

Devonian Tropical Plant Assemblages from Arctic Svalbard

Amy Louise Wyatt

A thesis submitted for the degree of
Doctor of Philosophy

Cardiff University
October, 2025

Summary

This thesis investigates the evolution, structure and ecology of Devonian plant assemblages from Arctic Svalbard, which during the Devonian lay in equatorial Laurussia. It integrates newly collected and historical material to reconstruct the development of early vascular floras and the rise of tree-dominated vegetation from the Silurian to the Frasnian.

Extensive fieldwork and the re-examination of historical collections have provided a basin-wide perspective on the diversity and distribution of early terrestrial plants. Detailed preparation using serial *dégagement*, camera lucida illustration, photogrammetry and microscopy enabled the documentation of both external and internal structures across a wide range of preservational modes. This approach has allowed the reconstruction of complete plants and the resolution of long-standing taxonomic and anatomical uncertainties.

Silurian and Early Devonian assemblages from the Siktefjellet, Red Bay and Wood Bay groups record low-lying vegetation dominated by small axial taxa such as *Zosterophyllum fertile* and *Psilophytites svalbardensis* sp. nov. By the Middle–Late Devonian, within the Mimerdalen Subgroup, the flora had diversified into complex forest ecosystems composed of arborescent plants with well-developed trunks, crowns and rooting systems. New analyses of *Svalbardia polymorpha* and *Actinopodium nathorstii* demonstrate that they represent different preservational states, clarifying the anatomy and morphology of *Archaeopteris* in Svalbard. Newly discovered material of *Protolepidodendropsis pulchra*, including a complete crown and root system, permits the first whole-plant reconstruction and defines its growth architecture and ecological role.

Together, these findings reveal that Mid-Late Devonian vegetation of Svalbard formed diverse, mixed forests in which different plants occupied distinct ecological niches across varied substrates. By combining new field evidence with anatomical and morphological data, this study refines the knowledge of equatorial Devonian floras and provides new insight into the emergence and environmental impact of the world's earliest forest ecosystems.

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Acknowledgements

I would like to acknowledge NERC for its sponsorship and financial support of this PhD project through the NERC GW4+ Doctoral Training Partnership. I am incredibly grateful for the opportunity to undertake this research and to spend the past few years pursuing my love of palaeobotany in the High Arctic.

First and foremost, I would like to thank my primary supervisor, Dr Christopher Berry, for his support, guidance and friendship throughout this project. I could not have asked for a more patient, understanding or talented palaeobotanist to guide me through it. I will always be grateful for everything you have taught me, for your endless palaeobotanical wisdom and most importantly, for always believing in me.

You have also been the best fieldwork companion I could have hoped for. There is no one else I would rather have beside me while scanning the horizon for polar bears, and my favourite fieldwork game will always be: is it a white rock, or a sitting polar bear?

I have learned far more from you than simply how to be a good palaeobotanist. You have taught me about hard work, patience and resilience, and how to stay grounded when things become difficult. I will always remember standing on top of Estheriahaugen, looking out towards the Nørdenskiöld Glacier and thinking how lucky I was to be there. None of it would have happened without your trust and encouragement. I know this is only the beginning of a lifelong friendship, and I look forward to the next bar and the next beer after a long day in the field.

I would also like to thank my secondary supervisors, Professor John Marshall, Professor Charles Wellman and Dr Paul Kenrick, for all of their expertise, advice and encouragement throughout this project.

John, thank you for your generosity, your companionship in the field and for sharing so much of your knowledge and experience with me. Without your support, both practical and financial, much of this project simply would not have been possible. Charlie and Paul, thank you for your patience, insight and wisdom over the years. I have learned a huge amount from all three of you and could not have asked for a better supervisory team.

I would also like to thank Lindsey Axe, our lab manager, for her technical expertise, patience and support throughout my PhD. Lindsey, thank you for always making sure we had what we needed, for answering what must have felt like an endless stream of questions and for doing it all with such good humour.

Special thanks must also go to the 2022 and 2023 fieldwork team, Roger Jones, Mike Newman and John Armstrong, for being the very best field companions I could have asked for and for somehow managing to convert me to Devonian fish.

Roger, who sadly passed away in 2024, is deeply missed. I will always treasure the long conversations we had about health, philosophy, academia and life while walking through the incredible landscape of Svalbard. You gave me hours of moral support at a time when I really needed it and always seemed to believe in me, even when I was finding things difficult. We regularly became so absorbed in conversation that we would eventually look around and realise

we had left everyone else about a mile behind us on the road to Pyramiden. I feel very lucky to have shared two field seasons with you and I will never forget them.

Mike, thank you for the endless entertainment and for sharing your incredible knowledge with me. The evenings in Pyramiden drinking beer and presenting our “fieldwork find of the day” remain some of my favourite memories from the trips. You can safely say that you succeeded in getting me excited about Devonian fish.

John, thank you for your kindness, understanding and the many conversations about music, life and politics. Sitting down with a beer and talking about Pink Floyd was a pretty perfect way to end a long day in the field. I like to think I managed to teach you almost as much about Devonian plants as you taught me about Devonian fish.

I would next like to thank my family, who have believed in me and supported me through all of this. To my mum, my biggest cheerleader, thank you for always backing my decisions and life choices, no matter how ridiculous or far-fetched they may have seemed at the time. To my nan, thank you for somehow always knowing when to leave me to get on with things and when I needed a bit of extra support. To my dad, thank you for always believing in me, particularly during the times when I struggled to believe in myself. To my sisters, Abi and Sophie, thank you for endlessly encouraging me and pushing me to do things I never thought I could. And to Sian, thank you for always showing up with love, care and reassurance. You have built me back up more times than you probably realise.

To my gramps, who passed away at the beginning of this project: although you are no longer here, I have carried you with me throughout it. I miss you enormously and I know you would be looking down on me now with a very proud smile.

I would also like to thank Lewys for his unwavering support, warmth and level-headedness during the final stages of this thesis. I am still not entirely sure how we made it through the chaos of those final three months, but somehow we did. Thank you for your patience, compassion and encouragement through all of it.

Last, but certainly not least, I would like to thank my best friends, Ryan, Emily and Oona, who have stood beside me through the whole thing. You have seen this journey from the beginning and have supported me through all of its highs and lows, both professionally and personally.

Ryan, I cannot really put into words how much your love, patience and guidance have meant to me. You have an incredible ability to give calm, rational advice at exactly the moment I need it, and your belief in me has carried me through some of the hardest parts of the past few years.

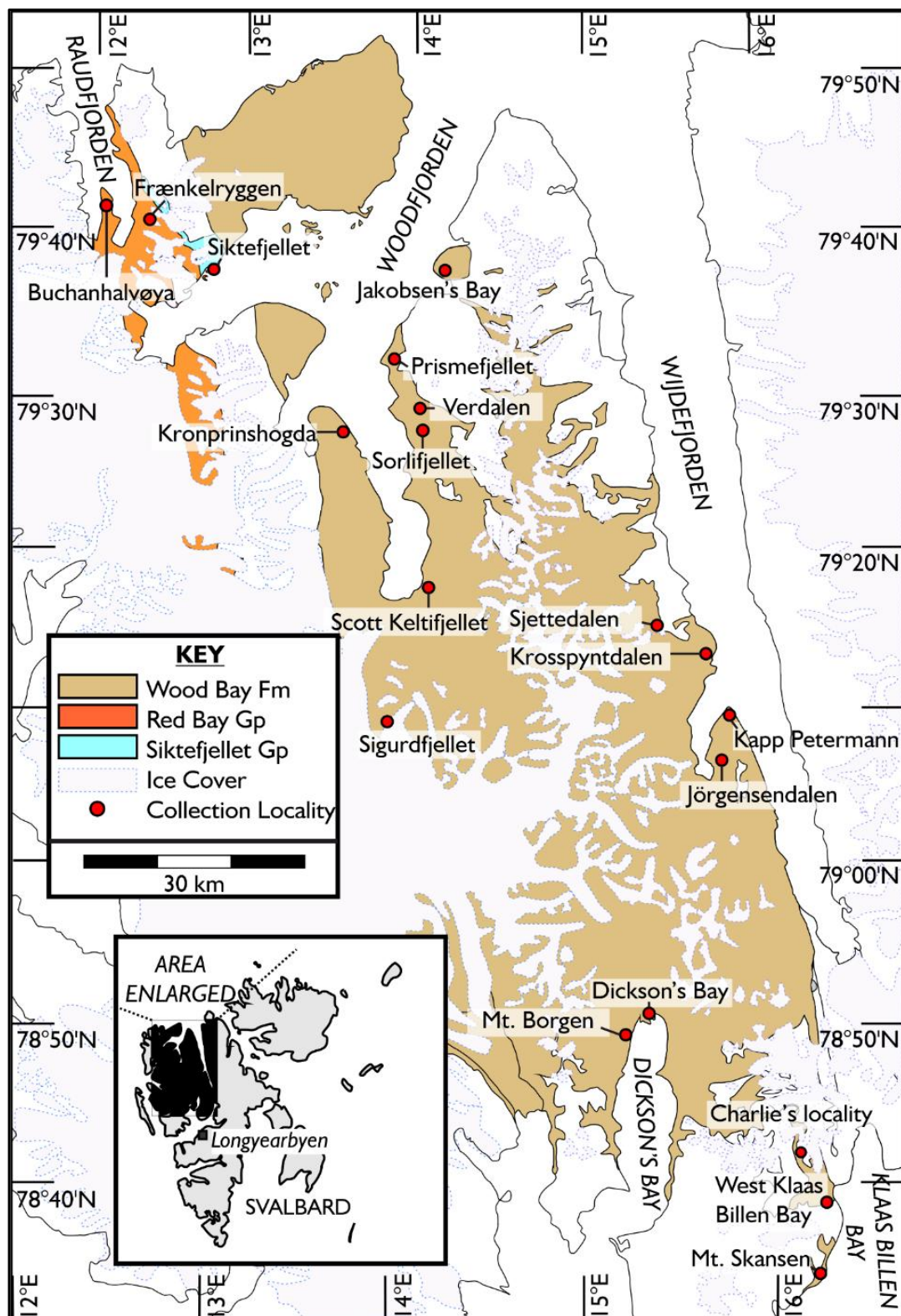
Emily, thank you for always being such a source of warmth and kindness, and for reminding me to eat, drink and generally look after myself when I have been far too stressed to remember to do any of those things. Your love and care have kept me going more times than you know.

Oona, thank you for being such a wise, funny and endlessly supportive friend and for sharing this journey almost to the day. There are very few people who understand quite as well what this whole experience has been like. Thank you for all of the encouragement, laughter and solidarity along the way. I am so grateful for you.

