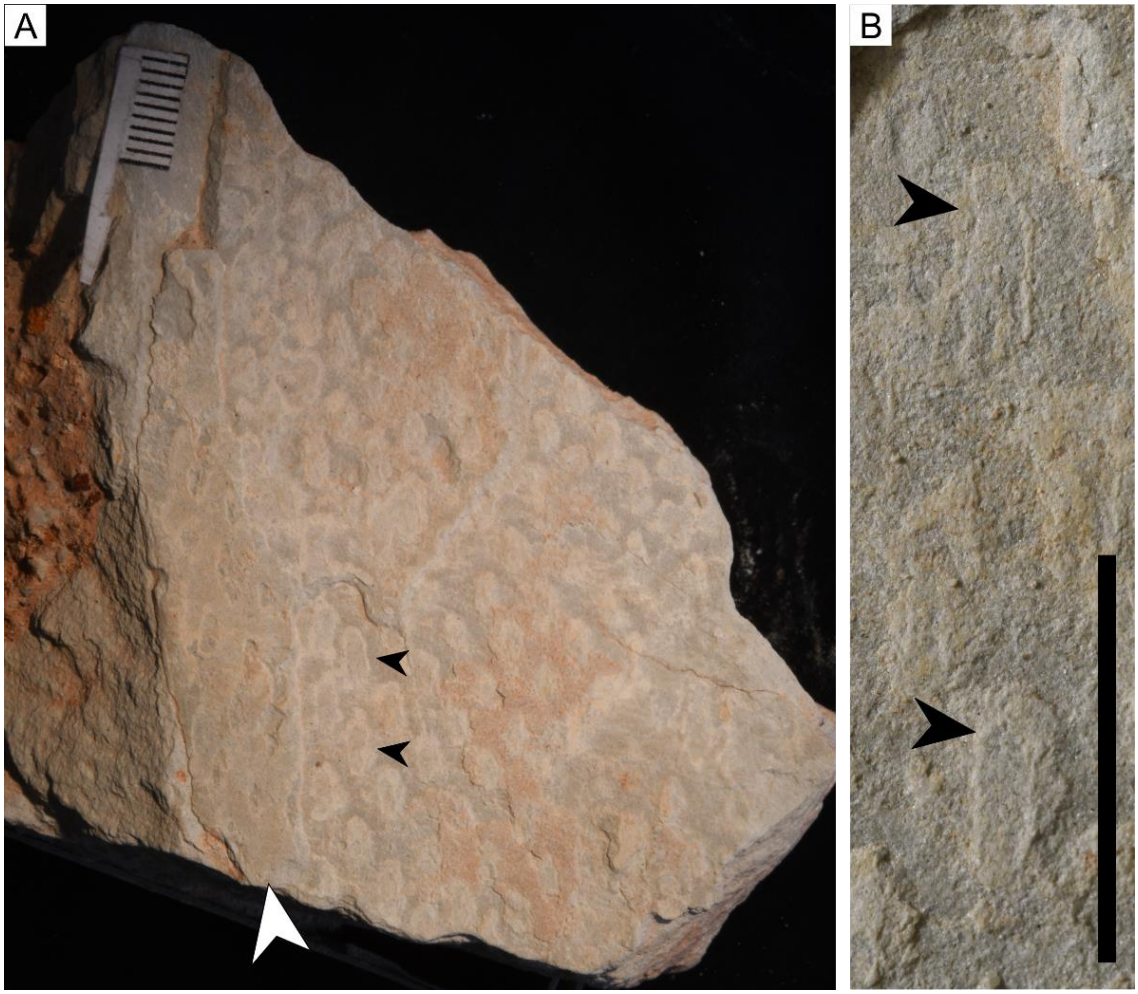

Figure 6.8: Large lycopod axis, AM 7709; **A)** General view of the specimen under cross-polarized illumination. White arrow indicates overlying surface of axis with smaller, depressed leaf bases. Black arrows indicate the position of leaf bases enlarged in (B) (scale at top left in mm). **B)** Enlargement of leaf bases under low-angled illumination from top left. Arrows indicate a transverse arch on each leaf base. A longitudinal ridge is also visible medially on the leaf bases (scale bar = 1cm).

6.4.2 Comments

Leaf bases on the specimen are compatible with those of lycopod axes, in their morphology and helical arrangement. The bases are not referred to as ‘cushions’, because of the term’s implication of leaf abscission (Thomas and Meyen, 1984). As the lateral margins of the specimen are not preserved, it is uncertain whether leaves remained attached to the bases, as this is usually where leaves will be visible if attached to lycopod axes at Coombs Hill.

The axis may well have been a hollow shell of outer cortex when it was buried, since putative opposing cortical surfaces of the specimen are separated by very little

thickness. The width indicates it to have belonged to an arborescent plant, with a trunk at least 6 cm wide. Its width may be indicative of its true width in life, as Rex and Chaloner (1983) have demonstrated that during compression, the apparent width of plant axes does not change.

The leaf bases are comparable to the those of the small arborescent lycopod *Longostachys latisporophylla* on which leaf cushions vary considerably in morphology, occurring where leaves have abscised from the plant (Cai & Chen, 1996). Those on the widest axes, up to 3 cm wide, are very similar to the ones described here, being fusiform in shape, and about 3 times as high as wide. A longitudinal furrow marks the centre of the cushion, and this corresponds exactly to the longitudinal ridge observed here, which is probably formed by an external mould of what was originally a furrow.

The scars on AM 7709 are also similar to those of the homosporous arborescent lycopod *Hoxtolgaya* Xu *et al*., 2012, also from the Givetian of China, but those on the latter are contiguous, without the interareas observed here.

Transverse arches of organic matter near the of top leaf bases of *Sublepidodendron songziense* Chen emend. Wang *et al.* 2003 were interpreted as false leaf scars, where the leaf had been truncated by parting of the rock matrix (Wang *et al.*, 2003). Leaf bases on axes of *S. songziense* are similar in size, shape and spacing to those described above, also preserving a longitudinal coal-filled ridge or groove. Hence, the leaf bases are interpreted as representing analogous structures to those on the Chinese arborescent form. Similar transverse arches on AM 7709 may represent false leaf scars. Evidence of ligule pits or parichnos scars is absent on the Coombs Hill specimen, as on *Sublepidodendron* (Wang *et al.*, 2003; Meng *et al.*, 2016), although poor preservation of AM 7709 may inhibit observation of such features.

Devonian isoëtalean lycopods all present a fusiform leaf cushions on larger axes. Those of *Longostachys* were considered by Cai and Chen (1996) to be almost identical to *Sublepidodendron.* The latter has a thicker trunk, with a diameter of up to 6.5 cm in *S. songzians*e. These two Chinese species have narrow isotomously dichotomizing distal branches bearing simple leaves and sporophylls arranged in terminal strobili, somewhat resembling those of ‘lycopod D’. *Sublepidodendron* has been suggested to have been as phylogenetically derived as Carboniferous Lepidodendrales, despite originating in the Late Devonian (Wang *et al.*, 2003).

Lack of observation of leaves inhibits taxonomic identification of the specimen. There are however some large lycopod axes in the Cape Supergroup worth comparing it to. Distinctive large axes, up to 80 mm in diameter previously reported from the Witpoort Formation are ascribed to *Leptophloeum rhombicum*, on the basis of bearing contiguous rhombic abscission scars (Prestianni and Gess, 2014). These are very different from those on AM 7709.

Isolated axes from the Upper Devonian Msikaba Formation at Port St. Johns, up to 70 mm in width, were described as *Longicatrix bulbosa* Anderson and Anderson 1985 and included in the Lycophyta. Some axes show unusual, distinctive bulbous swellings. One of the specimens (Anderson and Anderson 1985, Pl. 11, fig. 4) has fusiform scars arranged helically about the axis, somewhat resembling those on AM 7709, although lacking a central linear ridge or groove. Other axes ascribed to the genus by Anderson and Anderson, 1985, show a variety of scar patterns, and this is consistent with different modes of preservation and decortication in arborescent lycopods (Gensel & Pigg, 2010). A number of lycopod axes between 1 and 4 cm thick from Waterloo Farm were tentatively compared with *Longicatrix* (Gess & Hiller, 1995a). *Longicatrix* may well represent the decorticated axes of arborescent lycopods, but this has not been demonstrated.

AM 7709 is here kept in open taxonomy, as a large lycopod axis of probable isoëtalean affinity. It is plausible that ‘Lycopod D’, could represent the distal fertile organs of this form.

6.5 Megaspores of *Kowieria alveoformis*

Morphological similarities between ‘Lycopod D’, *Kossoviella* and *Kowieria* are recorded, but the described megaspores from the latter two genera preclude a close relationship between these taxa. An undescribed specimen of *Kowieria* allows clearer observation of its megaspores than on the holotype, reinforcing the distinction between it and *Kossoviella*.

6.5.1 Description of AM 5301

Collected by R.W. Gess in 1993, the specimen was illustrated by Gess and Hiller (1995a) but not included by Gess and Prestianni (2018) in their description of *Kowieria alveoformis*.

AM 5301 presents a scatter of megaspores, associated with sporophylls of *Kowieria*. One entire leaf demonstrates the characteristic falcate shape (Figure 6.9A) and the bases of other sporophylls emerge from the aggregation of spores, with an outward orientation (Figure 6.9B). The specimen appears to be a strobilus in an advanced state of decay, and no remains of sporangia are apparent. Disaggregation and decay of the leaves and sporangia appear to have exposed the spores.

Megaspores are round to sub-triangular, 0.9 mm to 1.1 mm in diameter, bearing trilete radial laesurae. The equatorial outline of each spore is surrounded by a dense spiny sheath. Individual spines are acuminate, extending radially, 0.4–0.7 mm in length and proximally around 0.1 mm wide. At least three of the megaspores have spines covering their entire perimeters (Figure 6.9B). There is no evidence of a prominent gula on any of the spores, although since their proximal face is presented, this would perhaps be pressed onto the spore face, and possibly obscured by dense mineralization.

6.5.2 Megaspores on the holotype of *Kowieria alveoformis* (AM 5297)

Megaspores preserved on the holotype AM 5297, are not very clear. Spores remaining within sporangia were examined, of which several are visible on the specimen. One *in situ* spore has a spiny ornament, and this can be partially discerned among the dense mineral of the sporangium (Figure 6.9C). Like the spores on AM 5301, it is around 1 mm in diameter, with a dense covering of spines, radially extending around 0.5 mm from the margins of the spore body.

6.5.3 Comments

These observations compliment the description of Gess and Prestianni (2018), where megaspores of *Kowieria* were described as being hologulate, 580–720 μm in diameter, covered by spines at least 150–200 μm long, with a prominent gula, though photographic images in the paper do not clearly illustrate these characters (Gess and Prestianni 2018, Plate II, Fig 3). The spiny nature of the spores is here confirmed, though a prominent gula was not observed. Spores herein described reach up to twice the size previously reported. Confirmation of the spiny nature of the spores confirms taxonomic distinction between *Kowieria* and *Kossoviella*, since more recent description of the latter taxon has provided clear illustration and description of its smooth walled megaspores (Orlova *et al.*, 2019).

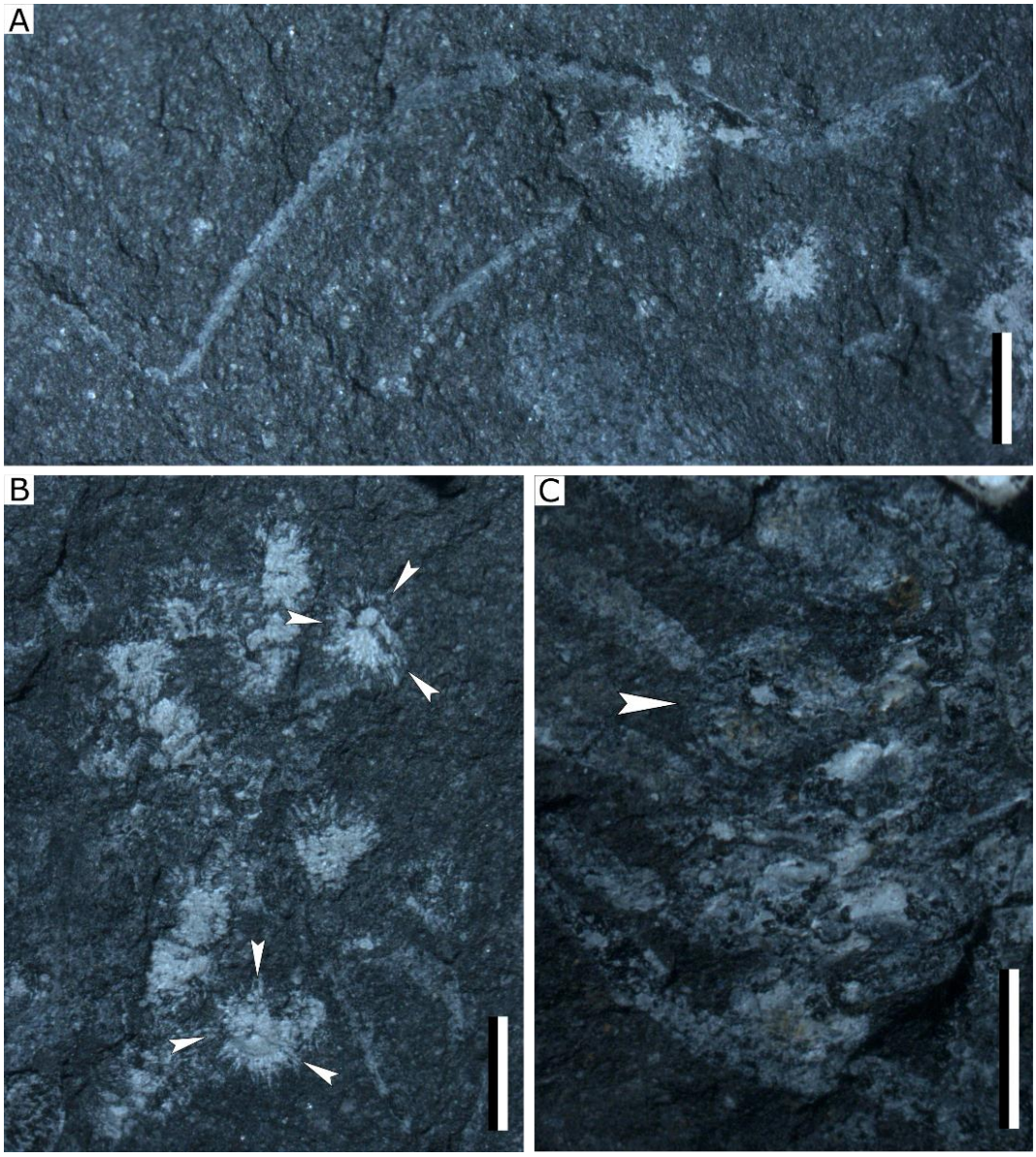

Figure 6.9: Megaspores of *Kowieria alveoformis*: **A)** AM 5301a, showing a typical falcate sporophyll with two megaspores alongside. **B)** AM 5301a, showing a scatter of megaspores. Small white arrows indicate radial trilete laesurae. **C)** AM 5297, arrow indicates an *in situ* megaspore. All scale bars = 2mm.

CHAPTER 7 – *ARCHAEOPTERIS NOTOSARIA* FROM COOMBS HILL

7.1 Introduction

Description of *Archaeopteris notosaria*, from Waterloo Farm, was significant as it extended the known distribution of the genus into high-palaeolatitudes (Anderson *et al*., 1995). *A. notosaria* is not as well understood as some Laurussian species. Prior to this study, the only fertile example of the plant was the holotype. The second known occurrence of the species at Coombs Hill provides new information on the architecture of the leafy lateral branch systems of the plant and their fertile organs.

New material from Coombs Hill preserves additional fertile units, including some in attachment to entire lateral branch systems, allowing for observation of the arrangement of fertile and vegetative structures at a larger scale than the Waterloo Farm material permitted. Some of the fertile structures are preserved in great detail, providing new perspectives on their morphology.

The range of variation documented in this study derives from the relatively small sample recovered thus far from Coombs Hill. Although revision of the species diagnosis is suggested, this will be withheld until a full comparative study of the Waterloo Farm collections has been performed.

7.2 Specimens studied

Vegetative parts: AM 7710 a + b, AM 7711 a + b, AM 7712

Fertile organs: AM 7710 a + b, AM 7713 a + b, AM 7714 a + b, AM 7716

7.3 Description of vegetative parts

Archaeopteris leaves are usually recovered attached to lateral branch systems at Coombs Hill where only a few specimens of isolated leaves were found. These lateral branch systems comprise penultimate axes with attached leafy ultimate axes. Two almost complete such units inform understanding of the overall architecture. Of the numerous partial remains of lateral branch systems, more informative specimens were selected in order to further elucidate details of the organs.