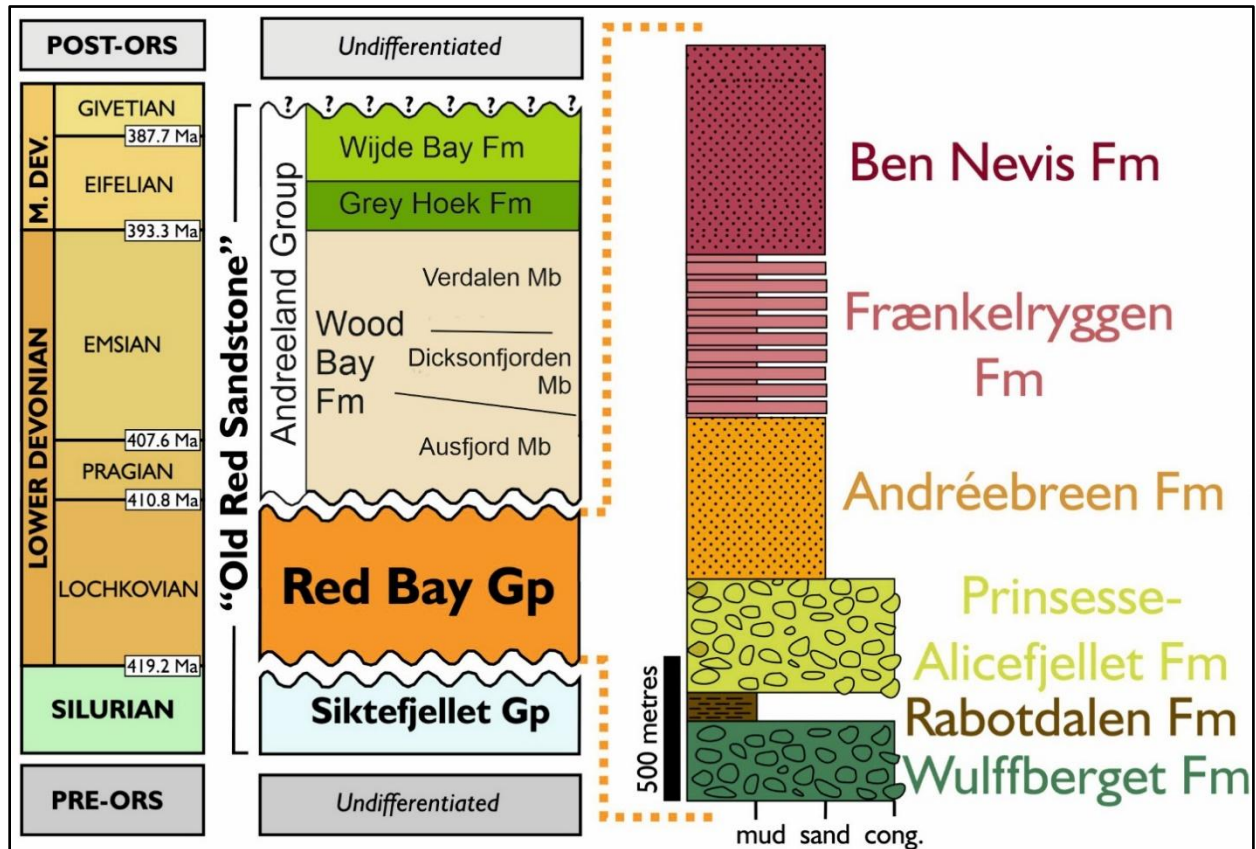
**Part I – Introduction,
Background and
Methodology**

Part II

**The Silurian and Lower
Devonian Diversity in
Spitsbergen**



Text Figure 1A. Geological map of North West Spitsbergen showing Silurian and Lower Devonian fossil plant localities. See Text Figure 1B for stratigraphy. Base map by Neil Davies.



Text Figure 1B. Stratigraphy of the Silurian and Devonian of North West Spitsbergen. Plant fossils are here described from the Siktefjellet Group (Silurian), the Andréebreen Formation (Buchananhalvoya), the Frænkelryggen Formation (Frænkelryggen), and numerous localities in the Ausfjorden and Dicksonfjorden Members of the Wood Bay Formation. For localities and geological map see Text Figure 2. Modified from Wellman *et al.*, 2022.

Introduction

The Silurian to Lower Devonian succession of northern Spitsbergen (Text Figure 1A-1B) preserves a rare stratigraphically continuous record of early land-plant assemblages deposited along the equatorial margin of Laurussia (Torsvik & Cocks, 2017; Davies *et al.*, 2021). This sequence captures the gradual colonisation of terrestrial and marginal aquatic environments through the Siktefjellet, Red Bay and Wood Bay formations, providing one of the few low-latitude records that document the diversification of early vascular plants across the Silurian–Devonian transition (Edwards & Wellman, 2001). Sedimentary facies within these formations record oxidised, intermittently wet floodplains and shallow lacustrine systems that supported patchy, low-diversity vegetation dominated by small, axial plants (Friend & Moody-Stuart, 1970; Davies *et al.*, 2021). The plant remains are typically fragmentary and frequently transported, representing initially opportunistic colonisers that occupied bar tops, levees and strandline muds. Nevertheless, the establishment of *Zosterophyllum* and other small axial plants led to the formation of deposits containing coprolites and trace fossils, indicating more stable habitats and increasingly complex terrestrial ecosystems.

Historical collections made during the English-Norwegian-Scottish and Høeg 1939 expeditions (Høeg, 1942), together with new material collected in 2018, provide an opportunity to reassess the Silurian - Lower Devonian flora of Svalbard.

Aims of the Chapter

This chapter synthesises the Silurian and Lower Devonian plant record of Spitsbergen, integrating historical and recent collections to reassess the composition, diversity and preservation of these assemblages. Its objectives are to (1) situate the Silurian and Lower Devonian plant assemblages of the Siktefjellet, Red Bay and Wood Bay formations within their documented stratigraphic and palaeoenvironmental framework. (2) Describe and re-examine key taxa to refine their morphological and systematic interpretation. (3) Assess the diversity and taxonomic composition of these assemblages across different localities. (4) Examine the flora as a possible exemplar of low-latitude Early Devonian vegetation during the rise of land plants.

2.1 Siktefjellet Group (Silurian)

Stratigraphy of the Area and History of Fieldwork

Siktefjellet Group outcrops in Liefdefjorden, inner Woodfjorden, North-West Spitsbergen (Text Figure 1A). The stratigraphy of the area was first defined by Gee & Moody-Stuart (1966). Unfortunately, it is the least well understood part of the Spitsbergen Old Red Sandstone and to date there has been continuous debate as to the age. Lack of bio-stratigraphical and palynological markers make it difficult to pinpoint an exact age, however a Late Silurian – very Early Devonian age is generally agreed upon (Gee & Moody-Stuart, 1966; Murašov & Mokin 1979; Friend, *et al.* 1997; Friend & Williams, 2000; Davies, *et al.* 2021). It forms the base of the Old Red Sandstone (ORS) basin (Leifde Bay Supergroup) in North Spitsbergen, lying unconformably beneath the Lochkovian Red Bay Group (Friend *et al.*, 1997, Text Figure 1B).

The Siktefjellet Group is composed of three formations: the Robotpasset Formation which forms the base of the group, the Lilljeborgfjellet Formation and the uppermost unit is the Albertbreen Formation (previously called the Siktefjellet Sandstone by Gee & Moody-Stuart, 1966). The Robotpasset Formation is 25m thick and composed of a coarse, angular breccia deposit; the Lilljeborgfjellet Formation is 400m conglomerate; finally the Albertbreen Formation is 1400m thick and is a mixture of fine and coarse grained, cross-bedded sandstone (Friend *et al.*, 1997).

The main expeditions to Siktefjellet have been largely to determine the general stratigraphy of the unit (Gee & Moody, 1966; Gee, 1972). Later expeditions by Friend *et al.* (1997) were to further elucidate and revise the stratigraphy. A handful of expeditions to collect megafossil and microfossil assemblages have been largely unsuccessful.

Murašov and Mokin (1979) reported the collection of *Taeniocrada decheniana* Kr. et Weyl., *Prototaxites psygmophylloides* Kr. et Weyl and *Hostinella* sp. from three localities at Siktefjellet (north-east, north-west and south). However, they did not provide any plates or information on where these collections are held, making confirmation or

interpretation difficult. They noted that, in the opinion of N. M. Petrosjan, the plant remains indicate a Lower Devonian age and compared the assemblages to those reported at Frænkelryggen by Høeg (1942). This comparison is challenging to verify. To date, there has been no other mention of plant macrofossils collected from this unit (Friend et al., 1997).

Palynological assemblages for this unit are very poorly preserved, described as much more thermally mature than the other regions of the ORS in Spitsbergen (Davies *et al.*, 2021). The overwhelming composition of the assemblages is of phytodebris (plant cuticles, tubes, tracheids, etc). Some poorly preserved spores are present; however, most are largely indeterminate with the exception of some rare cryptospore tetrads. The lack of megafossil and microfossil assemblages from this area makes further elucidation of the age very difficult.

Siktefjellet Locality

The material reported here consists of five newly collected slabs from two closely situated sub-localities within the same section, located below a conglomerate layer adjacent to a stream and a prominent waterfall. SKT-1 was at an elevation of 33 m, and SKT-2 at 90 m. Three slabs were collected from SKT-1 and two from SKT-2. The stratigraphic layers where the plant remains were found comprised light grey sandstone with abundant mica fragments.

All remains were preserved as coalified compressions, most of which were of very poor quality and largely indeterminate. The best-preserved specimen was a part and counterpart (SK1-1, Plate 1A, 1C) of probable *Prototaxites*. Only three specimens contained remains worth further discussion, while the other slabs held very small, indeterminate fragments of carbon.

Description of Remains

SK1-1 (*Prototaxites*)

Black carbonaceous remains 80mm long and 29mm wide with an undulating pattern present on both part and counterpart (Plate 1A, 1C). The details of the undulations are

more visible using binocular microscopy than photography, where the three-dimensional texture is lost. These remains probably belong to *Prototaxites*.

SK-1-2 (*Prototaxites*)

A single, unbranched, incomplete axis 13mm in length and 2.9mm in width (Plate 1B). There are two distinctive breaks in the axis, 6mm apart (Plate 1B, *white arrows*) which are probably shrinkage cracks. On the same slab there is another mass of carbonaceous matter (Plate 1B, *black arrow*), but the preservation is too poor for an accurate diagnosis. These remains probably belong to *Prototaxites*.

SK-2-1 (*Incertae sedis*)

Part (Plate 1D) and counterpart (Plate 1E) with a ribbon of poorly preserved carbonaceous matter, probably of plant origin. On the part, the remains are 6 mm in length and up to 1 mm in width in the widest portion. The remains in the counterpart are slightly less well preserved and smaller. These remains are too poorly preserved for taxonomic discernment.

Discussion

Little material was collected from this locality, and the preservation was very poor. However, these fossils represent the first plant material to be illustrated from the Siktefjellet Group. They suggest that with more focused time and effort, identifiable plant material could potentially be recovered. Further expeditions and studies at this site are needed to recover better-preserved specimens that can be suitably described.

It is likely that the remains described in this study belong to *Prototaxites*. This conclusion is not based on direct comparisons with *Prototaxites* but rather on the absence of any other taxon of comparable size that fits within the age and stratigraphic context of this unit.

2.2 Red Bay Group (Lochkovian)

Stratigraphy of the Area and History of Fieldwork

Red Bay is located within Raudfjorden, North-Western Spitsbergen (Text Figure 1A). First described in 1914 (Holtedahl, 1914), the strata lie unconformably above the ?Late Silurian Siktefjellet Group and beneath the Lower–Middle Devonian Andréeland Group of the ORS in North-West Spitsbergen (Text Figure 1B). The strata are Lochkovian in age and are well dated by a diverse vertebrate assemblage that is almost continuous through the sequence (Blieck & Heintz, 1979; Blieck & Heintz, 1983; Blom & Goujet, 2002). Other palaeontological evidence used to constrain the age of the strata includes fragmentary plant macrofossils described by Høeg (1942) and palynological assemblages (Wellman et al., 2022).

The Red Bay Group comprises six distinctive formations (Text Figure 1B). From the base of the group: the conglomerate Wulffberget Formation, mudstone Rabotdalen Formation, conglomerate Prinsesse- Alicefjellet Formation, sandstone Andréebreen Formation, the cross bedded sandstone and mudstone of the Fränkelryggen Formation and finally, the sandstone Ben Nevis Formation at the top (Wellman et al., 2022). The Ben Nevis Formation is the thickest of the six units (750m) and the Rabotdalen Formation is the thinnest.

The majority of expeditions to the Red Bay Group have been either to determine stratigraphy of the area (Holtedahl, 1914; Manby & Lybris, 1992; Thielemann, 1996; Thielemann & Thiedig, 1997; Dallmann, 1999; Piepjohn & Dallmann, 2014) or to collect vertebrates (Blieck & Heintz, 1979; Blieck & Heintz, 1983; Blieck, 1987; Ilyes, 1995; Blom, 2002). There have been a small number of expeditions to collect plant fossils and palynological samples that have yielded varying results (Piepjohn & Dallmann, 2014; Wellman, et al. 2022).

The plant fossil remains collected from the Fränkelryggen locality, Fränkelryggen Formation have yielded a small number of relatively poorly preserved fossils (Høeg, 1942; Schweitzer, 1999). These include *Pachytheca* sp, *Prototaxites* sp, *Hostinella* sp,

Gosslingia sp and the indeterminate remains of a single, unbranched axis Høeg (1942) called *Zosterophyllum*.

Collection Localities Used in this Study

New plant material from the Red Bay Group was collected from two locations (Text Figure 1A). The first, Frænkelryggen, in the Frænkelryggen Formation, initially identified by Strand and Størmer during Vogt's 1928 expedition, was described by Høeg (1942). Although locality details were imprecise, the material likely originates from the same site and stratigraphic levels (Shale I and Shale II) due to the presence of the stream mentioned by Høeg. Wellman's 2018 expedition collected material from three sub-localities at Frænkelryggen (Table 1). The second locality, Buchananhalvøya (Table 1), Andréebreen Formation, was found by Davies and others in 2018, with its stratigraphic

Locality Name	Sub localities	Coordinates	Collection Notes
Frænkelryggen	Frænkelryggen A	UTM Zone 33X, 0447278 E, 8848261 N	Just inside gulley entrance, 40 cm grey shale ... up top, surrounded by purple cross bedded sandstone. Lots of plant fragments. Must be one of the localities mentioned by Høeg.
	Frænkelryggen B	UTM Zone 33X, 0447288 E, 8848260 N	About 10m upstream & about 1m stratigraphically below. Another grey shale sandstone with similar plant fragments and a couple of fish plates. Probably the younger horizon mention by Høeg.
	Frænkelryggen C	UTM Zone 33X, 0447393 E, 8848241 N	Green sandstone collected from the N side of the gulley with scrappy plant fossils in it. Probably approximate to the stratigraphically lower plant horizon mentioned by Høeg.
Buchananhalvøya		UTM Zone 33X, 0444137 E, 8846806 N	Grey sandstones and shales, big mass of plant fragments found in the layer directly below sandstone.

Table 1. List of localities and sub localities where fossils were collected within the Red Bay Group. Included is the locality name, sub localities, coordinates and field notes from the collector (Berry).

context and associated illustrations detailed in Davies et al. (2021). It is the oldest locality to yield clearly identifiable plant remains in Svalbard.

Previously Reported Taxa

Five different taxa were described from Frænkelryggen (Høeg, 1942), collected on Vogt's 1928 expedition (Table 2). These taxa were redescribed by Schweitzer (Schweitzer, 1999) and were discriminated into four taxa and one indeterminate taxa.

Taxa described by Høeg, 1942	Taxa redescribed by Schweitzer, 1999
<i>Hostimella</i>	<i>Hostinella</i> sp.
<i>Zosterophyllum</i> sp.	Indeterminate axes
<i>Pachytheca fasciculata</i>	<i>Pachytheca</i> sp.
<i>Prototaxites</i> sp.	<i>Prototaxites</i> sp.
<i>Taeniocrada</i> (?) <i>spitsbergensis</i>	cf. <i>Gosslingia</i>
N/A	N/A

Table 2. Taxa collected from Frænkelryggen. Column 1 shows taxa described by Høeg (1942), column 2 the taxa analysed, and in some cases put into different taxonomic groupings, by Schweitzer (1999).

Previously Figured Specimens Tentatively Referred to ?*Gosslingia* sp.

Høeg 1942, Pl. 1, Fig 1-13. Pl. III

This text (Text Figure 2A-H)

This material comprises seven figured specimens of smooth axis fragments preserved across several slabs. Some slabs also contain globular to pear-shaped bodies associated with the axis fragments (Text Figure 2B–D). Høeg (1942) originally assigned these remains to the morphotaxon *Taeniocrada* as *T. spitsbergensis*. Schweitzer (1999) later suggested an affinity with *Gosslingia* on the basis of the kidney-shaped bodies and general branching morphology, but the preservation is too poor for a confident determination. The material is therefore best regarded as tentatively referable to ?*Gosslingia* sp.

The axis fragments are short, cylindrical, bare and dichotomously branched, with smooth surfaces (Text Figure 2B–E), and some specimens appear to preserve a very narrow central vascular strand. The largest axis, on the holotype (Text Figure 2A), measures 60 mm in length and 2 mm in width and bifurcates three times. Høeg described one axis as bearing a 0.7 mm thorn-like projection emerging at a near-right angle from the axis, although Schweitzer (1999) later suggested that this was a fragmented piece from another axis. I agree with this interpretation, given the poor preservation and the absence of any unequivocal organic connection.

Associated with the axis fragments are numerous spherical bodies, which Høeg described as “representing some kind of reproductive organ” (Text Figure 2B–D). These bodies are ovoid to kidney-shaped and range from 3–4.5 mm in length and 3–5 mm in diameter. Schweitzer interpreted these as probable sporangia of zosterophyllalean affinity on the basis of their shape, but noted that their poor preservation and lack of diagnostic attachment to an axis prevent secure determination.

Schweitzer argued that the remains lacked key characteristics of *Taeniocrada*, including terminally borne sporangia and clear distal dehiscence. He also considered the axes too slender for confident retention in that genus, although the very narrow vascular strand may have contributed to the original placement of the sterile axes there. Comparison with *Gosslingia breconensis* (Edwards, 1970) suggested similarities in the kidney-shaped sporangia and general branching pattern. However, a consistent feature of *Gosslingia* is the presence of sub-axillary tubercles, and these cannot be demonstrated clearly in the Spitsbergen material. I therefore agree with Schweitzer that the fossils are best removed from *Taeniocrada*, but I consider the material too fragmentary and poorly preserved for confident generic assignment. Although the sporangia resemble those of *Gosslingia breconensis*, the lack of unequivocal attachment between sporangia and axes, together with the absence of clearly demonstrable diagnostic vegetative characters, means that the remains are best treated as ?*Gosslingia* sp.

Prototaxites sp

Høeg 1942, Pl. 4., Pl. LXII, Fig 1.

This text: (Text Figure 2I-K)

The best preserved material comprises two specimens (PA 226, PA218) “which preserve *Prototaxites* as black, highly carbonised compression fossils. The most well preserved (PA226) contains flat, compressed coalified material that in some places appears to have long elements or tubular cells (Text Figure 2I-K). These tubular cells are parallel and appear as longitudinal striations with the naked eye, only visible in the best-preserved specimens.

Following treatment with hydrofluoric acid and embedding in paraffin, Høeg (1942) noted that after cutting the section transversely, characteristic tubes are visible which make up the interior of *Prototaxites*. These tubes are 10-15 µm diameter and circular-oval in circumference, depending on the level of deformation during the fossilization process. The tubes make up the main proportion of the tissue, sitting very close to one another but rarely coming into contact with the adjacent tube. The walls of the tubes are 1-3 µm in thickness. There is no regularity in the arrangement of the tubes and each tube remains undivided throughout the tissue.

Pachythea sp.

Høeg, 1942, Pl. I, Fig 15-16.

From Horizon II at Frænkelryggen, Høeg attributed a single specimen to *Pachythea* cf. *fasciculata* (Text Figure 2L–M). He also mentioned other dubious and indeterminate material that might belong to the same genus, but this specimen is the best-preserved example. The specimen is ovate in section, 3 mm in length and 2.5 mm in width. The medulla is compressed and forms a concave indentation on the surface of the specimen. The cortex consists of radiating channels extending outward from the medulla, each approximately 30 µm in diameter.

I agree with Schweitzer's (1999) reassignment of this material to *Pachythea* sp. rather than *P. fasciculata*. Although the specimen is poorly preserved, the preserved cortical structure does not show a fasciculate arrangement. In *P. fasciculata*, the channels are arranged in distinct fascicles of 1–5 filaments, whereas no such organisation can be demonstrated in the Frænkelryggen specimen. For this reason, the material is better treated as *Pachythea* sp. rather than assigned to a specific species.

Hostimella sp. (*Hostinella* sp – Schweitzer, 1999).

Høeg 1942, Text Figure 2.

This text (Text Figure 2N-P)

This single specimen (Text Figure 2N-P) is a bare, slender axis, 75mm in length with at least three separate dichotomies, all of which have snapped off just after the point of bifurcation. On at least two of the bifurcations, there is a single small, raised axillary tubercle. On one of the ramifications (Text Figure 2O), there is a small depression in the primary axis, probably where a lateral branch protrudes into the matrix.

The genus name *Hostinella* was originally introduced by Barrande in 1882, with *Hostin* meaning 'the village'. The orthographic variant *Hostimella* later emerging due to transcription errors, but *Hostinella* is now the accepted and valid name in palaeobotanical classification.

Zosterophyllum sp. (indeterminate axes – Schweitzer)

Høeg 1942, Pl. II Fig 1-10, cf. 11-13.

Several specimens of bare dichotomous axes fragments were collected from Horizon 1 at Frænkelryggen. Høeg attributed these remains to the genus *Zosterophyllum*, however Schweitzer disputed this and later described them as 'indeterminate axes fragments' owing to the fact that these branching patterns have been reported in other genera. I agree with Schweitzer's view owing to the poor preservation and fragmentary nature of the remains.

The axes are small, dichotomous, incomplete and bare. The largest axis is 1.2 mm wide and 55 mm long. At least two fragments have typical H or K type branching as found in

Zosterophyllum (Text Figure 1Q-S) and in the majority of specimens a central vascular strand is present. The details of the epidermis were extracted by cellulose peel, and it is composed of distinctive, longitudinal cells.

Text Figure 2. Taxa from Frænkelryggen described by Høeg (1942), collected during Vogt's 1925 and 1928 expeditions.

A. Part and counterpart of type specimen of *Taeniocrada spitsbergensis*, picture taken from Høeg (1942), Plate III, Fig 1-2. Scale bar 10 mm.

B. *T. spitsbergensis* with laterally attached body. Taken from Høeg (1942), Plate II, Fig 6. Scale bar 10 mm.

C. *T. spitsbergensis*. Counterpart of B. Taken from Høeg (1942), Plate III, Fig 7. Scale bar 10 mm.

D. *T. spitsbergensis* axis with laterally attached body. Taken from Høeg (1942), Plate III, Fig 5. Scale bar 10 mm.

E. Branched axes of *T. spitsbergensis*. Taken from Høeg (1942), Plate I, Fig 3. Scale bar 5 mm.

F. Bifurcating axis of *T. spitsbergensis*. Taken from Høeg (1942), Plate I, Fig 9. Scale bar 10 mm.

G. Bifurcating axis of *T. spitsbergensis*. Taken from Høeg (1942), Plate I, Fig 7. Scale bar 10 mm.

H. Bifurcating axis of *T. spitsbergensis*. Taken from Høeg (1942), Plate I, Fig 5. Scale bar 5 mm.

I. Reflected light section of *Prototaxites* sp, embedded in paraffin. Taken from Høeg (1942), Plate IV, Fig 1. Scale bar 5 mm.

J. *Prototaxites* sp. Taken from Høeg (1942), Plate VI, Fig 4. Scale bar 5 mm.

K. *Prototaxites* sp. Taken from Høeg (1942), Plate VI, Fig 5. Scale bar 5 mm.

L. *Pachythea fasciculata*. Taken from Høeg (1942), Plate I, Fig, 15. Scale bar 100 µm.

M. *P. fasciculata*. Taken from Høeg (1942), Plate I, Fig 16. Scale bar 100 µm.

N. *Hostinella* sp. Axillary tubercle present at the point of bifurcation. Taken from Høeg (1942), Text Figure 2B. Scale bar 100 µm.