7.3.1 Branching architecture

Complete (or nearly complete) penultimate branches (PUBs) from the studied sample are 56 and 61cm in length (Figure 7.1A, B). They each have a swollen base, 17.2–28 mm wide, which rapidly tapers to 8–10.5 mm, after which the axis is roughly parallel sided, tapering very gradually along its length to around 2 mm wide distally. Axes are represented by coarse mineralization and are often ornamented with parallel longitudinal striations. Their taphonomy suggests that that they were originally rigid and dense in structure.

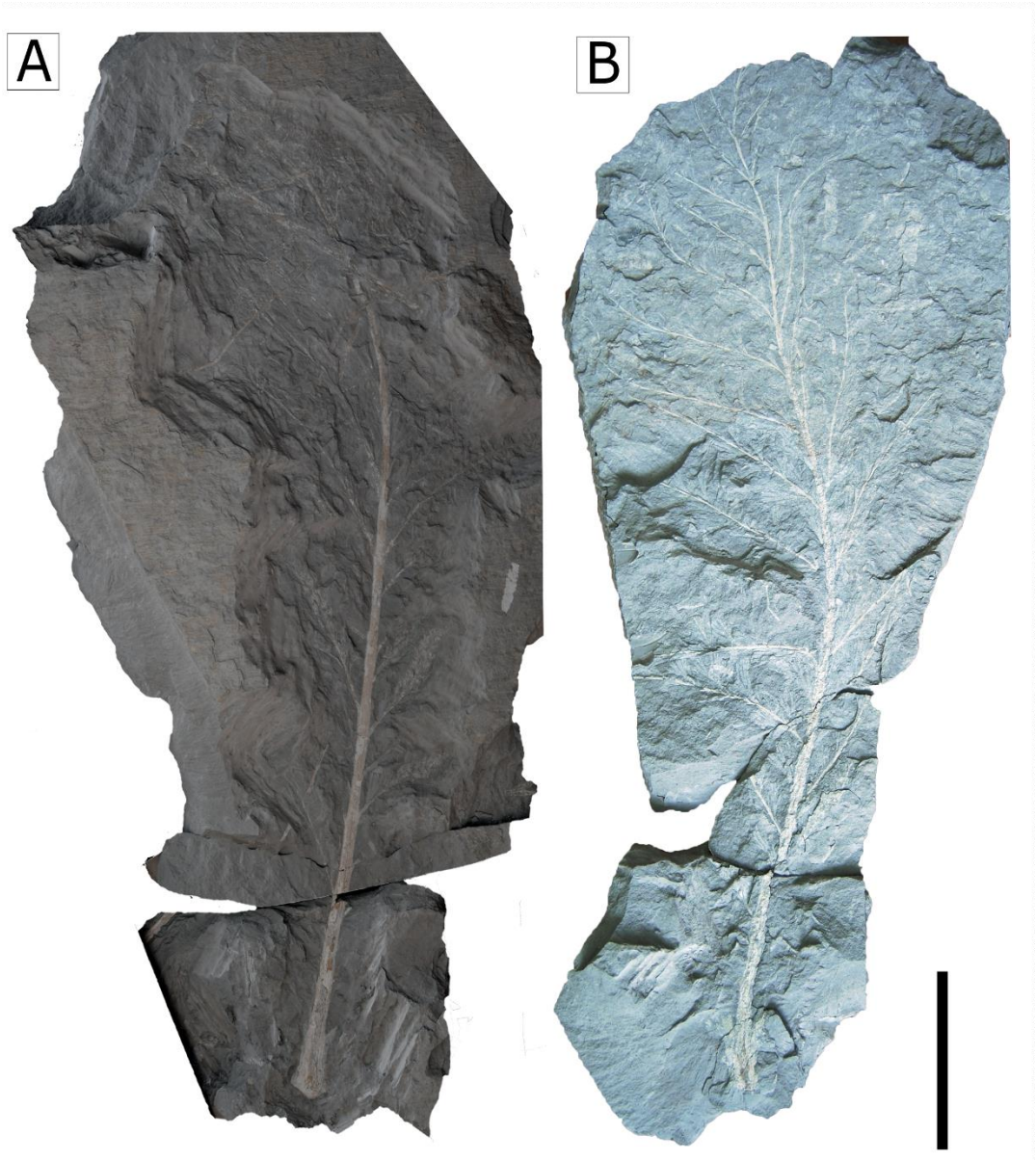

Figure 7.1: Lateral branch systems of *Archaeopteris notosaria*, **A)** AM 7713a, **B)** AM 7710. (A) and (B) to same scale (scale bar = 10cm).

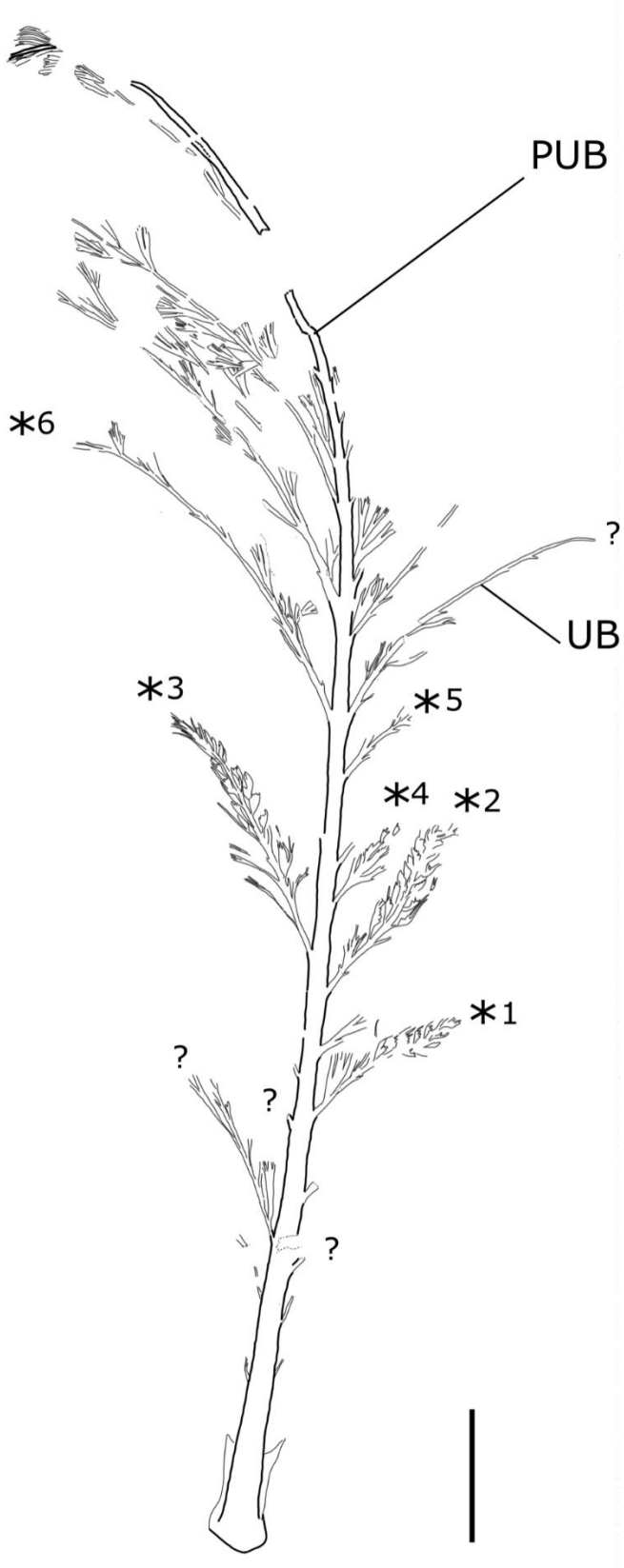

Figure 7.2: Line drawing of AM 7713 (Figure 7.1A). Fertile ultimate branches (UBs) are indicated by * and are numbered sequentially, putatively fertile UBs are indicated by ?. PUB indicates the penultimate branch and UB indicates an ultimate branch. Scale bar = 5mm.

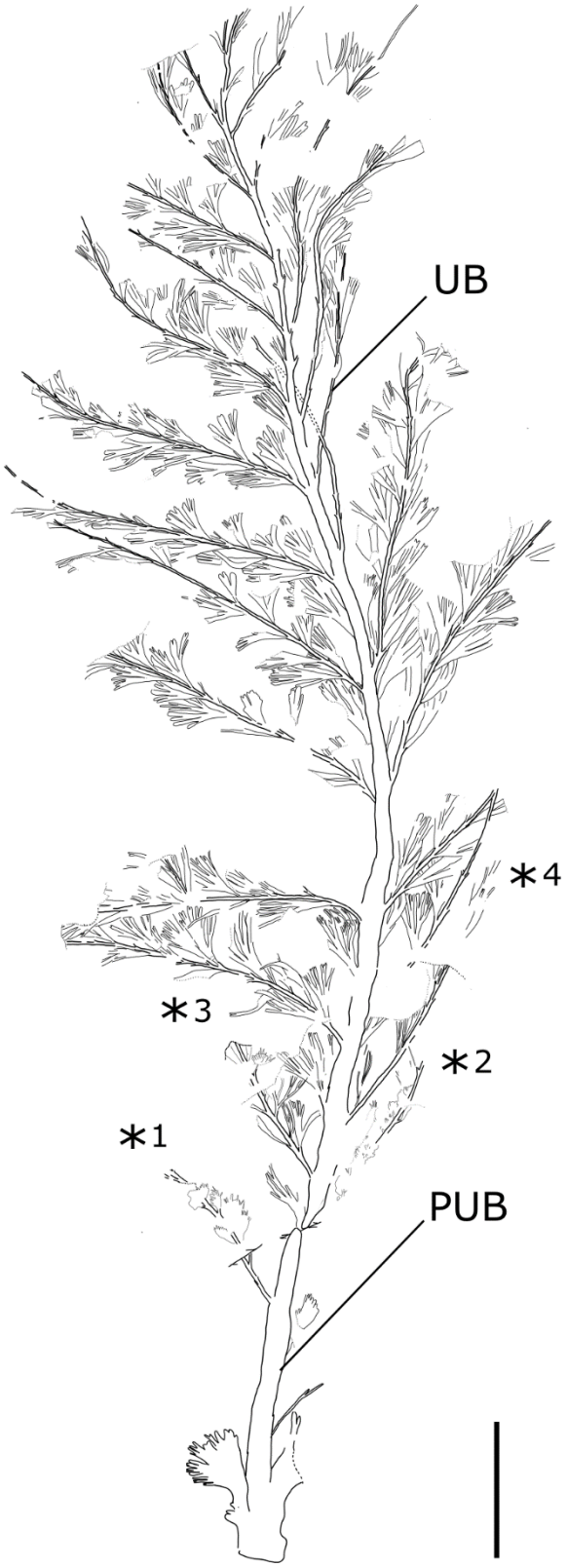

Figure 7.3: Line drawing of AM 7710 (Figure 7.1B). Fertile ultimate branches (UBs) are indicated by *, and are numbered sequentially. PUB indicates the penultimate branch and UB indicates an ultimate branch. Scale bar = 5mm

Attached on either side of the enlarged base of the PUBs are a pair of large, opposite leaf-like structures, termed **prophylls** (eg. Figure7.4C). Prophylls are wing-like, lacking the bilateral symmetry of typical leaves, and are more coarsely mineralized. They are larger than vegetative leaves, being up to 60 mm in length, and have a very long attachment to the PUB, from the base to between 20 and 52.5 mm, after which the blade extends a further 9.2–33,2 mm. They have a deeply dissected distal margin and are preserved with either a fan-shaped outline, or tapering to a point. The latter is probably taphonomic, representing the appearance of the prophyll when preserved side-on.

Ultimate branches (UBs) are 40 mm to 188 mm in preserved length, where completely preserved, decreasing in length towards the apex of a lateral branch unit. Proximally incomplete UBs on AM 7712 measure up to 15.5 cm in length (Figure 7.5D) and from the trajectory of a PUB preserved further along on the specimen a total probable length of 22 cm is suggested for the longest UB. Vegetative UBs are 1.5–2 mm wide at the base, and taper to 0.8–1 mm distally. Usually they curve slightly abaxially, although on AM 7710 they curve in an open S-shape, with branches on the both sides of the penultimate axis bending first in an anticlockwise and then in a clockwise direction (Figure 7.3). This curve likely results from taphonomic processes such as weak current action on the specimen during burial.

UBs diverge from the PUB at 20° to 45°, usually emerging in sub-opposite pairs. There is however some variation in this regard, particularly where fertile; as they may alternate, or two successive branches may emerge on the same side of the axis.

On AM 7713, the proximal and apical UBs are apparently paired sub-oppositely, whilst the fifth to seventh branches (which are the most densely fertile ones on this specimen (see Section 7.4) do not show a clear pairing, but are arranged somewhat irregularly (Figure 7.2). On another near-complete lateral branch system, AM 7710, the four most basal UBs (which are fertile) alternate, and are opposed by vegetative leaves, and thereafter all UBs arise in sub-opposite pairs (Figure 7.3). Pairs of UBs arise at intervals of 4–7 cm proximally on the PUB, reducing to 2–3 cm near the apex of the unit. Alternating UBs arise at increments of roughly half of that of paired (opposite to sub-opposite) ones.

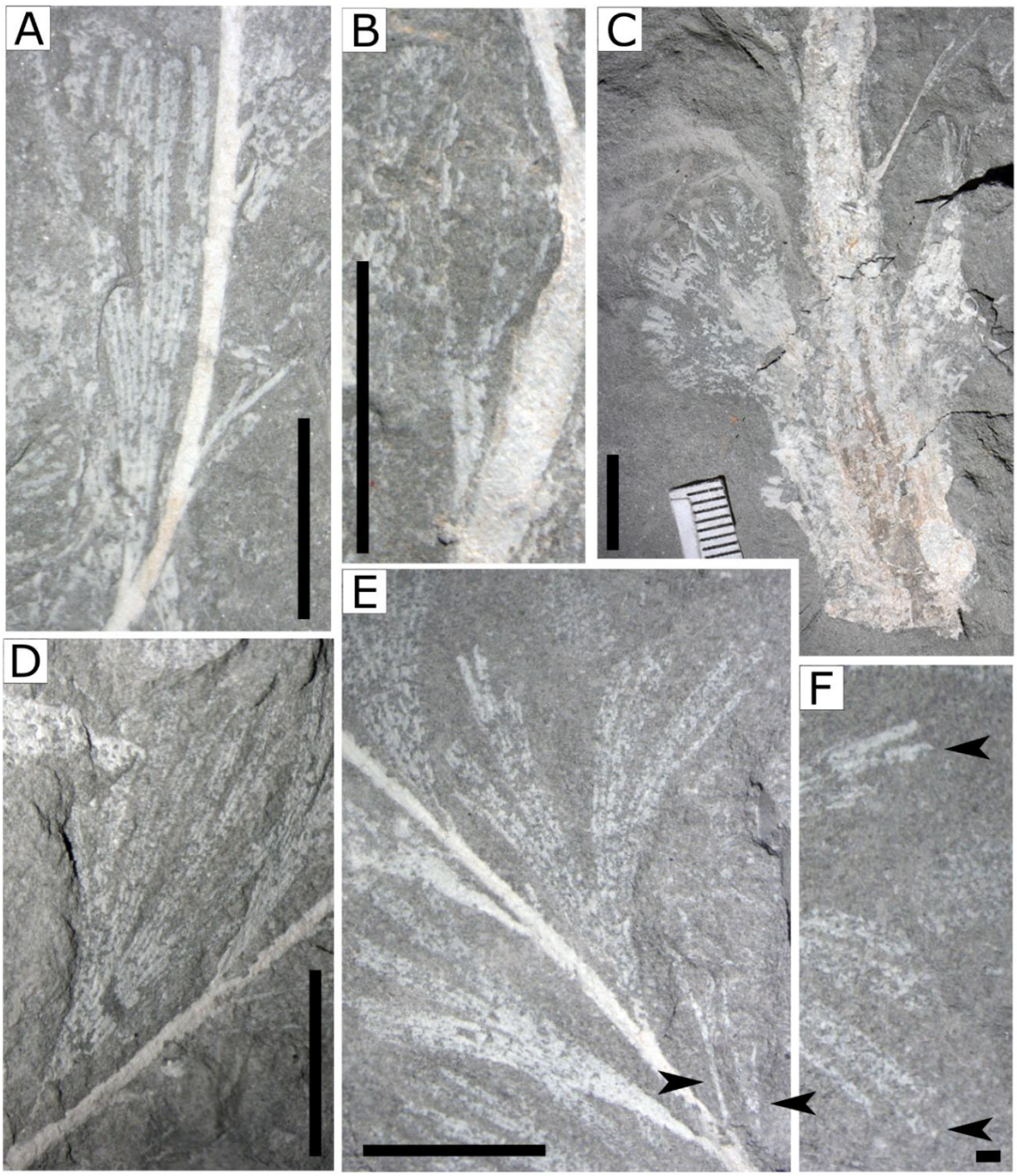

Figure 7.4: Enlargements from AM 7710; **A)** type 1 vegetative leaf (left) alternating with type 2 leaf (right) on an UB, **B)** type 2 leaf attached to PUB, **C)** basal prophylls of lateral branch system, **D)** type 1 leaf attached to an UB, **E)** type 1 and a pair of type 2 leaves (indicated by arrows) attached to an UB, **F)** enlargement from (E) rotated through 90˚ showing terminal segments each enclosing a pair of veinlets, indicated by arrows. All scale bars = 1 cm, except that in (F) = 1mm.