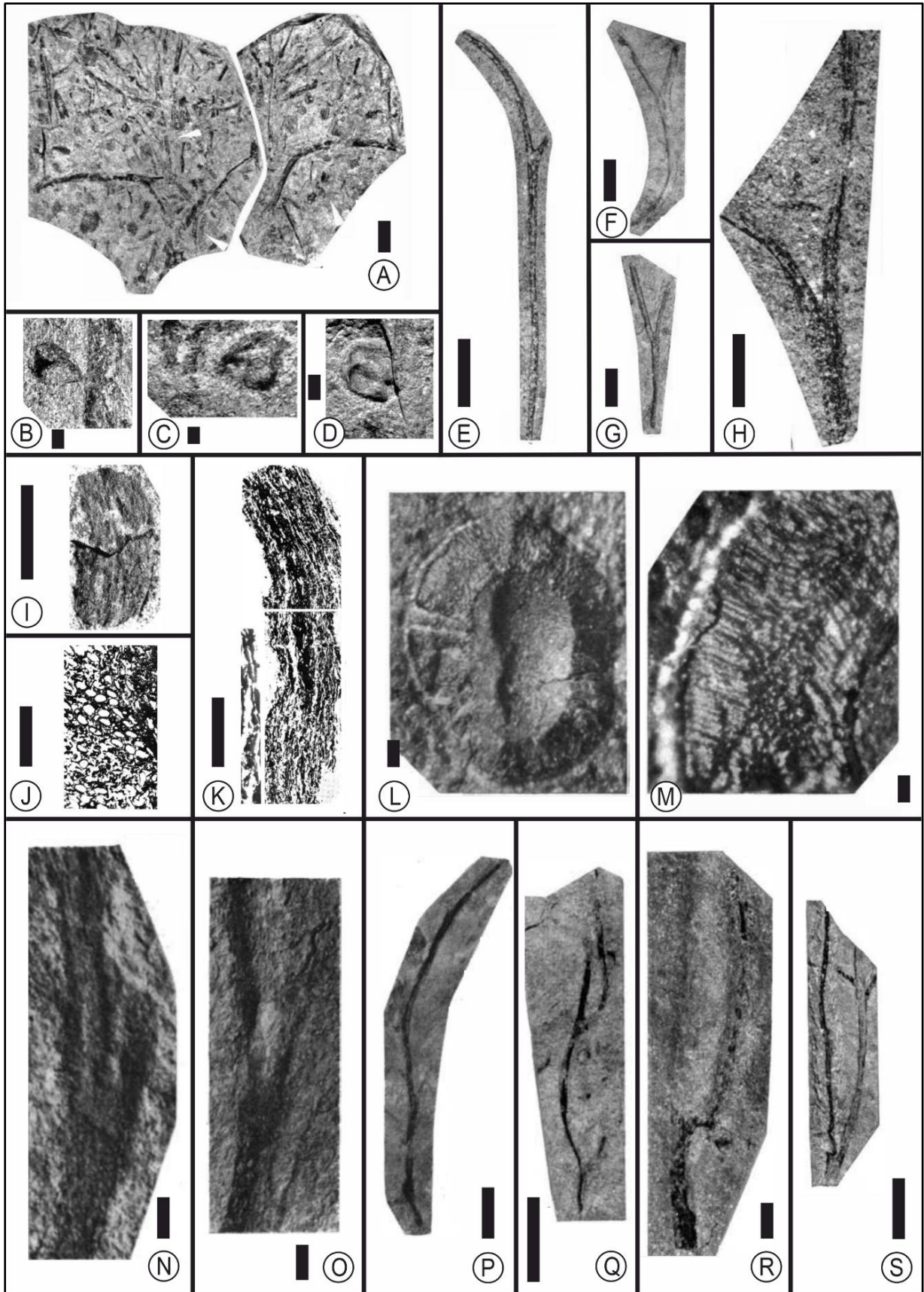
O. *Hostinella* sp. Axillary tubercle present. Taken from Høeg (1942), Text Figure 2C. Scale bar 100 µm.

P. Fragment of *Hostinella* sp axis. Taken from Høeg (1942), Text Figure 2A. Scale bar 10 mm.

Q. *Zosterophyllum* sp axis fragments. Taken from Høeg (1942), Plate II, Fig 1. Scale bar 10 mm.

R. *Zosterophyllum* sp axis fragment showing close up of bifurcation in Q. Scale bar 100 µm.

S. *Zosterophyllum* axis fragment showing at least two separate bifurcations. Taken from Høeg (1942), Plate II, Fig 9. Scale bar 10 mm.



2.2.1 *Zosterophyllum fertile* (Leclercq, 1942)

Description of Material Collected

The material comprises approximately 56 slabs collected from the Lochkovian-aged Buchananhalvøya locality, Andréebreen Formation, Red Bay Group (Text Figure 1). A detailed account of the locality and its sedimentology is provided in Davies et al. (2021, fig. 4, p. 7). The site coordinates are UTM Zone 33X, 0444137 E, 8846806 N. All specimens were catalogued under the prefix *18-Spits-25-*, where the final digit represents the specimen number within the collection. For brevity, specimens are referred to by number only (e.g. specimen 12 corresponds to *18-Spits-25-12*). Subsequent letters indicate different slabs belonging to the same specimen (e.g. A, B, C). In specimen 54 (*18-Spits-25-54*), two sporangial spikes occur on the same slab and are designated as left (L) and right (R).

The fossils are preserved in medium to dark grey shale containing abundant mica. The largest plant-bearing slab measures 35 × 26 cm. The length of the plant fragments ranges from 4.8 to 123 mm. Preservation varies, with fossils appearing as coalified compressions or impressions. Most specimens are moderately preserved. Five slabs contain fertile spikes; two of these preserve two spikes each, giving a total of seven fertile axes. The following description details the axes and fertile structures (sporangia and stalks) and aims to confirm and expand upon the original description of the species.

Axes

The axes are bare, fragmentary and incomplete, often terminating abruptly at the edge of the slab. The axes are often clumped together, lying parallel and overlapping one another (Text Figure 3). The majority of axes are straight and unbranched (Text Figure 3), only a small number of axes exhibiting branching.

In some specimens with a degree of mineral leaching, the yellow-orange residue sometimes makes discrimination of the axis from the matrix difficult (Plate 2A). Where the mineral leaching was severe, it was almost impossible to determine the outline of individual axes, especially where clumped together. The largest slab with the most

abundant axis fragments had >20 distinct, incomplete axis fragments present on the surface.

Unbranched axes range from 5-123 mm, average length 33 mm (N=70). The width of axes ranges 0.6-4.1 mm, average width 1.7 mm (N=96). Branching axes vary between 31-91 mm, average length 64.1 (N=12). Five specimens have a central strand of vascular tissue preserved either as a coalified black line (Plate 2H), or as an impression at the centre of the axis (Plate 2I). The width of the strand is between 144-180 μm , average width 159 μm .

On specimen 12, small discrete structures on the surface of the axis bulge out of the axis on the part (Plate 2F), and on the counterpart they form indentations (Plate 2G). These are present in a range of shapes but are mostly circular to ovoid. They range from 154-220 μm in diameter, 220 μm (N= 40) on average. These are likely small Microconchida (Caruso & Tomescu, 2012).

Branching patterns

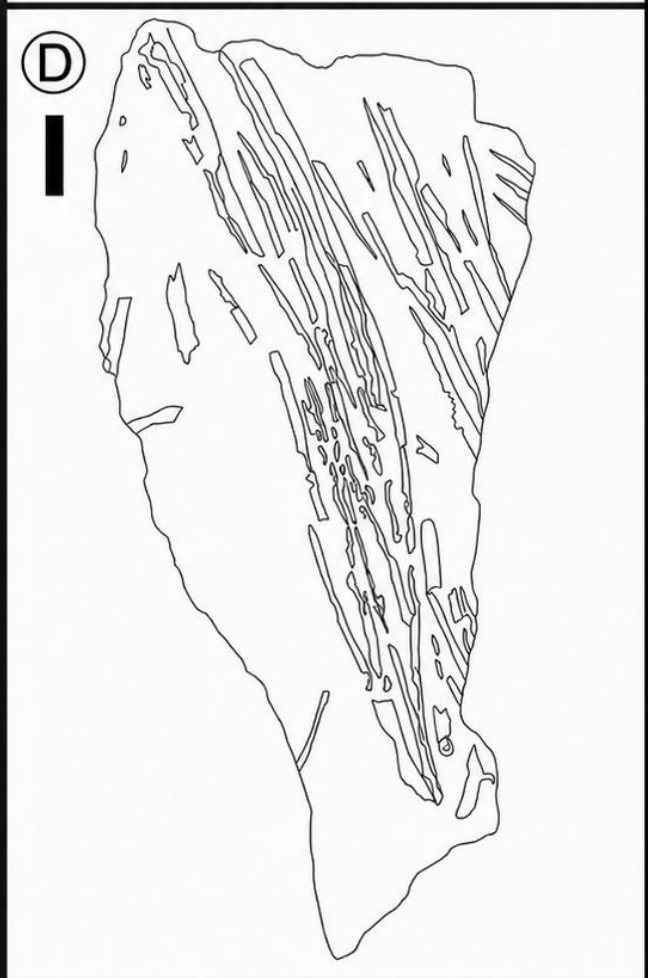
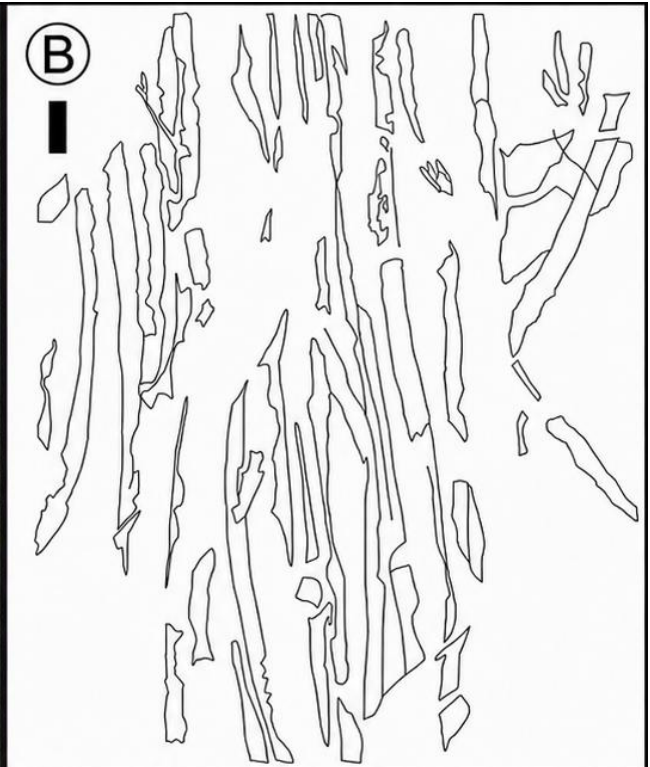
Branching is both isotomous and anisotomous. Seven specimens show isotomous bifurcations where daughter axes are approximately equal in width (1.0–1.2 mm) and diverge at angles of 55–65°. Because the material is fragmentary, axes are rarely preserved beyond the branching point. In specimen 5 (Plate 2C) the central angle between the two axes is 62° and both branches are ~ 1.1 mm wide. A few specimens show two or more successive isotomous bifurcations, one specimen (Plate 2D) displays three along a 47 mm segment, with 27 mm between the proximal and distal branch points.

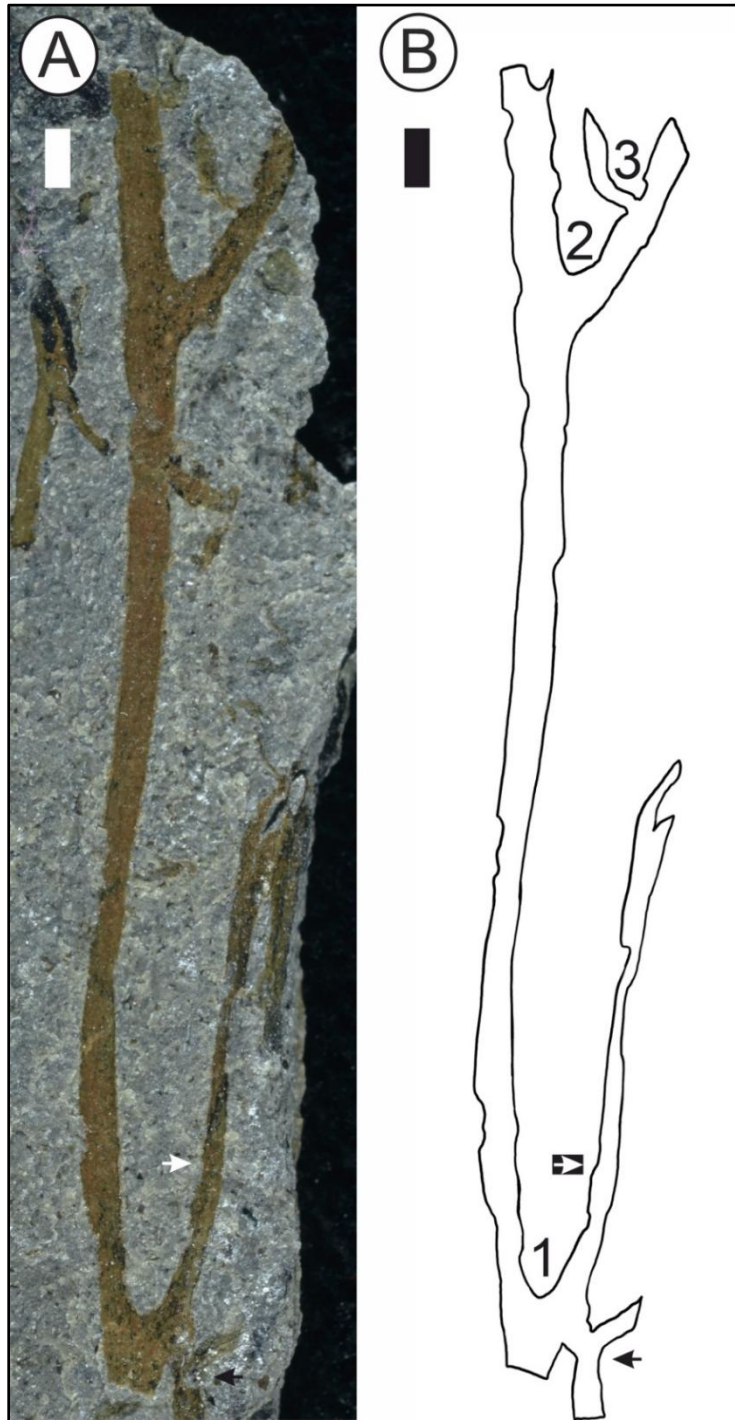
Another specimen shows more complex branching, combining K- and H-type arrangements with lateral offshoots and anisotomous dichotomies (Text Figure 4). Basally, the main axis dichotomises anisotomously (Text Figure 4; 1). The primary axis is 1.8 mm wide before bifurcation, widening to 2.8 mm immediately before division, and produces a narrower upright branch (0.9 mm) and a broader obliquely descending branch that forms a K-shaped configuration of lateral axes (Text Figure 4A–B; white arrow). The descending branch (1.0 mm) bifurcates again into a short obliquely

ascending axis (0.9 mm) and a downward-directed axis, forming an H-shaped arrangement (Text Figure 4A–B; black arrow). The unequal division and size disparity between the daughter axes indicate a proximally anisotomous dichotomy.

Distally, the same axis (1.8 mm wide) gives rise to a lateral branch (1.1 mm) at approximately 45°, curving gently towards the upright axis (Text Figure 4A; 2). A smaller branch (0.8 mm) arises 3.2 mm further distally from the inner margin of this lateral axis and also curves towards the upright (Text Figure 4A; 3). These features suggest that the proximal part of the specimen shows anisotomous branching associated with K- and H-type configurations, whereas the distal part preserves simpler branching. This is somewhat unusual, as K- and H-type branching in *Zosterophyllum* is more typically concentrated in clustered basal regions. The specimen may therefore represent part of a basal branching system, although its exact position within the plant remains uncertain owing to the fragmentary nature of the material.

Text Figure 3. Parallel, overlapping *Zosterophyllum* axes. A. Macrophotograph of oxidised overlapping axes found in 18-Spits-25-56. B. Line drawing of same (enhanced with ProCreate for iPad). Macrophotograph of oxidised overlapping axes fragments in 18-Spits-25-39. D. Line drawing of the same (enhanced with ProCreate for iPad). Scale bar in all is 10mm. Buchananhalvøya, Lochkovian.





Text Figure 4. Anisotomous K/H branching. Buchananhalvøya (Lochkovian). A. Axis with isotomous bifurcations and K type branching and possible H type branching. White arrow represents the distal axis which extends from the K type branch, black arrow depicts the basal axis extending from the same. B. Line drawing of axis. Specimen 18-Spits-25-12. Scale bar 2 mm.

Reproductive Structures

Terminology and measurements of individual sporangia

For zosterophylls, the term 'fertile spike' refers to closely inserted sporangia and supporting axis as one unit (Text Figure 5A). For individual sporangia (Text Figure 5B, C), the sporangial stalk is the short axis which attaches the sporangium to the axis (Text Figure 5C; *sporangial stalk*). The abaxial valve refers to the valve orientated away from the axis (Text Figure 5C; *abaxial valve*) and the adaxial valve refers to the valve orientated towards the axis (Text Figure 5C; *adaxial valve*). The dehiscence margin lies between the two valves and is often recognised as a thin strip of carbon at the margin of the compressed sporangium.

When describing individual sporangia on a single spike, each sporangia was given the prefix of S, followed by the row number from the apex of the spike and either A or B, where A represents sporangia on the left hand side of the spike and B represents sporangia on the right hand side of the spike, on the part (Text Figure 6). For example, S3B represents a single sporangium in the third row from the top, on the right hand side of the part. There is one specimen (56B) where the sporangia are not very visible, but the sporangial stalks are prominent. In this case, 'St' and instead of 'S' has been used marking the sporangial stalks rather than sporangium.

Description of Fertile Material

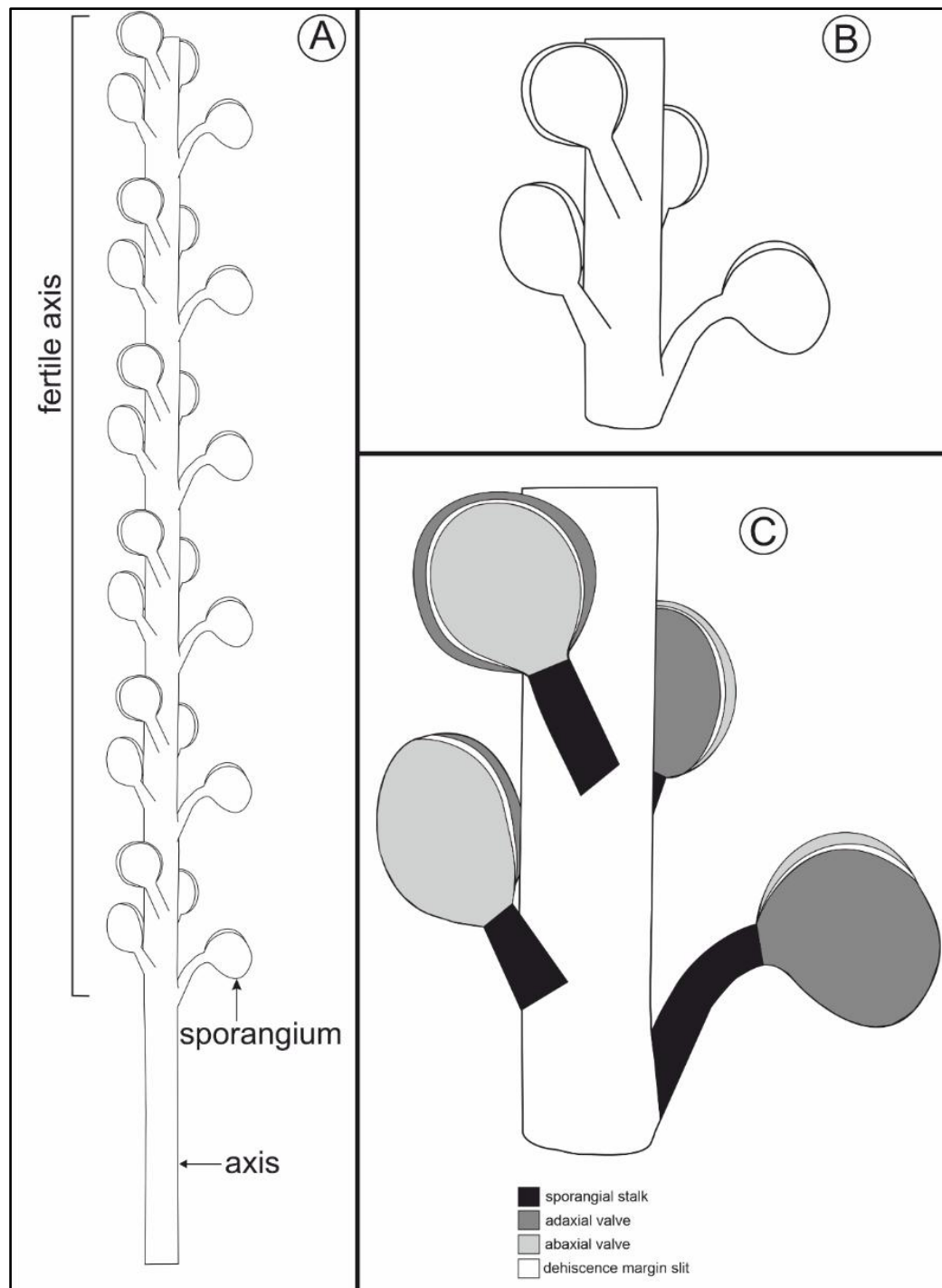
Five slabs include seven different fertile units. Three slabs had one individual spike preserved (12, 29, 39ii) whereas one slab had two fertile spikes preserved in close proximity (54L, 54R) and another had two fertile stalks preserved across two broken pieces of the same slab (56B, 56C). All fertile organs displayed relatively similar overall morphology and insertion of sporangia on the axis, despite displaying a high degree of taphonomic variability. This means that each of the fertile stalks varies in appearance quite considerably. Because of the high degree of taphonomic variability, different features of the sporangial morphology can be discerned in each of the specimens, resulting in a relatively complete picture of the overall sporangia morphology, and this