7.3.2 Leaf arrangement and morphology

Three distinct types of vegetative leaf occur on *Archaeopteris* from Coombs Hill. As all of these leaf types can be observed on a single specimen, AM 7711 (Figure 7.5), we are confident of their conspecificity. They are described in detail below.

Typical vegetative leaves as described by Anderson *et al.* (1995) occur in abundance attached to UBs and are best preserved on AM 7710 (Figure 7.4A, D, E, 7.7A). No clear pattern to their arrangement was determined. Clear understanding of their precise insertions on the ultimate branches was hampered by the three-dimensional arrangement of leaves, the multiple bedding levels on which leaves occur, and the lack of complete counterparts to the most informative specimens. Typical leaves are observed both in alternate and sub-opposite arrangement, with up to, at least 14 on an ultimate branch.

Typical leaves (type 1) are bilaterally symmetrical, wedge-shaped, with lateral margins that are outwardly curved or straight, and a distal margin that is deeply dissected terminating in 16 segments each enclosing a pair of veinlets (that is 32 veinlets in total). Parallel dichotomizing veinlets run the length of the leaf in parallel to the lateral margins. Three equally spaced, deep dissections extend from the distal margin to between 1/3 to 1/2 of the leaf length, dividing the leaf into four equal lobes. The middle dissection represents the first bifurcation of the leaf, and the two more lateral dissections indicate the second level of bifurcation. Splaying of the leaf influences the depth to which these dissections penetrate, but usually the middle one is the deepest. Each of the four lobes is bifurcated twice successively to produce four ultimate tips, each enclosing a pair of veinlets. Veinlets are a variable fraction of a millimeter wide and are rounded at the tip (Figure 7.4F). A total of 32 veinlets distally suggests 5 successive bifurcations, however, the vascular trace may divide before entering the leaf, as has been suggested by anatomical studies on *Archaeopteris macilenta* (Carluccio *et al.* 1966), which would suggest that the number of successive bifurcations of the veins within the leaf is four. Counting the number of veins can be difficult depending on the state of preservation and one can more consistently count the number of successive bifurcations/dissections of the leaf lamina (Figure 7.7A). Leaves range in length from 21–29.5 mm (n=13) and from 6.5–17.5 mm in width (n=13) and are around 1 mm wide at the base. A slight decrease in the leaf length along the ultimate axes was observed,

with the more distal leaves occupying the lower part of the size range. Typical (type 1) leaves are observed in attachment to ultimate branches only.

A second type of leaf (type 2) is smaller than the type 1 leaves and differs in being unwebbed, comprising delicate hair-like filaments (Figures 7.4A, B, E; 7.6B, D, G). These leaves are (at least) 15.7–22 mm long (n=4) and up to 6.5 mm wide distally. They successively divide two to three times, are 0.5–1 mm wide at the base, and produce filaments that are 0.2–0.3 mm wide, and of regular width. Observed in attachment to the UBs of all specimens included in the study, their full extent was estimated from only a few leaves that could be successfully prepared from the matrix. Due to their having a more delicate nature than the type 1 leaves they were not favoured by the plane of parting and were invariably partially embedded in the matrix. On AM 7711 some were well enough preserved to fully expose by *dégagement* (Figure 7.6B, G, E). Four were clearly identified along an incomplete ultimate branch on AM 7711, all extending from its adaxial (with regard to the PUB) margin. On this specimen and one other (AM 7710), two such leaves are clearly seen arising from an ultimate axis spaced around 2 mm apart (Figures 7.4F, 7.6B, E). Type 2 leaves are observable on all specimens studied, and on AM 7710 they were attached to most of the ultimate branches. AM 7710 also exhibits such a leaf in attachment to the penultimate axis (Figure 7.4B).

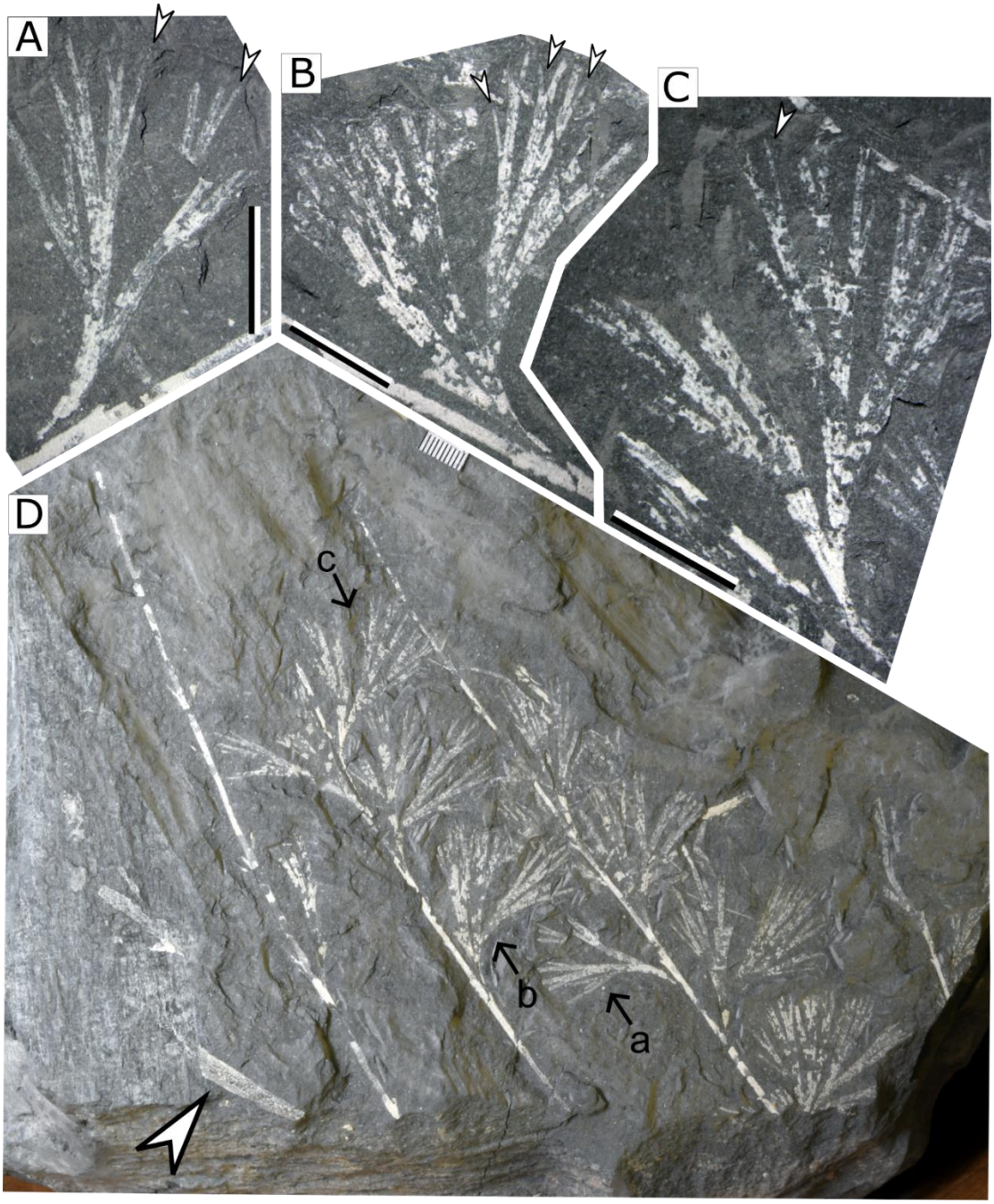

Figure 7.5: Portion of a lateral branch system (AM 7712); **A–C)** enlargements from (D) showing type 3 leaves attached to UBs, small white arrows indicate single terminal veinlets on leaves (scale bars = 1cm), **D)** whole specimen, large white arrow indicates PUB where it has been truncated and displaced by a slickenside, small black arrows with lower case letters indicate the respective leaves enlarged in A–C (scale = 10 mm, seen at top of image).

In addition to the two types already described, some vegetative leaves that otherwise resemble type 1 leaves, are larger (forming a distinct size class) and contain a greater number of vein bifurcations and leaf dissections. These type 3 leaves occur in direct attachment to PUBs and less commonly to UBs. They are 31.8–39.1 mm in length

(n=12) and 18.3–35.5 mm in width. These leaves bifurcate five or six times (Figure 7.7C), and hence produced approximately double (or more) the number of distal veinlets encountered on type 1 leaves (which have 32 veinlets). The first bifurcation of the leaf lamina usually occurs at around ¼ of the leaf length, more proximally than observed on type 1 leaves. Furthermore, despite their larger size, length of the 'petiole', or narrow basal part of the leaf prior to division is less than that of the typical leaves. Type 3 leaves are so large that it was impossible to see their entirety without destructive preparation of surrounding leaves and axes, and hence very few were prepared out completely. Large leaves are attached to the PUB on AM 7710 but not to the UBs. By contrast AM 7711 has type 1, 2 and 3 leaves attached to UBs, and only the larger type 3 attached to the PUB (Figure 7.6). AM 7712 has numerous vegetative leaves attached to its UBs and all conformed to type 3, but its PUB and corresponding leaves were not preserved. As noted above this specimen has the longest UBs of any in the collection. Where the large leaves were well enough preserved to observe the individual veinlets, it appeared that the distalmost successive bifurcation of the leaf lamina produced tips incorporating respectively a single and a pair of veinlets (arrows on Figure 7.5A, B, C). This asymmetry illustrates a more complex and variable structure than observed on the typical vegetative leaves. Type 3 leaves attached to the PUB of AM 7711 appeared to differ in symmetry from those on the other specimens (Figure 7.6A). The deepest dissection was not on the midline; rather these appeared to have two deeper lateral dissections, dividing the leaf into three unequal lobes.

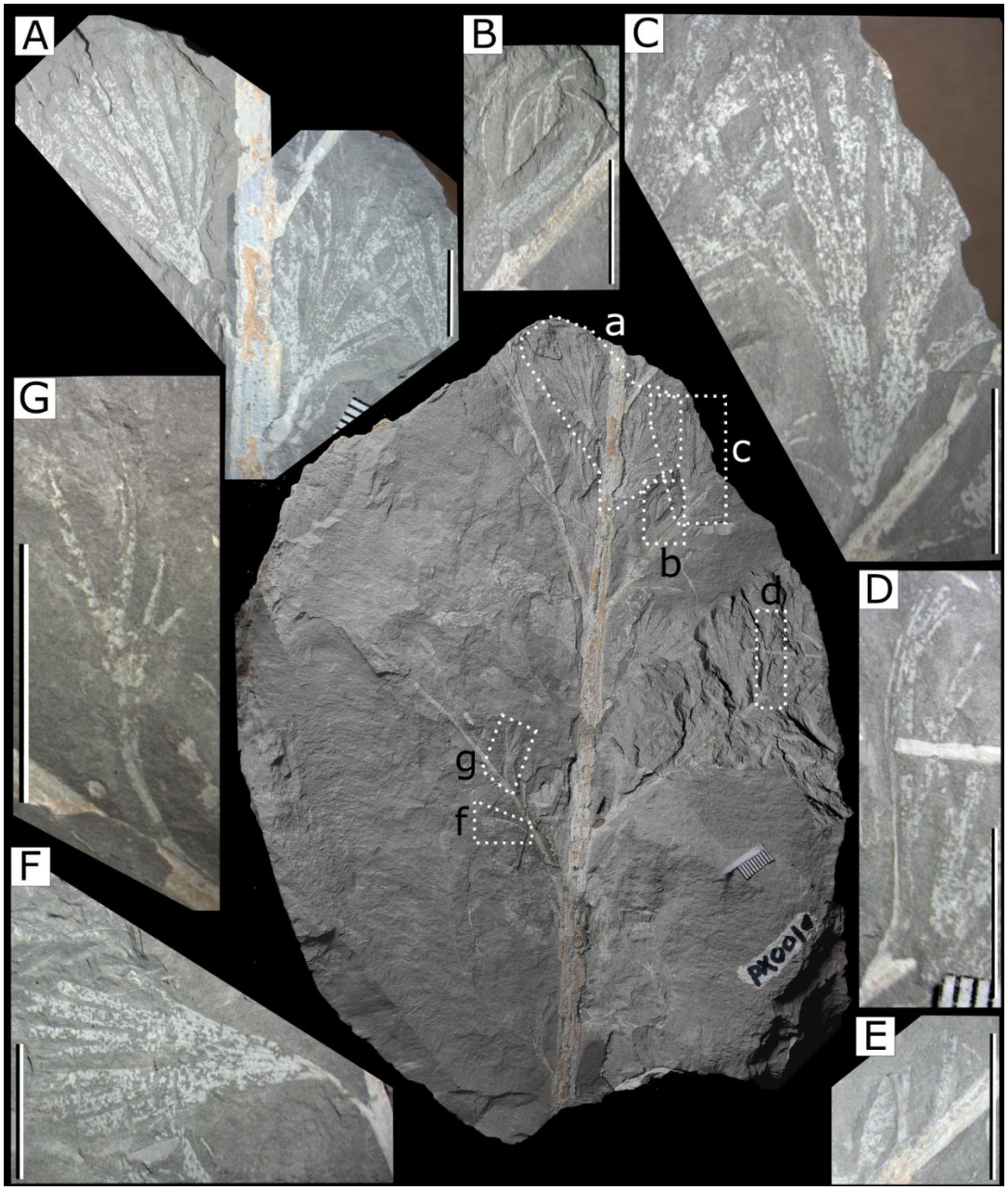

Figure 7.6: Partial lateral branch system of *A. notosaria* (AM 7711a – centre). **A-F)** enlargements from the specimen, their respective positions indicated on the centre photograph by lower case letters and demarked by stippled lines; **A)** type 3 leaves inserted on the PUB, **B)** two type 2 leaves attached to the UB (their insertions on the axis are only visible on the counterpart specimen, and are shown in (E)), **C)** type 3 leaf attached to an UB, **D)** type 2 leaf attached to an UB, **E)** insertions of two type 2 leaves shown in (B), from the counterpart (AM 7711b), which has been inverted to the correct orientation **F)** type 1 (?) leaf attached to an UB, and **G)** type 2 leaf attached to an UB. Scale bars for A–G = 1 cm. Scale for centre specimen in mm.