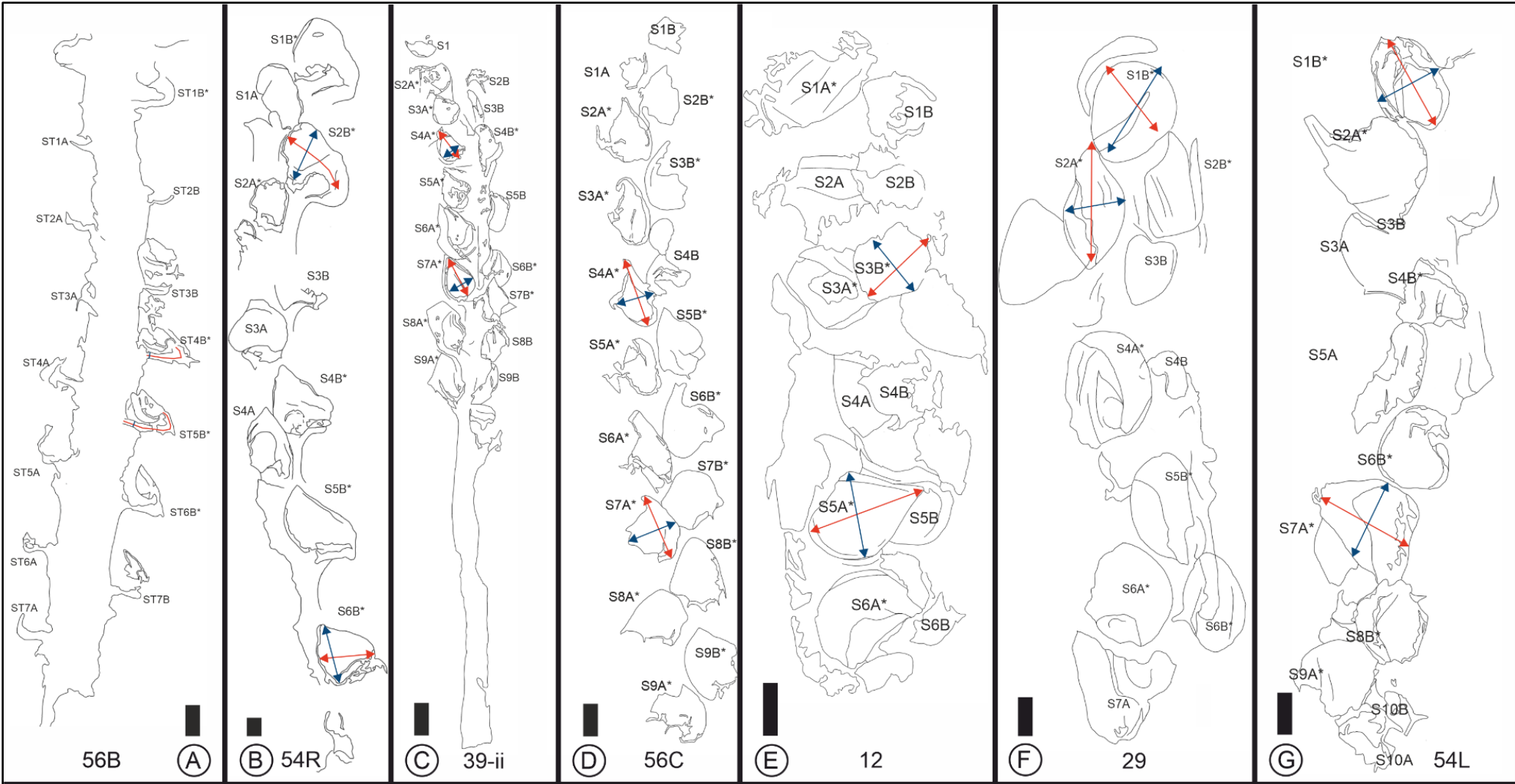
will be clarified first. Each of the specimens and the features that they elucidate will then be discussed in detail in the context of their orientation and taphonomy.

Sporangial Organotaxy

Sporangia are closely inserted alternately and are preserved in two opposed rows (Text Figure 7), forming a compact fertile spike. Because the specimens are preserved as compressions, it is difficult to determine whether this represents a strictly two-rowed arrangement in life or a loose helical arrangement compressed into two apparent rows. The term “two-rowed” is therefore used here to describe the preserved arrangement. The majority of specimens are preserved as incomplete fertile spikes. Only one spike is preserved with the vegetative axis below the sporangia visible, and it is unclear whether the spike is complete at the apex (39-ii, Plate 3A).

Text Figure 5. Diagram of a generalised *Zosterophyllum* fertile spike and individual sporangia, illustrating the preserved alternate two-rowed arrangement. This diagram is schematic and does not imply an opposite or decussate organotaxy. A. The entire fertile axis, including the fertile spike with individual sporangia and accompanying axis beneath. B. Line diagram of two pairs of sporangia, attached to the axis via sporangial stalks. C. Coloured diagram of B, with different shades of grey to represent the abaxial valve (light grey), adaxial valve (medium grey), sporangial stalk (black) and dehiscence margin (white) are also labelled. The axis which the stalks attach to is also coloured in white.





Key

Row A: Left hand row of sporangia

Row B: Right hand row of sporangia

↔

How sporangium/stalk length was measured

↔

How sporangium/stalk width was measured

*

Sporangia used in analysis, those without * were not measured because preservation was too poor or length and width of the sporangium could not be accurately determined.

39

Text Figure 6. Camera lucida interpretative drawings of each fertile spike collected from Buchananhalvøya. In A, only the sporangial stalks were measured but in B-G individual sporangia were labelled. *St* refers to stalk; *S* refers to individual sporangium. *A* denotes sporangia or stalks located on the left side of the spike, *B* denotes sporangium or stalks on the right side of the spike. The red arrows depict how sporangial length was measured and the blue lines denotes how sporangial width was measured. A well-preserved example and a poorly preserved example were chosen for illustration. Only sporangia with * after their label were deemed suitably preserved to take measurements. A. Specimen 56B. B. Specimen 54R. C. Specimen 39-ii. D. Specimen 56C. E. Specimen 12. F. Specimen 29. G. Specimen 54-L. Scale bar in all is 1mm.

Sporangial Stalk Morphology

There are four specimens where the sporangial stalk is visible (Plate 3A, E, F, G), but only two specimens where the insertion of the sporangium on the sporangial stalk is observed (54R: Plate 3E, 56B: Plate 3F).

The sporangial stalk can be divided into two distinctive limbs: a horizontal limb and a vertical limb. The horizontal limb of the stalk emerges from the axis (Text Figure 8; *black arrow*, Text Figure 9; *black arrow*) and recurves upwards and back towards the axis ~80° to form the vertical limb which connects the sporangium to the stalk (Text Figure 8; *grey arrow*, Text Figure 9; *grey arrow*). There is no clear line of demarcation between the back of the sporangium and the vertical limb of the stalk.

56B

The horizontal and vertical limbs of the stalk can be seen in two sporangia in 56B (St6B: Text Figure 8A-F, St7B: Text Figure 8GL). In both, the horizontal limb extends for 2.8 mm before recurving upwards. In St6b (Text Figure 8A), the vertical limb extends for 0.9 mm before the base of the sporangium is visible (Text Figure 8C, *grey shading*). In St7b (Text Figure 8G), the vertical limb extends for 0.7 mm (Text Figure 8I, *grey shading*).

The width of the horizontal limb varies with preservation. Immediately before the horizontal limb recurves upwards, in St6b the width of stalk is 0.7 mm (St6b, Text Figure 8A) and in St7b is 0.8 mm (Text Figure 8G).

54R

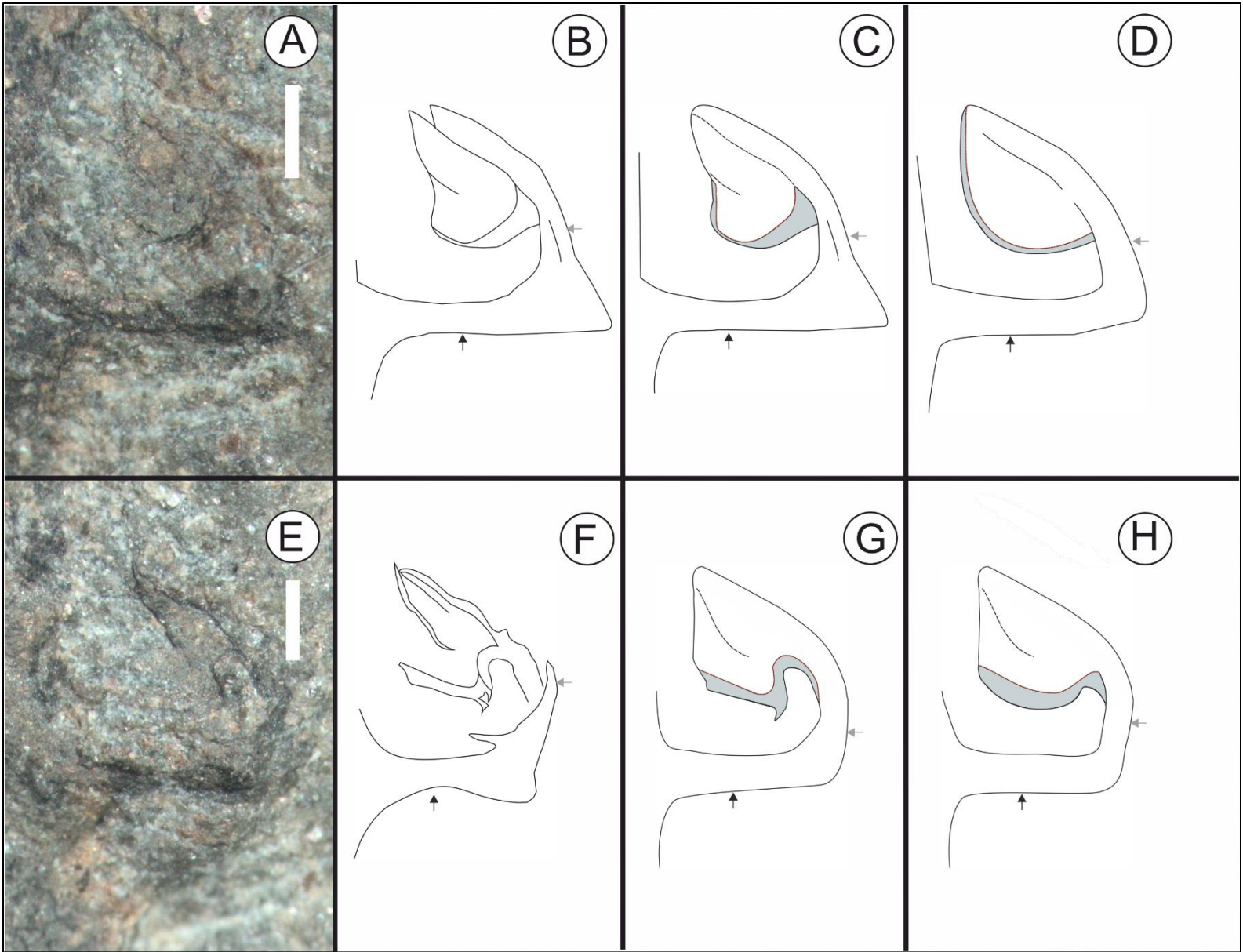
In 54R (S2A: Text Figure 9A, Text Figure 7; *white arrows*), the horizontal limb extends for 1 mm before recurving upwards to form the vertical limb, the length of which is obscured. In S2B (Text Figure 7, right sporangium), the horizontal limb of the stalk is 1.4 mm in length (Text Figure 7, right *white arrow*) and the vertical limb 1.2 mm. The width of the horizontal limb in S2A is 0.5 mm (Text Figure 7; left *white arrow*) and in S2B 0.7 mm (Text Figure 7; right *white arrow*).

54R provides insight into the orientation of the sporangial stalks relative to one another (Text Figure 7, Plate 3E). Sporangial stalks in row B are inserted at roughly 180° angles apart around the axis from sporangia in row A (Text Figure 6B, Text Figure 7, Plate 3F).