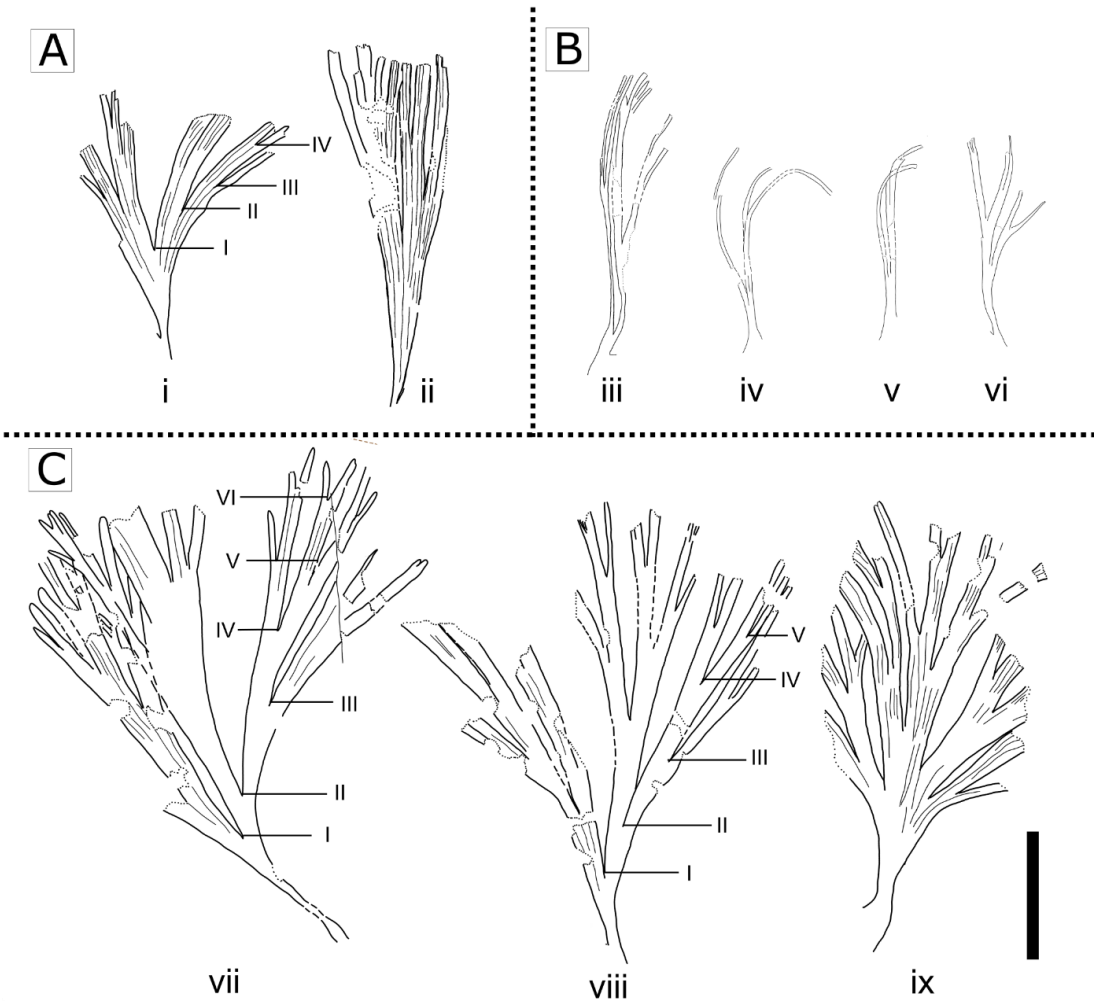

Figure 7.7: Line drawings of *A. notosaria* vegetative leaves; **A)** type 1 leaves, (i) from Fig. 7.4E, (ii) from Fig. 7.4A, **B)** type 2 leaves, (iii) from Fig. 7.6D, (iv) from an overlay of Fig. 7.6B and 7.6E (part and counterpart), (v) as for iv, (vi), from Fig. 7.6G, **C)** type 3 leaves, (vii) from Fig. 7.5B, (viii) from Fig. 7.5C, (ix) from Fig 7.6A. For A–C, small stipples indicate breakage of the fossils, larger stipples represent interpretive lines. Successive bifurcations of the leaf are indicated by capitalized Roman Numerals. All to same scale, scale bar = 1cm.

7.3.3 Remarks on vegetative leaf types

Vegetative leaves are represented by three distinct types, all of which occur on each of the three large specimens studied, except for the absence of Type 1 (‘typical’) leaves on AM 7712. On the basis of the studied material, it is noted that;

Type 1 leaves are ‘typical’ vegetative leaves characterizing *A. notosaria* (Anderson *et al.*1995), in that they are wedge-shaped, dichotomously veined with an anterior margin that has three deep dissections. Typical leaves terminate in 32 veinlets consistently, whereas *A. notosaria* is diagnosed as having leaves with up to 33 veins.

Type 2 includes small unwebbed leaves with at least two to three successive divisions. These usually arise from ultimate branches, and in a single instance was observed attached to a penultimate branch. They are filamentous structures distinct from the webbed type 1 and 3 leaves. All the specimens studied here had small leaves in attachment to vegetative ultimate branches with up to four found per ultimate branch, sometimes in pairs extending from the same side of the axis. They were probably more numerous than apparent but are underrepresented due to lower taphonomic and preparational potential than other types. It is possible that they may have been as numerous as typical vegetative leaves on the ultimate branch. As type 2 leaves occur on separate bedding planes from the typical vegetative leaves, and most commonly extended from the adaxial side of the ultimate branches, they are interpreted as having been inserted adaxially on the UBs.

Smaller leaves (type 2) were not hitherto recorded in this species. They resemble sporophylls (minus the sporangia), but are also similar to the vegetative leaves of *Svalbardia* and *Archaeopteris fissilis* (Andrews *et al.*, 1965; Matten, 1981; Jurina & Raskatova, 2014).

Diminutive filamentous leaves attached to *A. macilenta* ultimate branches were illustrated by Beck (1971; his figure 20), and were considered part of variation in the species. Fairon-Demaret and Leponce, (2001) observed diminutive leaves on vegetative ultimate branches of *A.* (*roemeriana*) *halliana* in addition to characteristic vegetative leaves. It was suggested that the small leaves occurred on the adaxial surfaces of branches, whilst the typical leaves were attached to abaxial surfaces, and both types were equally numerous on the branches. Their presence had already been predicted from the anatomical dorsiventrality in vegetative ultimate branches of this species, which produces leaf traces of unequal size ad– and abaxially (Kenrick & Fairon-Demaret, 1991). This ‘anisophylly’ was suggested to be an adaptation towards maximizing light interception (Fairon-Demaret and Leponce, 2001). Evidence presented here suggests that *A. notosaria* provides another example of anisophylly in *Archaeopteris* species.

Type 3 (large) leaves, with at least five successive bifurcations (Figure 7.7C), produce an estimated 64 (or more) distal veinlets. They are more deeply dissected than type 1 leaves, and, unlike the latter, often occur in attachment to PUBs. Two of three

specimens described here have type 3 leaves attached to UBs. Type 3 and type 1 leaves are similar in structure, but the larger form is more divided, with a marked initial subdivision resulting in at least double the number of veinlets.

These type 3 leaves are most clearly distinguished by size, occupying a separate, larger, size class than typical leaves. Being up to 39.1 mm long, type 3 leaves conform to the upper limit of the size range originally reported for leaves of this species (Anderson *et al*., 1995), in which they were considered to form a continuum of the variation rather than a distinct type. The diagnosis of *A. notosaria*, however, fails to note the far larger number of distal veinlets observed on the larger leaves (Anderson *et al*., 1995).

Type 3 leaves also differ from type 1 leaves in being apparently less symmetrical. For example, some large leaves attached to UBs show an odd number of terminal veinlets – a characteristic not observed on type 1 leaves. Others attached to a PUB appear to be three-lobed instead of four-lobed. The asymmetry and distribution of type 3 leaves is currently enigmatic, however more data on variation in this species is likely to be found in restudy of specimens already described by Anderson *et al.* (1995) and others subsequently added to the Waterloo Farm collection.

7.4 Description of fertile organs

7.4.1 Distribution of fertile material on the lateral branch unit.

Sporangia are borne on modified leaves (sporophylls). These are attached to UBs only within the studied sample. The two near-complete lateral branch units from the collection both bear fertile leaves, and therefore evidence the distribution of fertile material on the lateral branch system of this species. AM 7713 (Figure 7.1A, 7.2), has a penultimate axis 61 cm long with at least 20 UBs attached. Of the proximal ten, six bear fertile leaves, whilst the other four are either truncated at the base or too poorly preserved to determine whether fertile leaves are present. It is therefore possible that the ten most proximal UBs bore fertile leaves. The remaining – distalmost – UBs are all apparently fully vegetative. The other whole lateral branch system, AM 7710 (Figure 7.1B), has a penultimate axis 56 cm long and bears fertile leaves on the four most proximal of its 25 UBs. A less complete lateral branch system, specimen AM 7714 (Figure 7.8), shows four fertile UBs, and these appear to be the most proximal on the penultimate axis. It is therefore indicated that fertile leaves were borne on between four and ten of the most proximal UBs on a lateral branch system.

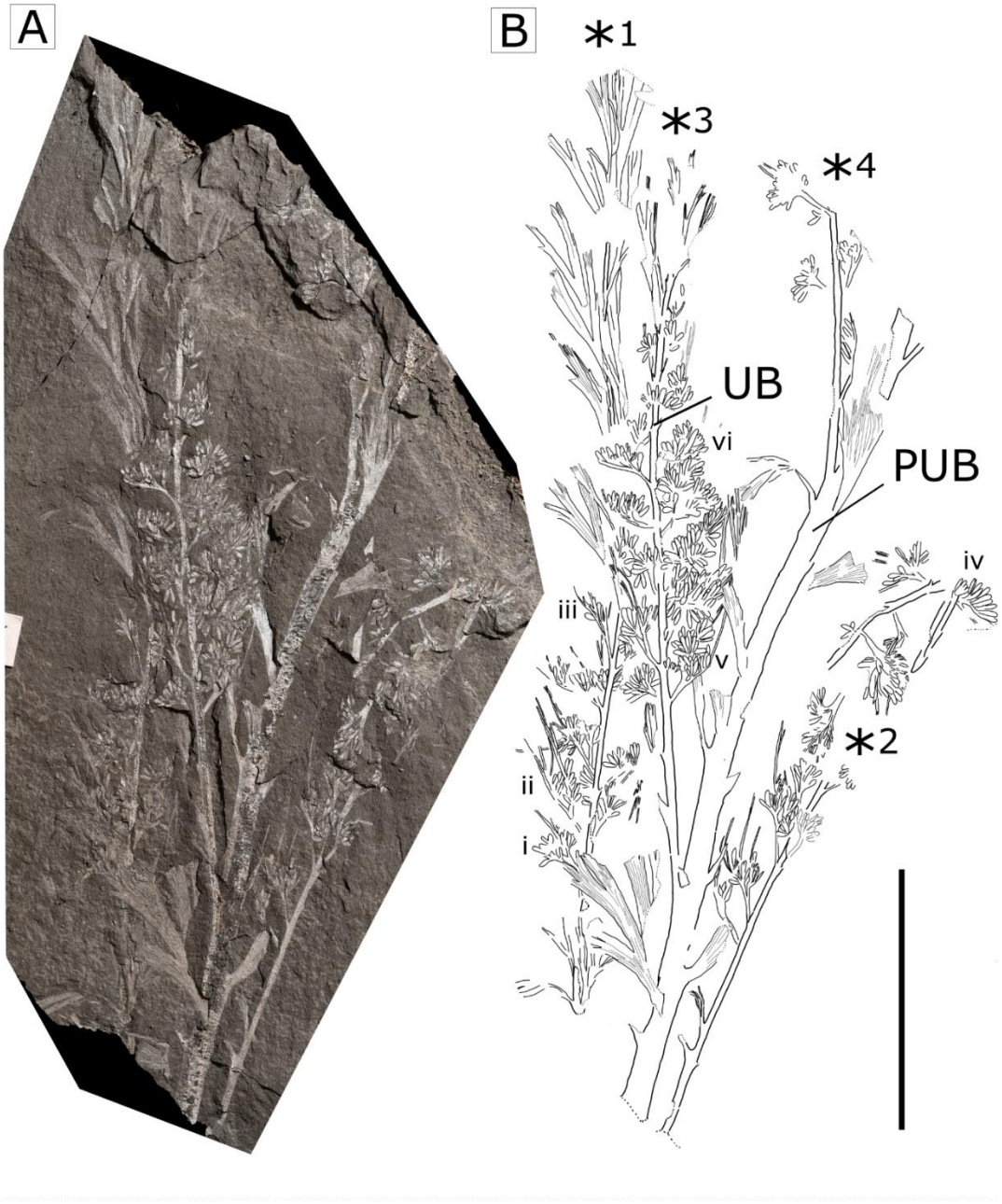

Figure 7.8: **A)** Portion of a fertile lateral branch system (AM 7714). **B)** Line drawing of the specimen in (A). Fertile UBs are marked with an *, and numbered according to the interpreted sequential origin on the PUB. Roman numerals indicate the sporophylls enlarged in Figures 12 and 13. (A) and (B) to same scale, scale bar = 5cm

7.4.2 Fertile ultimate branch morphology

Fertile UBs are between 80 mm and 188 mm in preserved length. Basally, axes are 1.5–2.5 mm wide, tapering evenly towards the apex, and bear up to 22 sporophylls (Figure 7.9B). Some have vegetative leaves attached proximally and distally to the fertile area on the branch, but this is not always the case, as some of the more heavily fertile

branches have very few or no typical vegetative leaves (eg. Figure 7.9B). Up to three (or four) type 1 vegetative leaves are attached proximal to the sporophylls on the axis, with up to ten being preserved distally, as exemplified by branch 1 on AM 7714 (Figure 7.8).

The number of vegetative leaves on a fertile UB varies along the lateral branch system, being greatest in number on basal fertile UBs, and fewer towards the distalmost fertile UBs, which usually lack vegetative leaves. This is observed most clearly on specimen AM 7713 (Figure 7.1A, 7.2), which has one or two proximal vegetative leaves on the first five (probably) fertile UBs, and none on more distal fertile UBs. Similar trends are evident on AM 7710 and AM 7714. AM 7714 (Figure 7.8) has four fertile UBs, and the number of proximal vegetative leaves on each fertile UB varies from three on the most basal, to none on the most apical. The number of basal vegetative leaves on branch 1 (Figure 7.8B) is probably more than three, as its origin is not seen on the specimen.

AM 7713 is the most heavily fertile specimen in the collection and demonstrates variation in the organisation of fertile leaves along the lateral branch system. The number of fertile leaves is greatest on UBs in the middle of the fertile area of the lateral branch system (UBs 2 and 3, Figure 7.2). As these leaves are densely packed about the UBs on the specimen, their number and insertions are difficult to determine, but they demonstrate clearly the highest number on any fertile UB in the collection. By contrast, the distal fertile UBs bear very few fertile leaves, although leaves with a sporophyll-like morphology (described below), but lacking sporangia, are numerous. The distalmost fertile UB (Figure 7.9D, F) has numerous leaves of this kind, and only four of them bear sporangia, each having six or less sporangia attached.

7.4.3 Sporophyll organisation

Sporophylls on UBs are usually borne in sub-opposite pairs, though sometimes alternately. On AM 7714, irregular and alternate arrangement of sporophylls tends to occur near the transition between vegetative leaves and sporophylls (Figure 7.10B). Pairs of sporophylls occur at fairly regular intervals, however, the spacing varies between consecutive pairs of sporophylls, and from specimen to specimen. The average spacing of sporophylls on ultimate branches from three different specimens (Figure 7.9A–C), calculated by dividing the number of sporophylls on the UB by the length of the fertile area, ranges from 2.15 to 4.96 mm. Variation in spacing of sporophylls is

illustrated in Figure 7.10, where two UBs are drawn to scale with sporophylls removed to show their insertions.

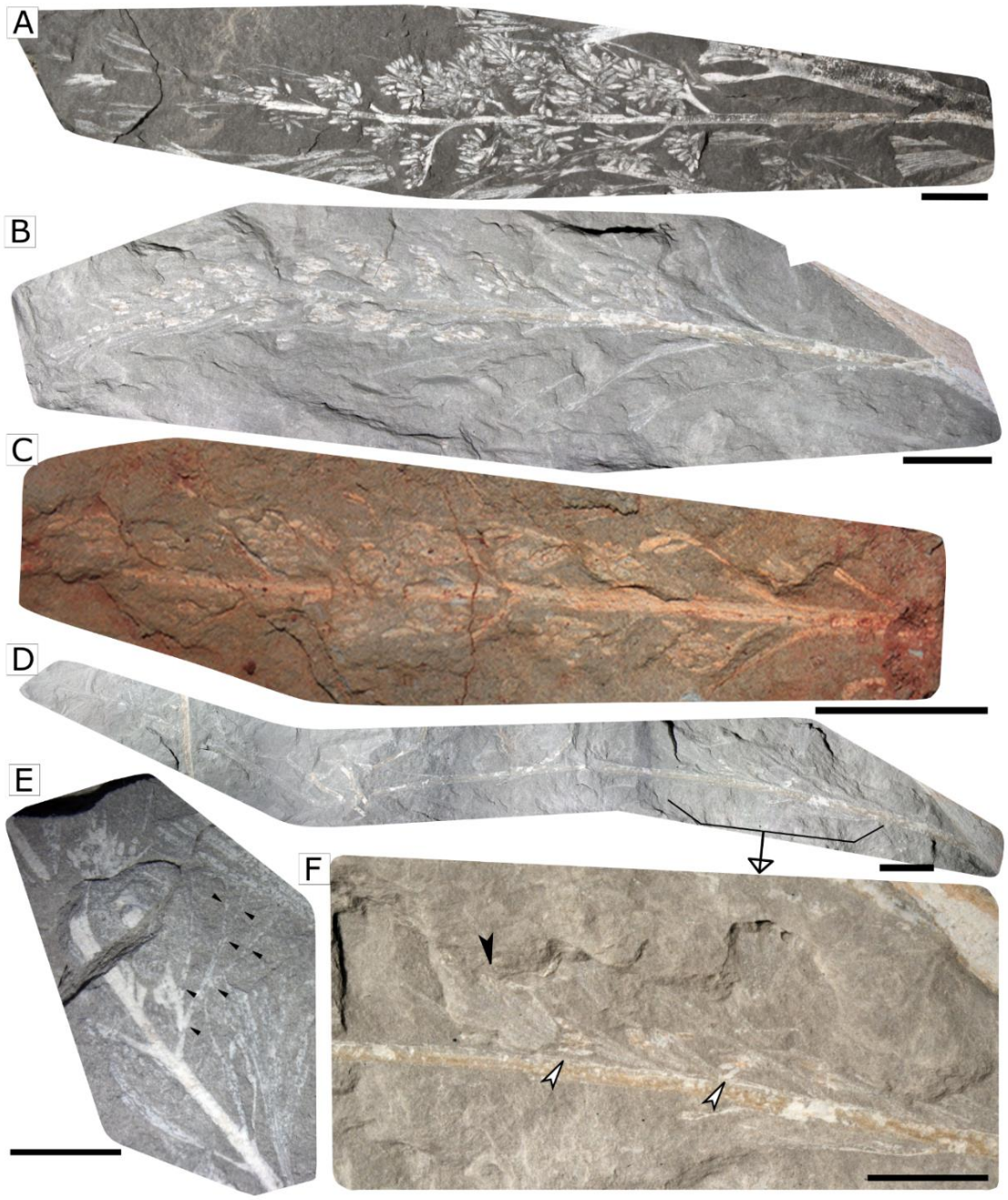

Figure 7.9: *A. notosaria* fertile ultimate branches; **A)** branch 3 from AM 7714a (Figure 7.8B), **B)** branch 3 on AM 7713 (Figure 7.2), **C)** an incomplete branch from AM 7716, **D)** branch 6 from AM 7713, **E)** proximal part of branch 1 on AM 7710 (Figure 7.3), black arrows indicate bifurcations of the sporophyll-like leaf which lacks sporangia, **F)** enlargement of the indicated region on (D) showing the only fertile leaves on the branch, sporangia are indicated by white arrows, a vegetative leaf is marked with a black arrow. All scale bars = 10mm.

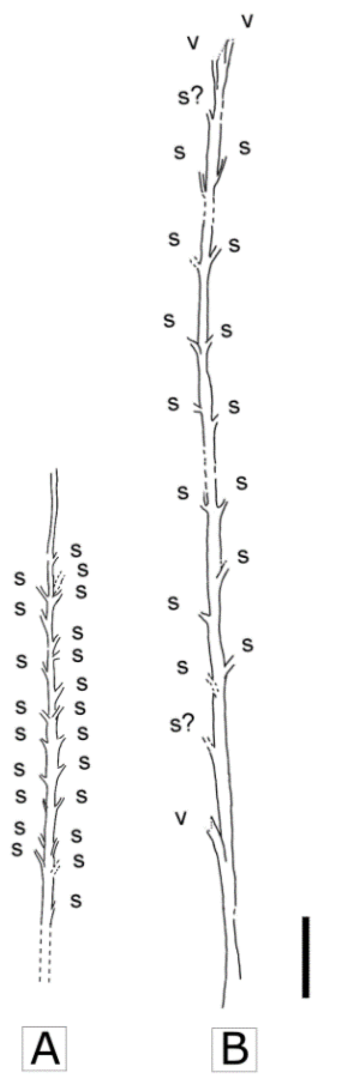

Figure 7.10: Line drawings of fertile UBs with sporophylls removed to show their insertions; A) AM 7716 (Figure 8C), B) AM 7714, (branch 3, Figure 7B; Figure 8A). (A) and (B) to same scale, scale bar = 1 cm, s = sporophyll, v = vegetative leaf.

Sporophyll attachments were sometimes exposed by *dégagement* where, for example on AM 7116 (Figure 7.9C, 7.10A), some of them extended from the underside of the axis, down into the matrix. Before preparation, pairing of sporophylls was not always detected, but pairing was found to be more consistent than was initially apparent.

7.4.4 Sporophyll morphology

Sporophylls are 16–32 mm long, with more sporangia-rich sporophylls falling towards the shorter end of this range. Sporophylls bearing fewer sporangia, by contrast, are longer. The sporophyll lamina dichotomises at four levels, possibly five in some cases

(Figures 7.12, 7.13). The leaf appears to divide on a single plane, transverse to the axis to which it is attached.

Sporophylls near to the vegetative area on the UB bear a lower number of sporangia, and there is a gradation in number of sporangia towards the most heavily laden sporophylls in the middle of the fertile area on each UB (Figure 7.9A, B, 7.11A, B).

Sporophylls are decurrent at the base, diverge from the ultimate branch at between 15 and 45° and are slightly recurved towards the axis. On AM 7714, the angle of sporophyll insertion increases with the number of sporangia on the sporophyll. Of the two specimens exhibiting complete fertile UBs, AM 7713 has sporophylls more densely arranged, and its leaves all diverge from the axis at less than 30°, with the angle decreasing towards the apex. The tight arrangement and the relatively low angle of divergence from the axis suggests that at the time of burial the fertile leaves were incompletely unfolded (Figures 7.9B, 7.11B). This contrasts with the condition of AM 7714, in which its fertile UBs are more elongate and its leaves more splayed, suggesting greater maturity (for comparison see Figure 7.11).

Figure 7.11: Line drawings of fertile UBs; **A)** branch 6 from AM 7713 (Figure 9B), showing a tight arrangement of sporophylls, **B)** branch 3 from AM 7714a (Figure 9A), showing greater spacing and splay of sporophylls than exhibited by (A). (A) and (B) to same scale, scale bar = 10mm.

In addition to being less compact, fertile branches on AM 7714 (a + b) represent the best-preserved examples. This permits detailed study of the structure of sporophylls utilising part and counterpart. Sporophylls divide 3–6 mm from insertion on the ultimate branch. The first division of the leaf is closely followed by another, and

subsequent divisions occur at increasingly larger intervals. Second order segments are 1–2 mm long, and third, fourth and fifth order segments are 2–3 mm, 3–4.5 mm and 4–10.5 mm (or more) respectively. The sporophyll lamina is proximally 0.5 mm–1mm wide, widening before division, and tapering distally. The naked final segments of a sporophyll stand proud of the overlapping mass of sporangia. Fully formed sporophylls are expected to produce 16 such 'tails' given the four times bifurcated leaves. A maximum of seven have been observed on a single leaf (Figure 7.13C), but on this particular leaf it appears that at least half of them are lost or hidden by matrix. Overlapping of the leaf filaments and sporangia prevents the entirety of any sporophyll from being observed, and destructive dégagement was avoided in consideration of the small sample available. On some leaves the 'tails' are forked distally as the last division of the leaf occurs notably distal to the level of sporangial attachment, representing a fifth bifurcation of the sporophyll lamina (Figures 7.12, 7.13). It is unclear whether all sporophyll bifurcations are equal, with more sporangia-rich sporophylls appearing more bilaterally symmetrical than those with less sporangia (compare Figures 7.12 and 7.13). The medial filaments appear to be longer, and the lateral segments more reduced, and possibly bearing fewer sporangia, giving the more sporangia-rich sporophyll a flabelliform shape (Figure 7.13).

Additional insights on sporophyll structure are provided by a non-sporangia-bearing leaf occurring at the transition zone near the base of a fertile ultimate branch on AM 7710 (branch 3 on Figure 7.3). This leaf nonetheless exhibits the morphology of a sporophyll, and is fortuitously preserved horizontally arranged on an exposed bedding plane (Figure 7.9E). The thin, filamentous lamina bifurcates four times prior to truncation by an overlying leaf. Divisions of the leaf are apparently all isotomous and well-splayed, producing a bilaterally symmetrical, cuneiform shape. The leaf is 17 mm in preserved length, and conforms to the basic morphology of sporophyll laminae described above.

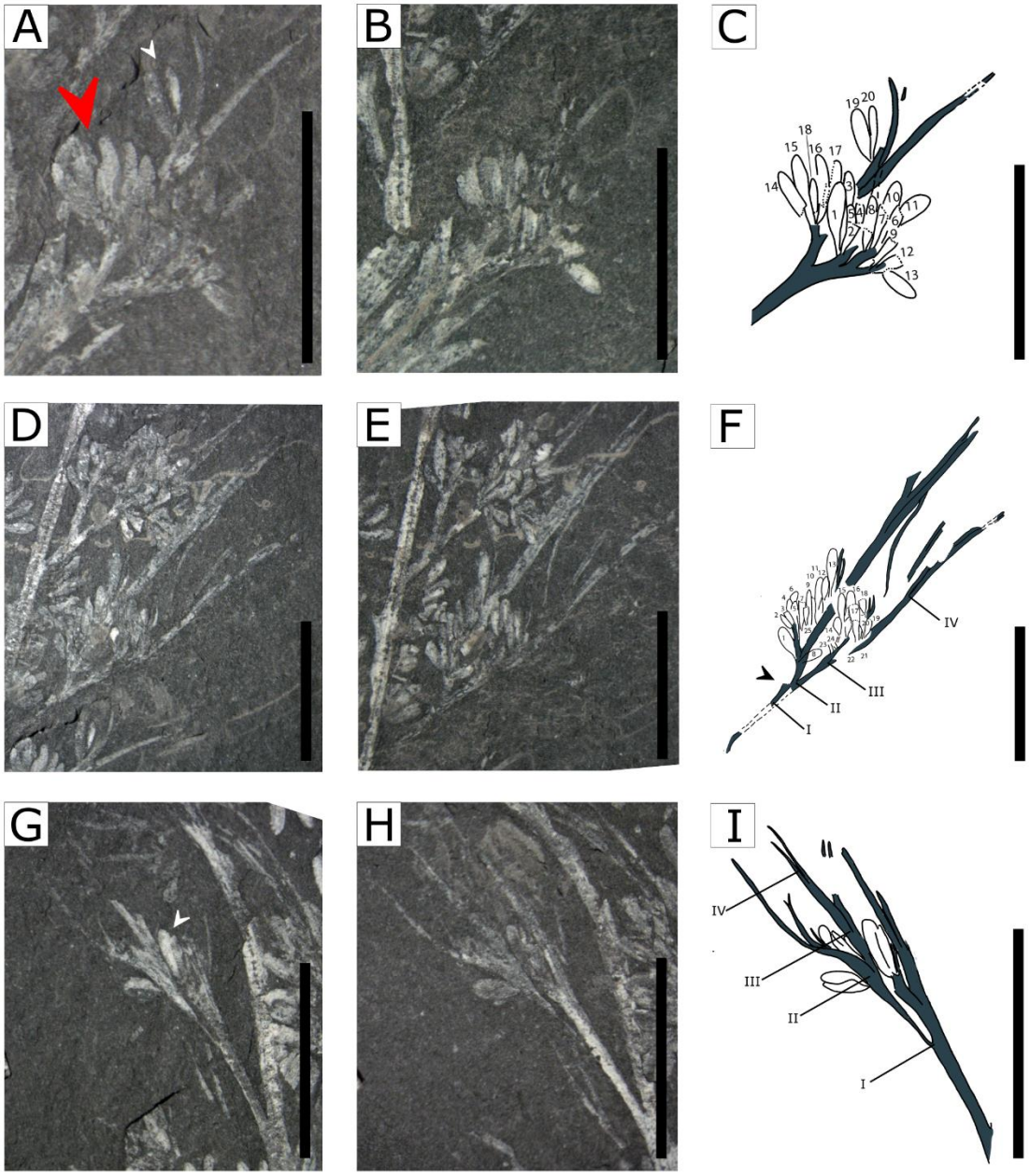

Figure 7.12 Detail of sporophylls i–iii from AM 7714 (a and B) (with reference to Figure 7.8B), **A)** counterpart to sporophyll i, large arrow indicates a 'whorl' of sporangia, small arrow indicates a pair of sporangia, **B)** sporophyll i, **C)** line drawing based on A and B, sporangia are numbered, sporophyll filaments are shown in blue, **D)** sporophyll ii counterpart, **E)** sporophyll ii, **F)** line drawing based on D and E, sporangia are numbered, capitalized Roman numerals indicate bifurcations of the sporophyll, arrow indicates first bifurcation of the sporophyll, sporophyll filaments are shown in blue, **G)** sporophyll iii, arrow indicates a pair of sporangia, **H)** sporophyll iii, counterpart, **I)** line drawing based on G and H, capitalized Roman numerals indicate bifurcations of the sporophyll lamina, sporophyll filaments are shown in blue. All scale bars = 10mm.

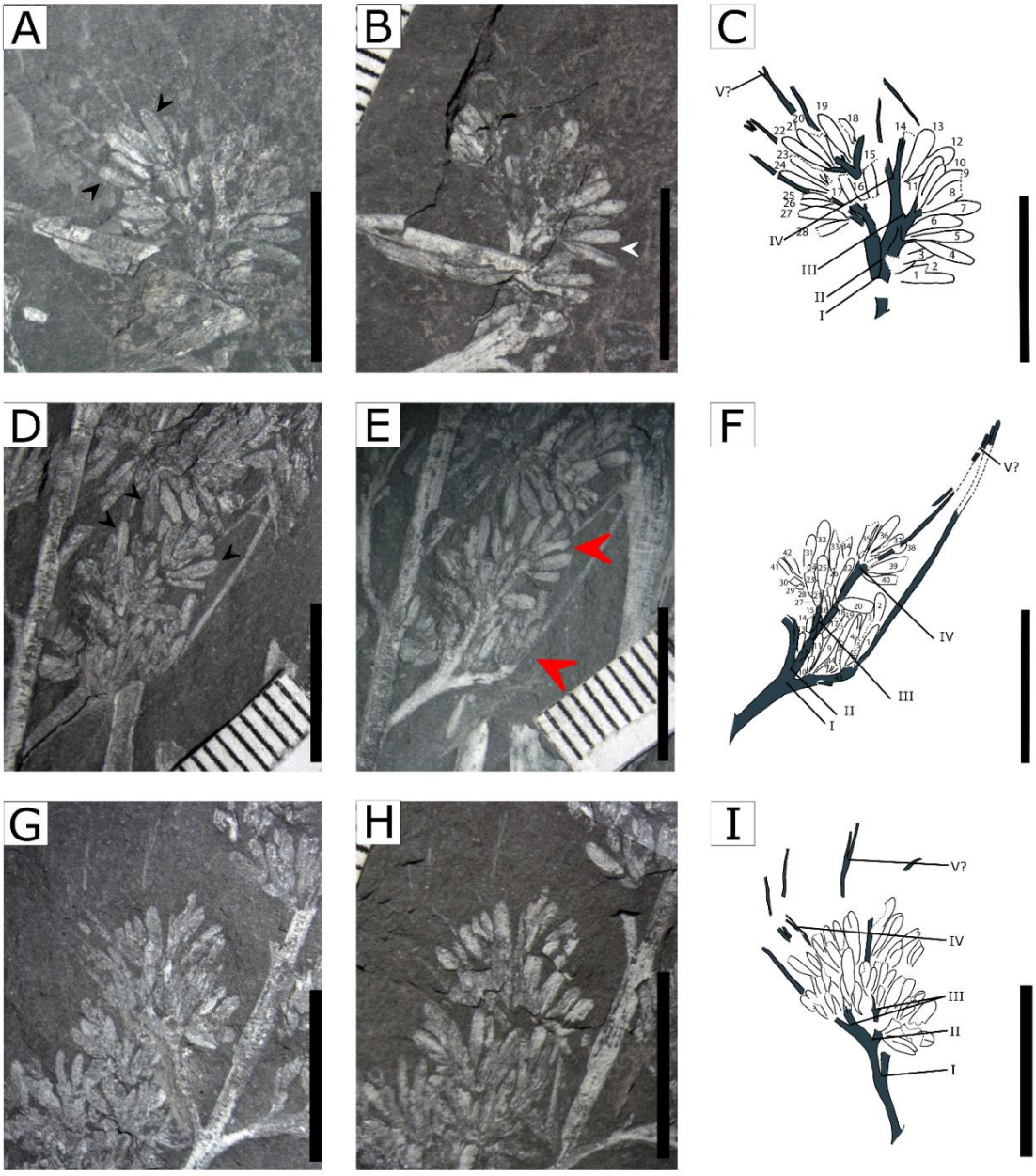

Figure 7.13: Detail of sporophylls iv–vi from AM 7714 (a and b), (with reference to Figure 7.8B), **A)** sporophyll iv counterpart, arrows indicate sporangia showing longitudinal line of dehiscence, **B)** sporophyll iv, arrow indicates a pair of sporangia, **C)** line drawing based on A and B, with sporophyll filaments shaded blue, **D)** sporophyll v, arrows indicate sporangia showing lines of longitudinal dehiscence, **E)** sporophyll v counterpart, arrows indicate 'whorls' of sporangia, **F)** line drawing based on D and E with sporophyll filaments shaded blue, **G)** sporophyll vi, **H)** sporophyll vi counterpart, **I)** line drawing based on G and H with sporophyll filaments shaded blue. Capitalized Roman numerals in (C), (F) and (I) indicate bifurcations of the sporophyll. Sporangia in (C) and (F) are numbered. All scale bars = 10mm.