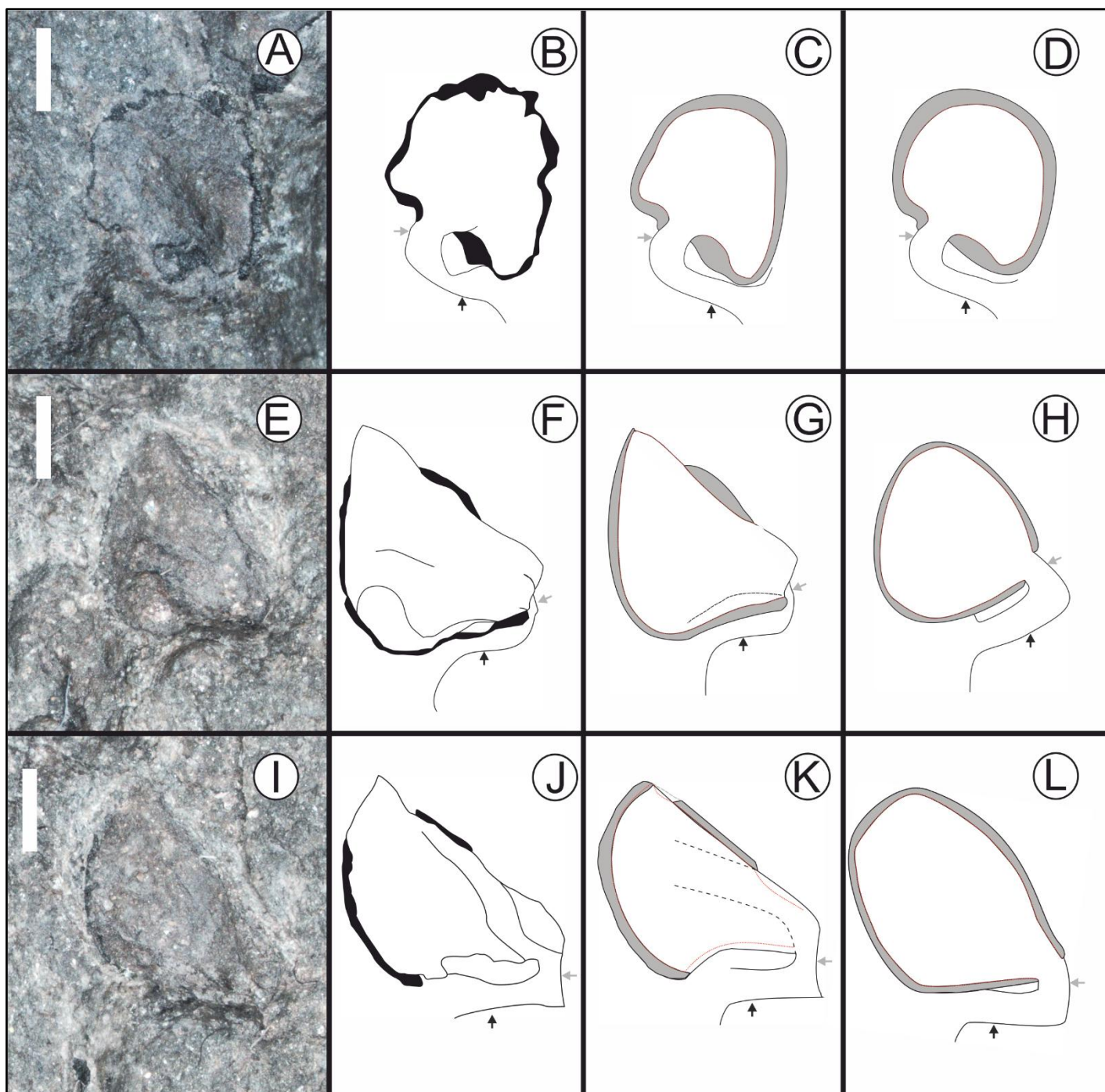
In conclusion, the sporangial stalks are preserved in two clearly defined alternating rows, positioned approximately opposite one another in compression. The horizontal limb of the sporangial stalk emerges at a right angle to the axis and extends for 0.7 – 1.4 mm before recurving upwards towards the apex of the spike. The vertical limb extends for 0.4 – 1.2 mm before joining the base of the sporangium. The width of the horizontal limb of the sporangial stalk before it recurves is 0.5 – 0.8 mm. Determination of the width of the stalk in other places is difficult because of preservation.



Text Figure 7. *Zosterophyllum fertile*, Buchananhalvøya. Two sporangia from 54R (S2B, S2A) inserted in two rows. Both sporangia are inserted onto the axis (grey arrow) by sporangial stalks (white arrows). Scale bar 500 μ m.



Text Figure 8. Interpretation of sporangial stalk morphology and sporangium insertion in sporangia St6B and St7B (specimen 56-B), showing variation in preservation of the sporangial stalk and sporangial morphology. A. Microphotograph of St6B. B. Camera lucida drawing of A. C. Interpretative line drawing of A in preservation position. D. Reconstructed diagram of A, illustrating the inferred pre-deformation arrangement with the sporangium held upright and the sporangial stalk terminating at its base. E. Microphotograph of St7B. F. Camera lucida drawing of E. G. Interpretative line drawing of F, slightly reconstructed to depict the likely pre-deformation morphology. H. Reconstructed diagram of E, showing the sporangium in an upright position with the stalk ending at its base. In all images, black arrows indicate the horizontal limb of the stalk, grey arrows indicate the vertical limb, and grey shading marks the dehiscence margin. Scale bar = 1 mm.



Text Figure 9. Interpretation of sporangial stalk morphology and sporangium insertion in S2A, S4B and S5B to show variation in sporangial stalk and sporangia morphology, specimen 54R. A. Microphotograph of S2A. B. Camera LUCIDA drawing of A. B. Interpretative line drawing of A in preservation position. C. Interpretative line drawing of A, slightly reconstructed to depict how the sporangium might have looked before deformation during preservation. D. Reconstruction of A to show sporangia with less compression. E. Microphotograph of S4B. F. Camera lucida drawing of E. G. Interpretative line drawing of E, slightly reconstructed to depict how the dehiscence valves may have been found. H. Reconstructive diagram of E showing what the sporangia may have looked like before deformation. I. Microphotograph of S5B. J. Camera lucida drawing of I. K. Interpretative line drawing of I in preservation position showing details of the stalk inserted into the back of the sporangia. L. Interpretative line drawing of I, slightly reconstructed to depict how the sporangium might have looked before deformation during preservation. Grey shading shows margin of dehiscence. Grey arrow shows vertical arm of stalk and black arrow shows horizontal limb of the stalk. Scale bar = 1mm.

Sporangial Morphology

Shape and Variation

Determining the exact shape of the sporangial valves is challenging due to preservation and taphonomic distortion. Sporangia appear ovate to elliptical in some specimens (Plate 3B–D; Plate 3B, D, G, H), spade-shaped in others (Plate 3G; Plate 4A) and teardrop-shaped in others still (Plate 3A, E; Plate 3C, F, I). In some cases, a range of apparent shapes occurs along the same spike (Plate 3E–G), reflecting compression and distortion during fossilisation (Plate 3C, E, F).

Dehiscence Margin

In some specimens, a possible dehiscence margin is visible as a narrow carbonised strip along part of the sporangial margin. Several sporangia preserve possible portions of this margin, although its full course is difficult to determine because of compression and folding of the valves (Plate 4B, C, E, H, I; white arrows). The average width of the margin is 0.2 mm (range 121–290 μm). The increased thickness of the margin suggests a reinforced zone of tissue along the line of dehiscence, similar to that shown in transverse sections (e.g. Edwards, 1969, fig. 21).

Valve Morphology

Specimen 56C (Text Figure 6D) provides the clearest evidence for the shape of the abaxial valve. Both rows of sporangia are preserved in face view, with those in row A folded across the axis and those in row B remaining more upright. Sporangium 53A (Plate 4B, Text Figure 12) displays an almost complete marginal dehiscence line, interrupted only where the stalk descends into the matrix on the left side of the sporangium, presumably attaching to the axis beneath. Sporangium 58B also preserves most of the margin, with the stalk descending into the matrix at the base of the sporangium and marked by a thick carbonised mass. In face view, the adaxial valve therefore appears rounded and slightly elongate, as indicated by the curvature of the dehiscence margin. This interpretation is supported by other specimens that show broadly rounded outlines in face view but lack clear evidence of stalk attachment (Plate 3C–D; Text Figure 6F–G).

When compressed such that the abaxial valve is viewed obliquely or folded (Text Figure 6B, S1B–S6B; Plate 3E; Text Figure 6A; Plate 3F), the dehiscence line is visible only along part of the exposed margin of the adaxial valve, mainly along the margin facing the axis and the proximal region adjacent to the stalk (Text Figure 9G–H, M–N; Text Figure 6A–C, G–I). In some sporangia, the proximal portion of the dehiscence margin curves towards the sporangium, producing a distinctly reniform outline (Text Figure 8C; Text Figure 9H), a feature supported by additional specimens (e.g. Text Figure 9B).

Although the abaxial valve is not definitively observed in any specimen, the orientation and curvature of the dehiscence margin which appears tangential to the axis, suggests that the abaxial valve likely mirrored the adaxial valve in overall shape and proportion.

Concluding Remarks

The sporangium is interpreted to sit upright or slightly inclined towards the axis, attached by a stalk that bends sharply from horizontal to near-vertical. In overall form, the sporangium is oval to slightly reniform, with a distinct dehiscence margin separating two morphologically similar valves.

Details and Taphonomy of Individual Fertile Specimens

Spike with clear sporangial stalks (56B, Text Figures 8, 10)

Specimen 56B comprises a fertile axis 215 mm long and up to 4.3 mm wide, preserved as a carbonised lateral compression. Although the sporangia are poorly preserved, this specimen provides key insights into the insertion and arrangement of the sporangial stalks. The spike is incomplete and preserves seven sporangial stalks arranged in two alternating rows (fourteen in total).

The position of the stalks is clearly defined (Text Figure 10). The average distance between alternating rows is 1.2 mm (range 0.8–1.5 mm) and between sporangia in the same row, 2.5 mm (range 2.1–3.0 mm). Each stalk has a broad, slightly decurrent base and emerges from the axis at approximately 90° (Text Figure 8B, H - black arrow). The horizontal limb thickens slightly before curving sharply upwards to form the vertical limb (Text Figure 10B, ST6B; Text Figure 6B, H - grey arrow). Where measurable, the combined length of the horizontal and vertical limbs averages 1.9 mm (range 1.5–2.3 mm) and the width of the horizontal limb before recurving is 0.4 mm (range 0.3–0.4 mm).

Preservation of the sporangia is poor, except for three on the right side of the axis that retain partial structure despite distortion (Text Figure 7; Text Figure 10 - STB5, STB6, STA7). The midline of each folded sporangium is inclined distally towards the axis. In ST6B, the lower margin of the sporangium curves upwards to meet the stalk (Text Figure 8A), suggesting an overall reniform shape

Spike with compressed sporangia and clear sporangial stalks (54R, Text Figures 7, 9, 11)

Although not particularly well preserved, this specimen provides important information on the insertion of the sporangia and the arrangement of the two rows relative to one another. The sporangia in the two rows are inserted alternately at approximately 180° around the axis. The specimen consists of a single incomplete spike, 390 mm in length and up to 4.7 mm in width, preserved as an unbranched impression. Along the length of the spike, at least ten sporangia are borne alternately in two rows (Text Figure 11B).

Sporangia S2A and S2B (Text Figure 7) provide the clearest evidence of how the two rows of sporangial stalks are inserted. S2A is slightly reniform in shape and preserved in abaxial view, with the valve and vertical portion of the stalk visible above the axis. S2B arises opposite to S2A, with the horizontal limb of the stalk emerging at a right angle to the axis and curving upwards to bear a nearly upright sporangium. In both S1B and S2B, the sporangial stalk appears continuous with the slightly distorted abaxial valve (Text Figure 11 S1B, S2B). The adaxial valve lies beneath the overlying abaxial valve, facing the axis, and is often crushed or obscured during preservation.

Towards the distal end of the spike, sporangia S6B, S5B and S4B incline towards the axis, so that most of the vertical limb and part of the horizontal limb of the stalk are obscured by the lower margin of the overlying sporangium (Text Figure 9G, M; Text Figure 11B). In five of the sporangia in row B (Text Figure 9B - S1B, S2B, S4B, S5B, S6B), a distinctive carbonised band occurs on the rounded left side of the sporangia (Text Figure 9B, *). In two sporangia the band is faint and indistinct, but in three it is clearly defined and represents part of the dehiscence margin. Proximally along row B, the degree of inclination of the sporangia towards the axis becomes more pronounced.

2.2.3.2.3 Spike with sporangia rotated laterally, in abaxial view (56C, Text Figure 12)

This specimen is moderately well preserved and represents one of the best examples of the overall shape of the abaxial valve (Text Figure 12; Text Figure 11B, *ab*) and the associated dehiscence margin (Text Figure 12, *; Text Figure 11, *). The specimen consists of an incomplete spike, 22 mm in length and up to 3.5 mm wide, preserved as a compression. Eighteen sporangia are present, arranged alternately in two rows (Text Figure 12). The preservation quality of individual sporangia is variable.