7.4.5 Sporangia

Sporangia are between 2.7–3.4 mm long and 0.5–1 mm wide, and measure within this range across all studied fertile specimens. A pedicel, or narrow stalk, about 0.5 mm long and 0.1–0.2 mm wide, expands upwards into an elliptical or club shaped body, which is widest at approximately its medial point. A longitudinal line of dehiscence was observed on some sporangia (black arrows on Figure 7.13A, D).

Up to 44 sporangia were counted in attachment to a single leaf (Figure 7.13F). Sporangia are generally very densely packed, and their precise attachment to the sporophyll is often obscure. It is clear however that sporangia emerge from the adaxial surface of the sporophyll, and in a few examples are attached in pairs (white arrows on Figures 7.12A, G, 7.13B). Where a leaf divides, two pairs of sporangia may emerge side by side, giving the impression of a whorl (red arrows on Figures 7.12A, 7.13E).

Sporangia were not observed in attachment to the proximal segment of a fertile leaf (prior to the first division), but are attached from after the first division until immediately prior to the fourth division (Figure 7.13C, F, I). On sporophylls bearing fewer sporangia, they are limited to the zone between the first and third divisions. These are usually asymmetrically borne (Figure 7.12C, F, I). One of the apparently less fecund sporophylls (Figure 7.12D–F) erroneously appears bilaterally symmetrical, as one of the daughter branches of the first bifurcation dives into the matrix underneath the other, such that the visible part of the leaf represents half of the leaf lamina (arrow on Figure 7.12F).

Sporangia removed from AM 7710b and AM 7714 revealed no evidence of internal spores when examined under SEM.

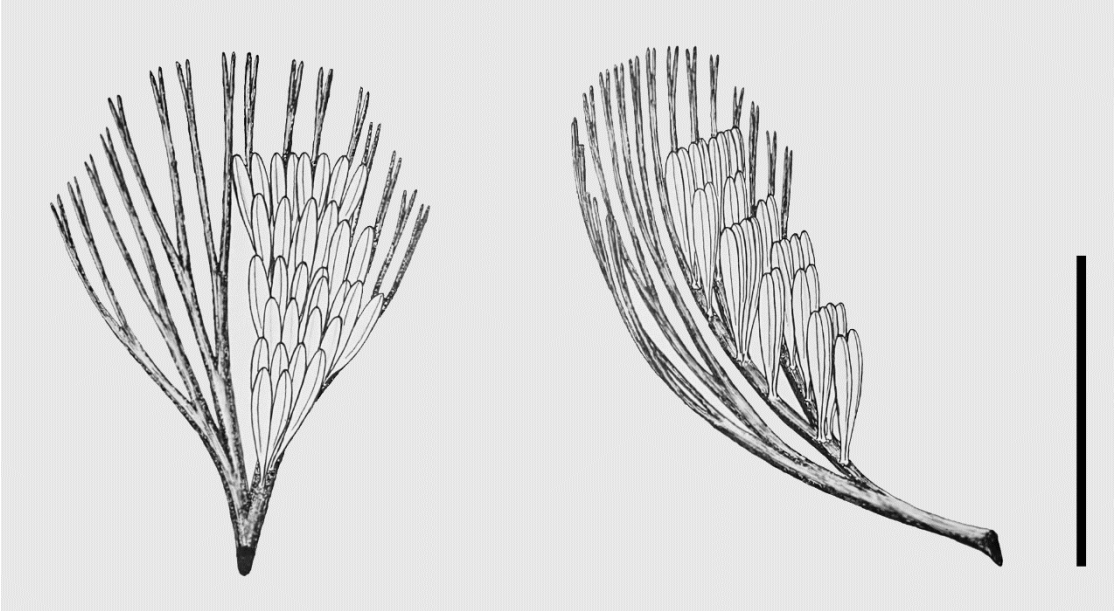

Figure 7.14: Suggested reconstruction of a mature *Archaeopteris notosaria* sporophyll with half of the sporangia removed, shown in frontal view (left) and oblique view (right). Scale bar = 10 mm.

7.4.6 Remarks on fertile material

The distribution of fertile organs on a lateral branch system is similar on all three closely studied specimens. Fertile leaves are borne on between four and ten of the most basal UBs. Among them, the most heavily laden UBs occur in the middle of the fertile region. Vegetative leaves are often borne proximally and distally to the sporophyll bearing region on an ultimate branch, and were greatest in number on the basalmost UBs on a lateral branch unit.

Both complete lateral branching systems studied are fertile and of the four other, less complete specimens, two are fertile. Neither of the remaining two partial specimens is conclusively infertile. However, the possibility of infertile lateral branch systems cannot be ruled out. From this (albeit small) sample, the majority of units were probably dispersed during, or after, the production of spores.

Fertile UBs were more disordered in their arrangement on the PUB than sterile UBs. In this dataset there is a positive correlation between irregular and alternate branching, and the presence of fertile leaves on the relevant branches. Indeed, few of the distinctly fertile UBs occurred in opposite pairs. Only one clear pair, the most distal fertile ultimate branches on AM 7713, could be identified.

Variation in the size of fertile UBs was compared to distribution of sporophylls. Shorter UBs bore sporophylls at a higher frequency than the longest fertile UB (AM 7714), which also had the highest average spacing of sporophylls. Correspondingly, sporophylls on the latter appeared to be more mature. This was evidenced by a greater degree of splay of the leaves, more numerous sporangia, and a wider angle of insertion on the axis. The tighter posture of sporophylls on the shorter branches appear to be at an earlier phase of development. By this argument, ontogenetic changes explain the great variation in spacing of sporophylls.

During burial most sporophylls have been rotated from their original perpendicular orientation, and it is therefore unlikely that all of the distal segments are expressed on a bedding plane, or that they can be exposed from the matrix without partial destruction of the leaf. However, they are so delicate as to be very difficult to prepare from the matrix. The methods required to expose the full extent of a sporophyll and its sporangia, were demonstrated by Fairon-Demaret *et al.* (2001) who were able to qualify the nature of a single sporophyll with great accuracy. Perhaps with the correct approach, their methods could be applied to *A. notosaria*, in order to test the observations of the present study. Lacking complete dégagement of sporophylls, it is hypothesised that many sporangia were not accounted for, and they could well be more numerous than counted.

7.5 Comparison with the holotype

The holotype of *Archaeopteris notosaria* (AM 4198 a + b) is the sole example of fertile structures of this species hitherto described. It is a portion of a lateral branch unit comprising a penultimate axis with characteristic leaves and four (possibly five) UBs attached. The two most proximal UBs on the specimen bear fertile leaves. It was diagnosed as having very short and compact fertile UBs, as long as wide, with up to five or six sporophylls spaced at intervals of 0.5 mm on the ultimate axis (Anderson *et al*., 1995). The compact nature of the fertile UBs was considered to be unique amongst *Archaeopteris* species.

The holotype was well illustrated, and interpreted correctly in the line drawing (Anderson *et al*., 1995, Fig. 3), hence there is no need to re-illustrate it here. However, the specimen was re-examined, and given the relatively well-preserved fertile material

from Coombs Hill, modification of some aspects of the original description are here proposed.

Although the holotype specimen is broken off at the base, it shows a slight bulging at this point, such as is usually seen at the base of a lateral branch system. Hence the holotype is most likely the proximal part of a lateral branch system, and the fertile UBs represent the most basal UBs thereof.

It was assumed that the fertile UBs on the holotype were complete, and the recorded dimensions (as long as broad) were unique amongst *Archaeopteris* species (Anderson *et al*., 1995). On re-examination, the specimen appears to have suffered some damage prior to burial, with some of the UBs having been torn off or bent backward. The apparent shortness of the fertile UBs likely results from preburial truncation.

Sporophylls are spaced at larger intervals than the 0.5 mm suggested in the description. Although difficult to observe the exact insertions due to poor preservation, an interval of 2–3 mm between successive pairs of sporophylls is suggested.

Sporangia are longer than the 2 mm suggested, being up to 3 mm in length.

Coombs Hill *Archaeopteris* fertile material is therefore similar to the holotype of *A. notosaria* in morphology of sporophylls. Sporophylls on the latter are not visibly branched, suggesting that they have been preserved side on, as with some of the Coombs Hill material, particularly the more compact fertile branches. In this case, the remainder of the sporophyll is likely concealed by matrix.

Further similarities include the size and shape of sporangia, their positions on the adaxial surface of sporophylls, and the proximal position of fertile UBs on the lateral branch system. The spacing of sporophylls is similar between the holotype and the most densely spaced fertile UB from Coombs Hill. It is therefore possible that the holotype specimen represents an early stage in the opening of the fertile UB. This possibility was already suggested by Anderson *et al.* (1995), but they preferred to interpret the compactness of the holotype fertile UBs as a taxonomic character.

7.6 Comparisons with other *Archaeopteris* species

7.6.1 Size of lateral branch systems

Lateral branch systems vary in size within *A.* species (Beck, 1962). Understanding of their range in size is however hampered by incomplete preservation of the lateral branch systems, as very few published records of complete lateral branch systems were found during this review. One complete lateral branch system of A. *halliana* is roughly 45 cm long (Cloutier, 2013). Fairly complete specimens, probably representing the major part of lateral branch units are illustrated by Arnold (1937); Phillips *et al*. (1972); Fairon-Demaret *et al*. (2001) and Kräusel and Weyland (1941). Arnold (1937) illustrates a partial lateral branch unit of *A. macilenta* which he reports as having a length of 14 in (35 cm). A partial specimen of *A. macilenta* illustrated by Phillips *et al*. (1972) has a length of around 20 cm. A partial specimen of *A. halliana* illustrated by Fairon-Demaret *et al*. (2001) is around 10 cm long. A drawing of an apparently nearly complete specimen of *A. halliana* was provided by Kräusel and Weyland (1941), although unfortunately no scale bar was provided. Complete lengths of *A. notosaria* lateral branch systems attained during this study are 56 and 61 cm. *A. notosaria* has been estimated as having lateral branch units up to 75 cm in length (Anderson *et al.*, 1995). The data suggests that *A. notosaria* branch systems may have attained a greater length than other known *Archaeopteris* species.

7.6.2 Morphology and arrangement of vegetative leaves

Archaeopteris notosaria has vegetative leaves that are wedge-shaped, and deeply dissected. It differs from *A. fissilis* which has unwebbed vegetative leaves, and *A. halliana* and *A. obtusa* (and similar species - see chapter 2.5) which have vegetative leaves with nearly entire margins. *A. notosaria* shares with *A. macilenta* deeply dissected vegetative leaves, but those of the latter are flabelliform rather than wedge-shaped, widest at their midway, and each of the segments of the leaf terminates in a delicate hair-like tip. The latter character has not been recorded in *A. notosaria*. The leaves of *A. notosaria* are superficially similar to *A. sphenophyllifolia*, but the latter is one of the less well understood species. Partial specimens were briefly described by Arnold (1936) and only a single fertile fragment was tentatively included in the species. His qualitative description of the vegetative leaves, as wedge-shaped, deeply dissected, into four or five lobes, is consistent with type 1 vegetative leaves of *A. notosaria*. Kräusel and Weyland (1941) re-illustrated a drawing of the holotype, and they

considered the species to not belong to *Archaeopteris*. Carluccio *et al*. (1965) considered *A. sphenophyllifolia* a synonym of *A. macilenta*. Re-study of *A. sphenophyllifolia* is required for definitive comparisons with *A. notosaria*, in order to exclude synonymy.

Archaeopteris notosaria has only been described from South Africa, but evidence from the literature suggests that it may have had a wider distribution. *Archaeopteris* with *notosaria*-like leaves from the Upper Devonian of Colombia were distinguished from the species on the basis of larger size (Moreno-Sánchez, 2004). The size range is not reported, but leaves of up to around 40 mm are illustrated (Moreno-Sánchez, 2004), which is insignificantly larger than type 3 leaves of *A. notosaria* (up to 39 mm in recorded length). It appears that only type 1 leaves illustrated in Anderson *et al*. (1995) were selected for morphometric comparison with the Colombian material (Moreno-Sánchez, 2004). The wedge-shaped, deeply dissected leaves of the Colombian specimens are most similar to those of *A. notosaria*. Other *Archaeopteris* species including *A. macilenta* and *A. obtusa* also occur in the Colombian Upper Devonian.

A possible record of *A. notosaria* was reported from the upper member of the Campo Chico formation in Venezuela (Upper Devonian) (Berry *et al.*, 2000). The remains have not been described though.

Archaeopteris cf. *halliana* from the Famennian of South China, has leaves that are wedge-shaped and deeply dissected, on average 14 mm long (Guo & Wang, 2009). Despite the deeply dissected vegetative leaves, around 40 specimens were attributed to *A. halliana* on the basis of similarities in sporophyll morphology (Guo & Wang, 2009). Lacking complete *dégagement* of sporophylls this approach may be misleading. Vegetative leaves of the Chinese material strongly resemble those of *A. notosaria*, except that the recorded size ranges of leaves and sporophylls are lower than those for *A. notosaria*.

Like most species of *Archaeopteris*, vegetative leaves of *A. notosaria* are borne both on the ultimate branches, and on the penultimate branch (Beck, 1962; Scheckler, 1978; Fairon-Demaret & Leponce, 2001). Type 3 vegetative leaves attached to some PUBs in the Coombs Hill material are larger than the typical vegetative leaves. Beck (1971) recorded abnormally large vegetative leaves attached to *A. macilenta* PUBs, but no other record of this character was found during this review.

Type 2 vegetative leaves are small, unwebbed and probably borne on the adaxial surfaces of ultimate branches. Similarly, smaller, unwebbed leaves were uncovered by *dégagement*, in attachment to the adaxial surfaces of ultimate branches of *A. halliana* (Fairon-Demaret & Leponce, 2001) and *A. macilenta* (Beck, 1971) and hence, 'anisophylly' may be a character shared by *Archaeopteris* species with webbed vegetative leaves (Fairon-Demaret & Leponce, 2001).

7.6.3 Distribution of fertile ultimate branches on the lateral branch system

A. notosaria bears its fertile ultimate branches at the base of the lateral branch system. In this regard it is similar to *A. fissilis* and *A. macilenta* (Beck, 1960; Andrews *et al.*, 1965), but differs from *A. halliana* which is considered to have a fertile area in the middle of the lateral branch system with basal and apical branches being sterile (Fairon-Demaret *et al*., 2001). The possibility of entirely fertile lateral branch systems in *A. halliana* was not excluded. Specimens suggesting a wholly fertile lateral branch system in *A. halliana* were also described by Phillips *et al*. (1972). *A. obtusa* was also suggested to bear wholly fertile lateral branch systems (Andrews *et al*., 1965). Thus, *Archaeopteris* species with entire, or nearly entire vegetative leaves are indicated to bear wholly fertile lateral branch systems, whilst those with dissected, or unwebbed leaves are recorded as bearing fertile leaves proximally on the equivalent unit.

7.6.4 Fertile leaves bounded proximally and distally by typical vegetative leaves

Sporophylls of *A. notosaria* are attached to ultimate branches, and are frequently bounded proximally and distally by typical vegetative leaves. This character is common among species of *Archaeopteris* (Beck, 1960; Phillips *et al*., 1972, Fairon-Demaret *et al*., 2001). Vegetative leaves are greatest in number on the most basal fertile ultimate branches on the lateral branch system of *A. notosaria*, and this character is shared with *A. halliana* (Fairon Demaret *et al*., 2001). In *A. fissilis*, it is the reverse, with the number of sterile leaves increasing on the more apical fertile ultimate branches (Andrews *et al*., 1965).

7.6.5 Gradation between vegetative and fertile leaves

In *A. fissilis, A. macilenta* and *A. halliana*, gradation between vegetative leaves and fully formed sporophylls has been described. Kenrick and Fairon-Demaret (1991) illustrated leaves of *A. (roemeriana) halliana* which they termed 'transitional leaves', that were morphologically intermediate between vegetative leaves and sporophylls.

Half of the leaf was a flattened blade, much like a typical vegetative leaf, and the other half was unwebbed, and bore sporangia like a sporophyll. Transitional leaves are borne at the boundary between the respective areas on an ultimate branch. A similar gradation was observed in *A. notosaria* leaves in the present study, in that the number of sporangia on a fertile leaf is reduced close to the vegetative bases and tips of the ultimate branches and sporangia may be absent on such leaves. No half vegetative and half fertile transitional leaves were, however, observed on specimens of *A. notosaria*. The changes in leaf morphology along a fertile ultimate branch were referred to as 'allomorphosis' by Fairon-Demaret *et al.* (2001). This character appears to be common among species of *Archaeopteris* (eg. Beck, 1962).

7.6.6 Arrangement of sporophylls

Sporophylls are arranged with variable frequency on the ultimate axes of *A. notosaria*, but are not as densely arranged about the ultimate branch as those of *A. halliana*, on which average spacing of 0.6 mm/sporophyll (Kenrick and Fairon-Demaret, 1991) and 1.5 mm/sporophyll (Phillips *et al.*, 1972) has been reported. This character was unfortunately not quantified in *A. macilenta*, and we cannot extrapolate this information from illustrations, but a dense arrangement is suggested (Carluccio *et al.*, 1966). With an average spacing of sporophylls between 1.5–5 mm, the fertile ultimate branches of *A. notosaria* are significantly less compact than those of *A. halliana* and probably *A. macilenta*.

The paired insertion of sporophylls on *A. notosaria* is consistent with either a decussate interpretation (Beck, 1971; Phillips *et al.*, 1972), or a paired helical interpretation (Carluccio *et al.*, 1966), but differs from the simple helical interpretation of Fairon-Demaret *et al.* (2001). The apparent orientation of pairs of sporophylls however, does not suggest a perpendicularly alternating 2/1 decussate phyllotaxy. From the radially symmetrical xylem noted in ultimate branches of both *A. halliana* (Kenrick & Fairon-Demaret, 1991) and *A. macilenta* (Carluccio *et al.*, 1966), the evidence presented here favours a paired –or double– helical insertion.

7.6.7 Morphology of the sporophyll

Sporophylls of *A. notosaria* bifurcate at four or five levels, in contrast to those of most other *Archaeopteris* species in which three or less orders of bifurcation have been observed (Andrews *et al.*, 1965; Phillips *et al.*, 1972; Fairon-Demaret *et al.*, 2001). The

one other exception is *A. macilenta*, which had up to several divisions of the sporophyll (Carluccio *et al*., 1965).

Sporophylls are also longer in the South African species than in other known *Archaeopteris*, usually more than 20 mm, and up to 32 mm in length. Fertile leaves were on average 10 mm in length in both *A. halliana* and *A. fissilis* (Andrews *et al*., 1965; Fairon-Demaret *et al*., 2001). In *A. macilenta* they were recorded as up to 10 mm in length (Phillips *et al*., 1972), although Carluccio *et al*. (1966) reported in the same species fertile leaves usually less than 20 mm, up to 25 mm long.

7.6.8 Number and arrangement of sporangia on the sporophyll

In terms of number of sporangia on a sporophyll, *A. notosaria* exceeds all other known species with up to 44 (probably more) on a sporophyll. Previously the largest number were reported on a leaf of *A. halliana*, which had 39. *A. macilenta* was reported as having between 2 and 20 sporangia per sporophyll (Carluccio *et al.*, 1966). This is supported by the suggestion that *A. fimbriata* (considered a synonym of *A. macilenta* by Kräusel and Weyland, 1941), had half, or less, the number of sporangia on a sporophyll compared to *A. halliana* (Andrews *et al.*, 1965). The same is suggested for *A. fissilis* (Andrews *et al.* 1965). The latter is interpreted as bearing sporangia mostly on the assumed proximal undivided segment of a sporophyll (Andrews *et al.* 1965). In *A. notosaria* and *A. halliana*, sporangia are generally not borne on the proximal undivided segment of the sporophyll except in rare cases in *A. halliana* (Fairon-Demaret *et al*., 2001).

CHAPTER 8 – DISCUSSION

8.1 Summary

Fossil floras at Coombs Hill and Waterloo Farm preserve relatively intact remains of Late Devonian plants from Southern Africa. New lycopod taxa and remains of the progymnosperm *Archaeopteris notosaria* are described in this dissertation, contributing toward a project to document high-latitude floral diversity of Devonian Gondwana. The presence of leaves attached to lycopod stems at these sites allows more detailed taxonomic description than has previously been possible with regard to southern African material. Lacking completely preserved leaves, many of the specimens included in this study would remain under the names '*Haplostigma'* and *'Archaeosigillaria'*, as recorded from Coombs Hill prior to taxonomic study (Harris, 2017). Lycopod material presented here enables diagnosis of four new species, increasing the number of lycopod species recorded from the Witpoort Formation to six (excluding *'Haplostigma'* and *'Archaeosigillaria'*). A possible seventh lycopod taxon is represented by large dispersed sporophylls reported from the Waterloo Farm locality (Gess & Hiller, 1995a). *Palaeostigma* was included in the Lycophyta by Anderson and Anderson (1985), but is here retained in *incertae sedis* as its true affinities are uncertain (Berry & Fairon-Demaret, 2001).

8.2 Preservational bias

Although lycopods are considered the dominant plant group of the Devonian Period (Taylor *et al*., 2009), including in South African strata of that age (Plumstead, 1967), lycopod remains at Coombs Hill do not dominate the flora by abundance. Of at least 70 plant fossils collected at Coombs Hill, 15 have preliminarily been identified as lycopods. The remainder includes 11 *Archaeopteris* specimens, as well as a variety of undescribed remains. Taxonomic study may yet show that the largest proportion of identifiable plant remains are attributable to putative iridopteridaleans. The perceived dominance of lycopods in the Mid-to Upper Devonian of South Africa may, in part, be an artefact of preservation. Pertinent to this, a carbonaceous mudstone horizon near the base of the Witpoort formation at Rabbit Ridge, a few kilometres away from Coombs Hill, which is interpreted as being more distal to the plant bearing habitat, suggests a sorting bias in favour of lycopods (Harris & Gess, in prep.). The Rabbit Ridge locality

is palaeontologically dominated by a monospecific lingulid brachiopod fauna with sparse associated plant remains, indicative of a marine-dominated lagoonal environment (Harris & Gess, 2018). The fragmentary state of the Rabbit Ridge plant remains suggests a greater distance of transport than that implied by the preservation of many specimens at Waterloo Farm and Coombs Hill. Lycopods, some attributed to *'Haplostigma',* were far more dominant among plant fossils at Rabbit Ridge than at Coombs Hill. Fossil plant remains in channelized quartzitic sandstones underlying the Rabbit Ridge mudstone comprise almost exclusively lycopod fragments (Harris & Gess, in prep.).

The inner cortex of protolepidodendralean lycopod axes, comprising spongy parenchymatous tissues (Banks, Bonamo, & Grierson, 1972), may have increased buoyancy, allowing further transport of their remains than those of other plants. This may help to explain dominance of lycopod remains at Rabbit Ridge, and may also apply to stratigraphically lower strata of the Bokkeveld and Lower Witteberg Groups, where occurrences of marine restricted invertebrates suggest more distal sedimentary environments. Lagoonal shales at Coombs Hill and Waterloo Farm preserve relatively intact plant remains as a result of their proximity to the plant habitat, and may be more indicative of true diversity on the coastal lowlands than shallow marine strata.

8.3 Comparison of diversity between Coombs Hill and Waterloo Farm

Although not clearly dominant in terms of abundance, Lycopsida is likely the most diverse group of plants occurring in the Witpoort Formation. Lycopod species described above include three probable herbaceous taxa, and a putative arborescent form (its proposed habit supported by additional fossil evidence – see below). Lycopods 'A', 'C' and 'D', derive from Coombs Hill and are not known to occur at Waterloo Farm. Of three definitive lycopod species known at Waterloo Farm, *Leptophloeum rhombicum, Kowieria alveoformis* and 'lycopod B' none are represented at Coombs Hill. The latter two do, however, have possible sister species at Coombs Hill. This preliminary result suggests that taxonomic differences between the localities can occur at the **α**-taxonomic level.

Table 8.1: Tracheophyte taxa from Witpoort Formation localities Waterloo Farm and Coombs Hill. Green shading indicates a species occurring at both localities. Yellow shading indicates remains of undescribed higher-level taxa occurring at both localities. Red shading is for taxa that are only present at one of the localities. * indicates identification by pers. comm. by Prestianni and Gess (2019).

Taxa		Reference	Locality	
Class or Order	**Genus and species**		**Waterloo Farm**	**Coombs Hill**
Incertae sedis	*Palaeostigma robusta* And. & And. 1985	Gess and Hiller, 1995a	Present	Present (?)
Incertae sedis	'*Dutoitia' alfreda* Plumstead 1967	Gess and Hiller, 1995a	Present	Present (?)
Zosterophyllopsida	Undescribed zosterophyll	Gess and Hiller, 1995a	Present	Present
Lycopsida	*Leptophloeum rhombicum* Dawson	Prestianni and Gess, 2014	Present	Absent
	Kowieria alveoformis Gess and Prestianni	Gess and Prestianni, 2018	Present	Absent
	'*Haplostigma*' (Schwartz) Seward	Gess and Hiller, 1995a	Present	N/A
	Colpodexylon Banks 1944 sp. nov. A	This study	Absent	Present
	C. sp. nov. B	This study	Present	Absent
	'Lycopod C' gen. nov. sp. nov.	This study	Absent	Present
	'Lycopod D' gen. nov. sp. nov.	This study	Absent	Present
	Lycopod indet. (isolated sporophylls)	Gess and Hiller, 1995a	Present	Absent
Progymnospermopsida	*Archaeopteris notosaria* And. *et al*. 1995	Anderson *et al.*, 1995	Present	Present
	Archaeopteris sp. indeterminate	Gess and Hiller, 1995a	Present	Absent
Sphenopsida	*Rinistachya hilleri* Prestianni and Gess 2018	Prestianni and Gess, 2019	Present	Absent
Iridopteridales	Undescribed putative iridopteridalean	Gess and Hiller, 1995a (plates 35-37) *	Present	Present
Cladoxylopsida	Undescribed putative cladoxylopsid	Gess and Hiller, 1995a (plate 21) *	Present	Present
Gymnospermopsida	Undescribed putative seed plant	*	Present	Present

Notable is the absence of *Leptophloeum rhombicum* at Coombs Hill. With the relatively high preservation and observation potential of its large robust axes, and distinctive appearance of its rhombic leaf cushions, it can be stated with some confidence that the species did not occur on the shores of the Coombs Hill lagoons. *Leptophloeum* casts are widespread in quartzites throughout latest Devonian strata in the Cape Fold Belt (Theron, 1960; Thamm & Johnson, 2006), and also in shale at Waterloo Farm (Prestianni & Gess, 2014). Deposition of the Coombs Hill sequence may predate the earliest occurrence of this cosmopolitan taxon in South Africa. The stratigraphic age, within the Famennian, of Coombs Hill is currently uncertain, though it is likely older than Waterloo Farm and *Leptophloeum's* absence from the site therefore suggests its potential usefulness as a biostratigraphic marker for the upper Witpoort Formation.

The only plant species which definitely occurs at both localities is *Archaeopteris notosaria*, which is currently represented by these two occurrences. Analysis of undescribed components of the Witpoort collections may yield further shared taxa, but at this early stage of taxonomic description of the floras, comparisons of many groups are tentative. In addition to Lycopsida and Progymnopsida, plant fossils putatively ascribed to Zosterophyllopsida, Iridopteridales, Cladoxylopsida and Gymnospermopsida are recognised at both localities (Table 8.1). With clear differences in lycopod diversity, it would be premature to attempt to evaluate the degree of overlap between the floras, prior to rigorous taxonomic study of all groups.

8.4 Protolepidodendralean lycopods

In the genus' first confirmed record from high palaeolatitude strata, two new *Colpodexylon* species are described in Chapter 4. They provide evidence of closely related, but clearly distinct species at the two relevant localities. The Waterloo Farm species ('lycopod B') is compared to short-tipped *Colpodexylon* species, with which it is similar in having proportionately short leaf tips. Its leaves are, however, more than double the length of any previously known short-tipped species. Aside from lengths of the leaf tips, it bears an overall similarity to the Coombs Hill derived 'lycopod A', in terms of leaf base morphology and arrangement, and the size of leaves prior to trifurcation. This latter species is comparable to the long-tipped *Colpodexylon* species, including the type species *C. deatsii* from the Lower Frasnian of New York State, to

which its leaves are most similar. It is distinguished from *C. deatsii* on the basis of slightly longer leaves, with differing proportions in length of leaf tips, as well as fewer leaves per pseudowhorl. Significantly the new species are between 10 and 20 million years younger than the last known appearance of *Colpodexylon.* This South African occurrence implies that the genus persisted at higher latitudes substantially longer than in the palaeotropics.

This occurrence extends the geographic distribution of *Colpodexylon,* as recent palaeomagnetic projections of the Late Devonian (Torsvik & Cocks, 2011, 2013; Domeier & Torsvik, 2014) place South Africa well beyond 60°S or even 70°S, possibly within the Antarctic circle (the latitude beyond which the sun does not rise on midwinters day) (Gess & Ahlberg, 2018). According to these projections, New York *Colpodexylon* were situated near the palaeotropics, whilst Venezuelan and Columbian occurrences would have been situated at mid-latitudes. Although possibly occurring on either side of the tropic parallel, these North and South American countries would have occupied a similar palaeogeographic region along the converging coastlines of Laurussia and Gondwana. Floral distributions support a hypothesis of proximity between these regions (Berry *et al.*, 2000). The western margin of Gondwana suggests a plausible land route for taxonomic exchange during the Middle–Late Devonian. A further record of the genus comes from China, although the taxonomy of Chinese *Colpodexylon* is controversial (see 4.3.2). The Chinese blocks extended into the northern hemisphere, occupying a disparate position offshore from the north-eastern margin of Gondwana.

It is currently uncertain whether *Colpodexylon* is represented among Middle Devonian protolepidodendralean lycopods from the Bokkeveld Group of South Africa (notably *Haplostigma*) (Plumstead, 1967; Penn-Clarke *et al.*, 2019). It is therefore impossible at this stage to decide whether like *Haskinsia, Colpodexylon* had an extensive latitudinal distribution during the Middle Devonian. Since the present occurrence is not contemporary with other occurrences, it is equally parsimonious to suggest that *Colpodexylon* migrated from low to high latitudes during the Late Devonian.

Another, probably herbaceous, species, ‘lycopod C’ is ascribed to a new genus and species within Archaeosigillariaceae. An important character of Archaeosigillariaceae is the presence of ‘leaf base sediment bodies’, often forming contiguous hexagonal

patterns on the stem (Berry and Edwards, 1997). ‘Leaf base sediment bodies’ were recognised on two of the Coombs Hill specimens but were absent on the assigned holotype, possibly as it was insufficiently fragmented at the time of burial to have been filled internally by sediment. Five specimens on three rock slabs were included in the new genus and species due to shared leaf morphology. The holotype (AM 7705) preserves a distal axis, at least twice bifurcated, and covered by persistent leaves. Near to the apex of the plant, sporangia are borne on the adaxial surfaces of sporophylls that are identical to the vegetative leaves. This specimen is unique because arrangement of fertile structures in Archaeosigillariaceae is not formerly known. Affinity to Protolepidodendrales has been suggested on the basis of a probable herbaceous habit and divided leaves (Berry & Fairon-Demaret, 2001; Gensel & Berry, 2001). ‘Lycopod C’ exhibits a key protolepidodendralean feature, of sporophylls isomorphic to vegetative leaves, supporting inclusion of Archaeosigillariaceae in Protolepidodendrales.

The record of *Archaeosigillaria* in South Africa has been challenged by Berry and Edwards’ (1997) literature review of the genus. In the present dissertation, examination of the holotype has identified characteristic leaf base sediment bodies. Only the truncated bases of leaves are preserved on the specimen, but an overall similarity in leaf base morphology and arrangement allows the possibility that *A. caespitosa* is related to ‘lycopod C’. Lacking leaf morphology, however, their conspecificity cannot be confirmed. *A. caespitosa* is retained for leafless archaeosigillariid axes of the described morphology.

Specimens of the two probable herbaceous lycopod species were among the more common plant remains recovered from the lagoonal sediments at Coombs Hill. *Colpodexylon sp. nov.* ‘A’ and ‘lycopod C’ belong to lycopod families considered as low-growing and probably limited to under a metre in height (Berry and Fairon-Demaret 2001). The two species represented do not co-occur in the same layer. ‘Lycopod C’ is the most abundant plant collected at the Plant Press layer, occurring with a relatively large lycopod trunk, putative zosterophyll as well as putative iridopteridalean axes with at least three orders of branching. This layer comprised some of the larger and more complete remains of plants, and their cross-cutting relationships suggest rapid burial in the lagoonal mud. *Colpodexylon* only occurs at Inner Outcrop, amongst putative iridopteridalean, zosterophyll and *Archaeopteris* remains,

approximately ten metres lower in the stratigraphy. Changes in recorded diversity are evidence for a dynamic depositional system at Coombs Hill, where composition of preserved floras is influenced by shifts in local environment and degrees of transport.

Protolepidodendralean herbs may have pioneered the shifting banks of waterbodies, and possibly comprised part of an understory layer in more complex ecosystems (Berry & Fairon-Demaret, 2001). With the disappearance of herbaceous lycopods in the tropics by the Famennian, more derived plants may have taken over their ecological role (Berry & Fairon-Demaret, 2001). *Rhacophyton* was an ecological generalist, and probably the most abundantly preserved plant taxon in the Famennian of Laurussia (Fairon-Demaret, 1986; Scheckler, 1986). An early seed plant from Hampshire Formation (Famennian, USA) is suggested to have been a pioneer of levees and banks bordering waterbodies (Rothwell, Scheckler, & Gillespie, 1989). Despite being replaced in tropical regions by the Famennian, protolepidodendralean lycopods managed to persist in colder, high-latitude environments exemplified by the Witpoort Formation, until at least the Upper Famennian, and possibly until, or beyond, the end of the Devonian Period. The presence of Devonian-like plant communities in the Tournasian (Lower Carboniferous) of Argentina, indicated the possibility that high-palaeolatitude regions acted as refugia for Devonian plants during the Late Devonian biotic crisis (Prestianni *et al.*, 2015), and data presented here supports their hypothesis.

8.5 Arborescent and/or heterosporous lycopods

The presence of arborescent lycopods at Coombs Hill is suggested by a large lycopod axis bearing well-spaced, fusiform leaf bases, like those observed on isoëtalean lycopod trunks (Chapter 6). Its 6 cm preserved width strongly supports its interpretation as the trunk of a rhizomorphic lycopod of large stature, comparable in size to the largest trunks of isoëtalean *Sublepidodendron* from the Famennian of China. The latter was, using ‘allometric’ principles, interpreted as reaching 4–6 m in height based on a 5 cm wide trunk base (Wang *et al.*, 2003).

‘Lycopod D’, occurring at Inner Outcrop, less than 10 m lower in the stratigraphy represents a possible distal branch of a rhizomorphic lycopod. Its terminal strobili, simple, elongate microphyllous leaves and anisomorphic, pedicellate sporophylls with an enlarged, spoon-like base for attachment of a single adaxial sporangium, are among the characters shared by most Devonian heterosporous lycopods (Cai & Chen, 1996;

Wang & Berry, 2003; Evreïnoff *et al.*, 2017; Orlova *et al.*, 2019). The strobilus of monosporangiate forms commonly includes sporophylls with additional modifications, including a ligule, heel, keel and/or alations (See Table 6.1). The group is considered the most derived amongst heterosporous lycopods (DiMichele & Bateman, 1996; Wang *et al.*, 2003). More basal amongst the supposed heterosporous clade, are species with bisporangiate strobili (DiMichele & Bateman, 1996). 'Lycopod D' is likely affiliated to these less derived forms. It is strikingly similar to Russian taxon *Kossoviella timanica* in appearance and structure. Elongate, narrow, bifurcating strobili, and needle-like leaves and sporophylls are shared characters (Orlova *et al*., 2019). The species are distinguished by fine crenulations along the proximal margins of sporophylls in the Russian taxon. Entire margins are shared by sporophylls of 'lycopod D' and *Kowieria* from Waterloo Farm, which are somewhat similar, but not identical, in size and proportion, and differ consistently in posture. On current evidence it cannot be unequivocally ascertained whether their similarities indicate a close relationship or result from convergence. Although *Kowieria* and *Kossoviella* both have bisporangiate terminal strobili, morphology of their respective megaspores precludes a close relationship between them. The lack of well-preserved spores of 'lycopod D' inhibits further exploration of its possible relationship to either genus.

As yet the stature of many Devonian heterosporous taxa is uncertain, but the earliest known examples of the group, including Middle Devonian genera *Longostachys* and *Chamaedendron* were diminutive trees reconstructed as between 0.5 and 1.5 m in height (Cai & Chen, 1996; Berry & Fairon-Demaret, 2001). By the Mid–Late Devonian, lycopods reached at least 5 m in height (Berry & Marshall, 2015). Remains of likely arborescent lycopods are widespread by the Famennian (Fairon-Demaret, 1986; Scheckler, 1986; Gensel & Berry, 2001; Meng *et al.*, 2015; Wang *et al.*, 2019). They are represented in the south of Gondwana by the cosmopolitan form *Leptophloeum rhombicum* and (probably) *Kowieria alveoformis* from the Witpoort Formation. Remains from Coombs Hill including the aforementioned partial lycopod tree trunk as well as a distal cone bearing axis indicates at least one additional species of tree lycopod present in the high-latitude Famennian.

8.6 *Archaeopteris notosaria*

New fossil material of *Archaeopteris notosaria* presented in Chapter 7, evidences another likely arborescent species at Coombs Hill, and adds characters to the known architecture of the species. Vegetative and fertile characters are explored in detail in the chapter and compared with other species of *Archaeopteris.*

A. notosaria was originally diagnosed as having uniquely compact fertile units on the basis of a single, incomplete fertile specimen (Anderson *et al*., 1995). Contrary to the species diagnosis, *A. notosaria* is characterized by fertile branches that are less compact than in other *Archaeopteris* species. The new material exhibits a great variability in density of sporophyll packing. Correlation between spacing of fertile leaves on a branch, splay of fertile leaves and branch length indicates that this variability may reflect ontogeny.

Distinguishing features of *A. notosaria* fertile organs include sporophylls that are larger, more divided, and bear a greater number of sporangia than previously recorded for *Archaeopteris* species. Vegetative leaves are also larger than those of the better known *Archaeopteris* species. Vegetative leaves of *A. notosaria* are deeply dissected, in a manner intermediate between the unwebbed leaf form of *A. fissilis* and nearly entire leafed species such as of *A. halliana*.

Aside from a similar architecture, characters in common with other *Archaeopteris* species include anisophylly (Fairon-Demaret & Leponce, 2001) and allomorphosis (Fairon-Demaret *et al.*, 2001), shared with *A. halliana* and *A. macilenta*. Forms with dissected leaves, including *A. fissilis, A. notosaria* and *A. macilenta*, appear to bear fertile material proximally on the lateral branch system, whilst those with more entire leaves are hypothesised to bear entirely fertile branch systems (see 7.6.3).

Similarities in leaf morphology between *A. notosaria* and Laurussian taxon *A. sphenophyllifolia* are suggested. The latter species is, however, too incompletely known for detailed comparisons. Their relationship should be explored if the New York material is re-studied. Fossils comparable to *A. notosaria* have also been reported from the Upper Devonian of China (Guo & Wang, 2009), Venezuela (Berry *et al.*, 2000) and Colombia (Moreno-Sánchez, 2004).

The connection between *Archaeopteris* and *Callixylon* has established that *Archaeopteris* species are responsible for the largest woody tree stumps of the Devonian Period (Beck, 1960; Taylor *et al*., 2009). In contrast to *Callixylon* wood, penultimate axes of *Archaeopteris* produce a single layer of secondary xylem, suggesting that they were short-lived, ephemeral structures (Scheckler, 1978). At Coombs Hill, the usual preservation of leafy lateral branch systems whole, with characteristic prophylls ('stipules' of Beck, 1962), emerging from the swollen base, supports the notion of these as the deciduous units of the tree (Beck, 1971; Meyer-Berthaud *et al.*, 1999; Algeo *et al.*, 2001). Overall architecture of lateral branch systems is closely comparable to those of the better-known species, *A. macilenta* and *A. halliana*. Very little data was attained from the literature on the full size attained by *Archaeopteris* lateral branch systems, but from illustrations of partial specimens (eg. Andrews *et al*., 1965; Carluccio *et al*., 1966; Fairon-Demaret *et al*., 2001), *A. notosaria* may have had larger lateral branch systems than other species. As no large woody stumps have been recovered at Coombs Hill, there is, as yet, no clear evidence of the size attained by *A. notosaria* at the site.

Archaeopteris is considered to have been a pioneer, being the first plant to produce laminar leaves (Osborne *et al.*, 2004) and was probably longer lived, and far more deeply rooted than any contemporary taxon (Algeo and Scheckler, 1998; Stein *et al*., 2020). With roots penetrating to more than a metre in depth, and spreading over a horizontal radius of up to 11 m (Stein *et al*., 2020), it was able to access subsurface moisture previously unavailable to plants, and in turn, contributing to soil formation (Algeo & Scheckler, 1998), whilst in all likelihood creating new shady niches for plants of lesser stature. Full sized *Archaeopteris* trees may have reached 20–30 m, or more, in height (Beck, 1962, 1981). The lack of documented woody axes has previously, however, cast doubt on the stature of *Archaeopteris* trees at high latitudes. In reference to the Waterloo Farm occurrence of *Archaeopteris*, a recent climate modelling study lamented the lack of published evidence for large woody axes, stating that as a result, 'the phenology of archaeopterid forests in these (high-palaeolatitude) zones is unknown' (Le Hir *et al*., 2011 p. 206). It is important that large woody axes such as that illustrated in Chapter 2, which is around 30 cm at the base, be described in detail in order to better understand these early trees.

We may speculate that at Coombs Hill, *Archaeopteris* trees inhabited lowland areas at a distance from the lagoonal banks, in preference of drier habitats, as has been reported from palaeotropical Laurussia (Scheckler, 1986). Only the shed leafy branches were brought into the lagoonal environment, perhaps during continental flooding events. Their complete state of preservation suggests a minimal of transport. *Archaeopteris* remains are far more common at Coombs Hill than those of the arborescent lycopod. However, it may have had a greater preservation potential, both as a result of its assumed deciduous habit, and the probability that many lateral branch systems were dispersed from a single plant.

8.7 Palaeoecology

Detailed studies on Upper Devonian floras from Laurussia provide insights into palaeoecology of the two groups studied in this dissertation. Interfingering terrestrial and marine sediments from the Hampshire Formation (Appalachian basin, USA), indicate distinct ecological roles for *Archaeopteris* and arborescent lycopods. Both are commonly preserved in coal forming lowland swamp deposits, but their taphonomy usually indicates contrasting degrees of transport (Scheckler, 1986). According to Scheckler's detailed palaeoecological study, in contrast to the cosmopolitan genus, *Rhacophyton*, neither *Archaeopteris*, nor arborescent lycopods, occupied swamp habitats. Arborescent lycopods are suggested to have occupied fringes of marshes and were not yet adapted to living within swamps as their later Carboniferous relatives were. Their taphonomy also implied a separate habitat to that of *Archaeopteris*, which was indicated to have preferred drier floodplain habitats (Scheckler, 1986). Their widespread association during the Famennian is however suggested as the arborescent lycopod *Cyclostigma kiltorkense* co-occurs with *Archaeopteris* in uppermost Devonian strata across much of Laurussia (Fairon-Demaret, 1986). Coombs Hill provides evidence for a similar association, with *Archaeopteris* as a dominant element of the flora, whilst exceedingly rare remains of an arborescent lycopod indicate its presence nearby. Due to its rarity, it is unlikely that the arborescent lycopod grew on the fringes of the lagoonal habitat, but like *Archaeopteris* may have preferred more well-drained areas away from the site of deposition.

The earliest *in situ* forests on Earth were not monospecific archaeopterid stands, as suggested for several Upper Devonian localities (Algeo and Scheckler, 1998). Large

cladoxylopsids, and lycopsids were also well-represented. Extensive lycopod forests are preserved *in situ* in the Famennian of China (Wang *et al*., 2019), and in a more limited geographic area in the lower Upper Devonian of Svalbard (Berry & Marshall, 2015). Localities in the upper Middle Devonian of New York State, comprising the earliest known forests, preserve *in situ* rooting systems attributed to all three of these groups co-inhabiting coastal lowland forests (Mintz, Driese, & White, 2010; Stein *et al.*, 2020).

The lack of *in situ* remains at Coombs Hill precludes understanding of their ecological preferences such as has been demonstrated in North American strata. Taxonomic analysis of putative Cladoxylopsida remains at Coombs Hill and Waterloo Farm, may yet determine whether the three groups comprising early tropical forests during the Devonian, are also represented amongst the earliest known high-latitude forests.

Though Witpoort Formation fossils provide the earliest record of trees at high latitude, it is uncertain whether or not earlier unrecorded trees may have preceded them. If trees were present in southern Gondwana prior to the Famennian, they may well not have left a record due to less favourable sedimentary facies for plant preservation lower in the Cape Supergroup. Palynological evidence, however, suggests hypothetical attenuation of latitudinal vegetation zones during the Famennian, allowing the spread of lowland forests into high palaeo-latitudes (Streel *et al.*, 2000), and indicating that forestation of Earth only became a global phenomenon by the Famennian.

CONCLUSIONS

Although our understanding of early forestation in the south of Gondwana is still in its early stages, Coombs Hill and Waterloo Farm provide evidence for a diversity of trees, which include *Archaeopteris notosaria* and arborescent lycopods at both localities. *A. notosaria* lateral branch systems are interpreted as the ephemeral distal appendages of an arborescent plant, but its size cannot be estimated on current evidence from Coombs Hill. Undescribed woody trunks from the Waterloo Farm locality may yet indicate the size attained by *A. notosaria* and other tree species. Absence of large woody axes at Coombs Hill suggests that the *A. notosaria* living environment was not adjacent to the site of deposition. The Coombs Hill occurrence considerably enhances understandings of the morphology of fertile and vegetative structures of this species, allowing for more detailed comparison with other *Archaeopteris* species. Further investigations at these localities will develop insights gained thus far, providing more data on the taxonomic composition, stature and ecology of the earliest known high-latitude forests.

As yet *Archaeopteris notosaria* is the only species recorded from both localities. Known lycopod species indicate no $\boldsymbol{\alpha}$ -taxonomic overlap between members at Coombs Hill and Waterloo Farm though both sites preserve both herbaceous and arborescent lycopods. Higher order taxonomy suggests a great similarity in floral diversity, but this is seemingly not reflected at the species level. Further comparison between these two macrofloral assemblages will require accurate taxonomic analysis of a wider range of groups.

Taxonomy of plant fossils allows insights into wider distributions of floras. *Colpodexylon* species described here extend the range of the genus by 10–20 million years. Similarly, members of the lycopod family Archaeosigillariaceae may have survived during the Late Devonian biotic crisis by persisting in a southern Gondwana. Fertile structures attached to the new archaeosigillariid strongly support its inclusion in Order Protolepidodendrales. Herbaceous protolepidodendralean lycopods may have been replaced in the tropics by a Late Devonian radiation of seed plants and other pioneering species, but their persistence at high latitudes indicates this region as a refugium for these primitive lycopod taxa.

Strata of the Witpoort Formation provide an abundance of material for taxonomic study, which is expected to continue to provide insights into Famennian plant

morphology and taxonomy, high latitude plant diversity, and both local and global stratigraphic ranges of plant lineages. Palaeoecological syntheses such as those undertaken on material from Laurussian deposits will derive from further rigorous investigation of both the stratigraphic and sedimentary setting of Witpoort Formation (and other Cape Supergroup) localities, and their floral make up.

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