In the left row, the upper sporangia (Text Figure 12A - S2A–S6A) are rotated so that the midline of the sporangium and its stalk are perpendicular to the axis. In at least three of these sporangia, remnants of the sporangial stalk are visible (Text Figure 9B, *st*). The vertical limb of the stalk emerges from the left side of the sporangium (the back of the abaxial valve), while the horizontal limb is folded beneath, between the axis and the adaxial valve. The clearest example of this arrangement is S3A (Text Figure 12), where

the sporangial stalk arises from the abaxial valve approximately halfway up the height of the sporangium (Text Figure 11B, *st*; Text Figure 12, white arrow).

Sporangia in row B are less well preserved. The lower sporangia (Text Figure 11B - S9B, S8B, S7B) are preserved in face view, with the vertical limb of the sporangial stalk folded underneath the sporangium. This configuration is most clearly visible in S8B. In sporangia S2A–S5A (Text Figure 12B), a distinctive thickened carbonised margin outlines the valve and represents the dehiscence margin, measuring 223 μm thick (range 183–290 μm).

Spike crushed with an overlaying axis (39-ii, Text Figure 13)

The specimen is preserved as a compression, and where the carbonised material has been removed a clear impression is visible (Text Figure 13). The axis is 457 mm long, with the portion bearing the spike measuring 270 mm in length and up to 3.6 mm in width. It is uncertain whether the apex of the spike is complete. The spike is preserved with the axis overlying the sporangia, or this slab may represent the counterpart (Text Figure 13B, *ax*). Seventeen sporangia are preserved in two rows (Text Figure 13B). Sporangia in the left row (A) are better preserved than those in the right row (B), which are partly obscured by the overlying axis.

The lower portion of the spike provides a good indication of how paired sporangia are arranged relative to one another, even though individual sporangial morphology is obscured. Distally, the sporangia become increasingly distorted by compression.

At the base of sporangia S7A, S8A and S9A, a small protrusion from the overlying axis may represent a sporangial stalk joining the back of the sporangium (Text Figure 13B, *?st*). In S8A, there is no clear demarcation between this presumed stalk and the valve at the back of the sporangium. Given the position of the stalk, this surface likely represents the abaxial valve, although its outline has been distorted by rotation and compression during preservation (Text Figure 13B, *?ab*).

Spike with sporangia crushed laterally (12, Text Figure 14)

This specimen consists of a short fertile spike, 133 mm in length and 3.3 mm in width. Because of the poor preservation, it is unclear whether the spike is complete, although this is unlikely given its size and the number of sporangia. Initially, four poorly preserved sporangia were visible, but after serial *dégagement* a further two pairs were revealed on the basal portion of the spike (Text Figure 14; S5A–S5B and S6A–S6B).

An unbranched axis overlies the left portion of the spike, 133 mm in length (Text Figure 14, ax). *Dégagement* of the basal region shows that this axis lies directly above the sporangia, suggesting it may represent the original axis that bore the sporangia prior to preservation.

On five sporangia in the left row, a clear and distinctive carbonised margin outlines the exposed sporangium and likely represents the dehiscence margin (Text Figure 14; *). The average width of this margin is 175 μm (range 121–242 μm). Because of the poor preservation, it is difficult to determine which portion of the sporangia are exposed, and the position of the stalk relative to the sporangium cannot be determined.

Poorly preserved spike with sporangia in various orientations (18-Spits-25-54-L, Text Figure 15)

This specimen contains a poorly preserved fertile spike, 17.6 mm in length and up to 3.3 mm in width, with at least ten sporangia preserved largely as impressions. It is unclear whether either the apical or basal portion of the spike is complete, or which direction represents the apex. A partially preserved axis occurs on the right side of the specimen, 122 mm in length and up to 10 mm in width.

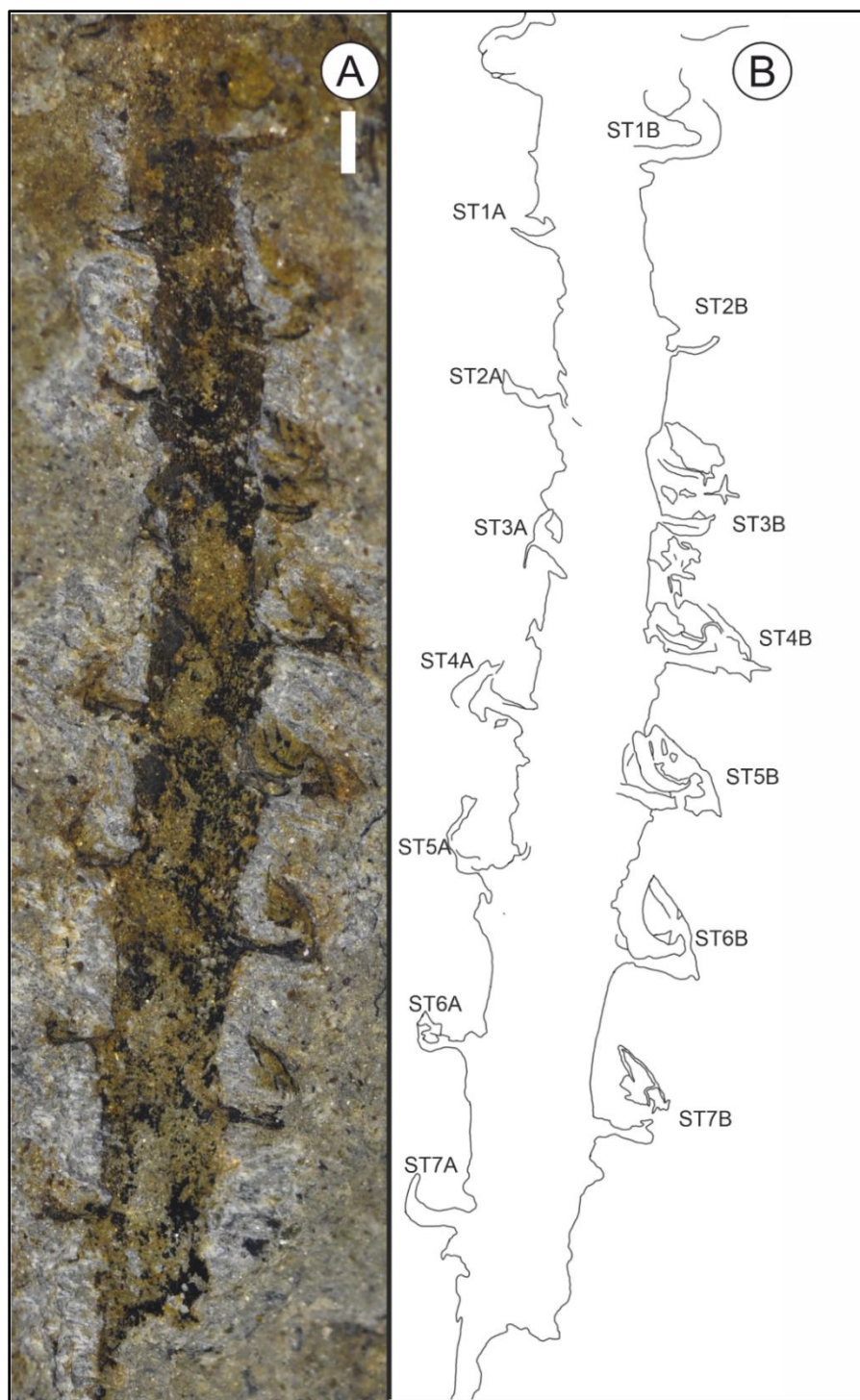
At least ten sporangia are present, three of which appear to form pairs (Text Figure 6F; Text Figure 15). The majority are ovate in shape but poorly preserved, with finer morphological details obscured by compression.

Poorly preserved spike with possible sporangial stalk (29, Text Figure 16)

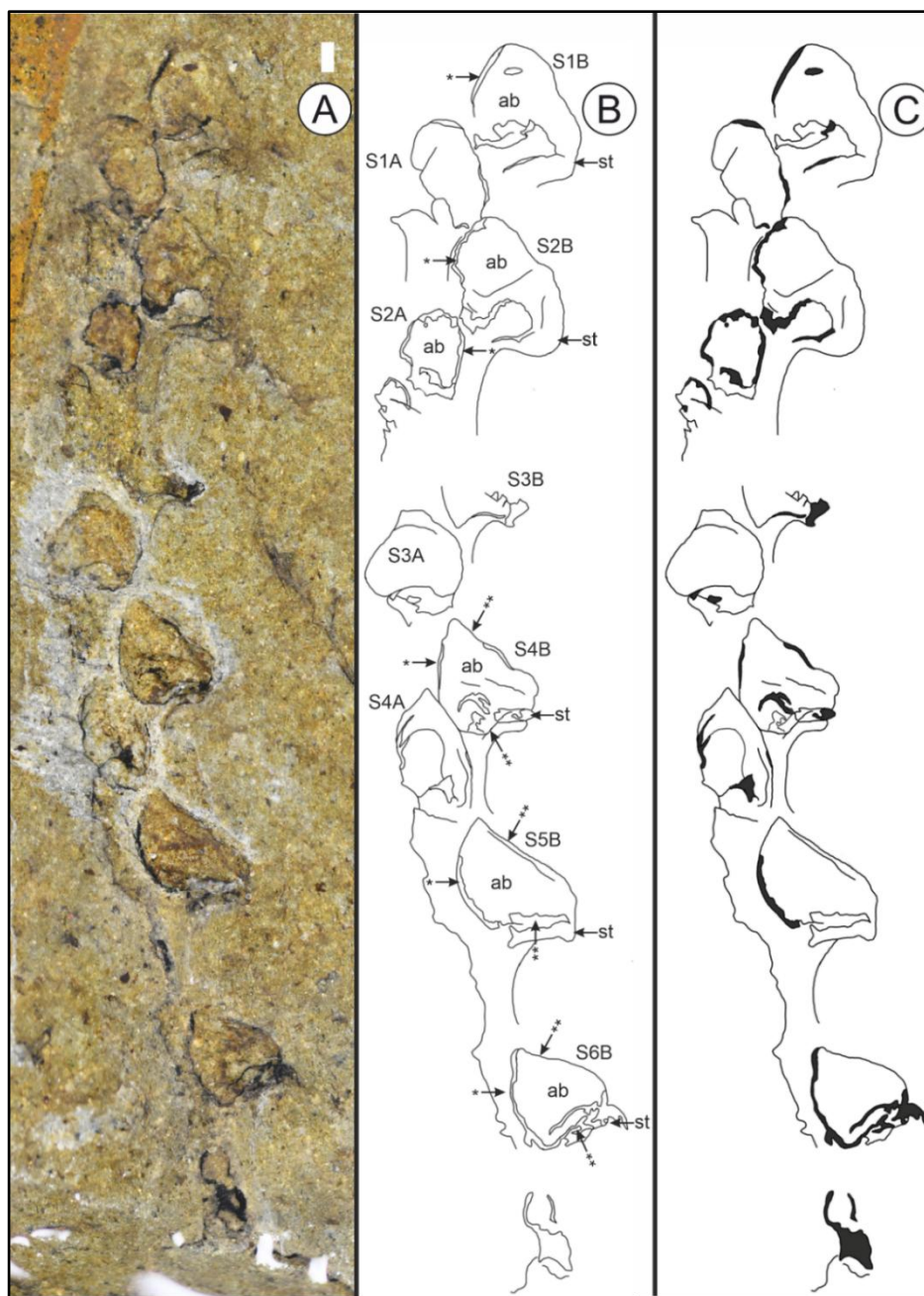
This specimen measures 183 mm in length and up to 3.2 mm in width and is poorly preserved as a compression. Both the basal and apical regions of the spike appear incomplete. Along its length, twelve sporangia are visible, four of which occur in

apparent pairs along two rows of the axis, though all are poorly preserved (Text Figure 6G; Text Figure 16). Because of the poor preservation, it is difficult to determine the orientation of the sporangia or which end of the spike represents the apex.

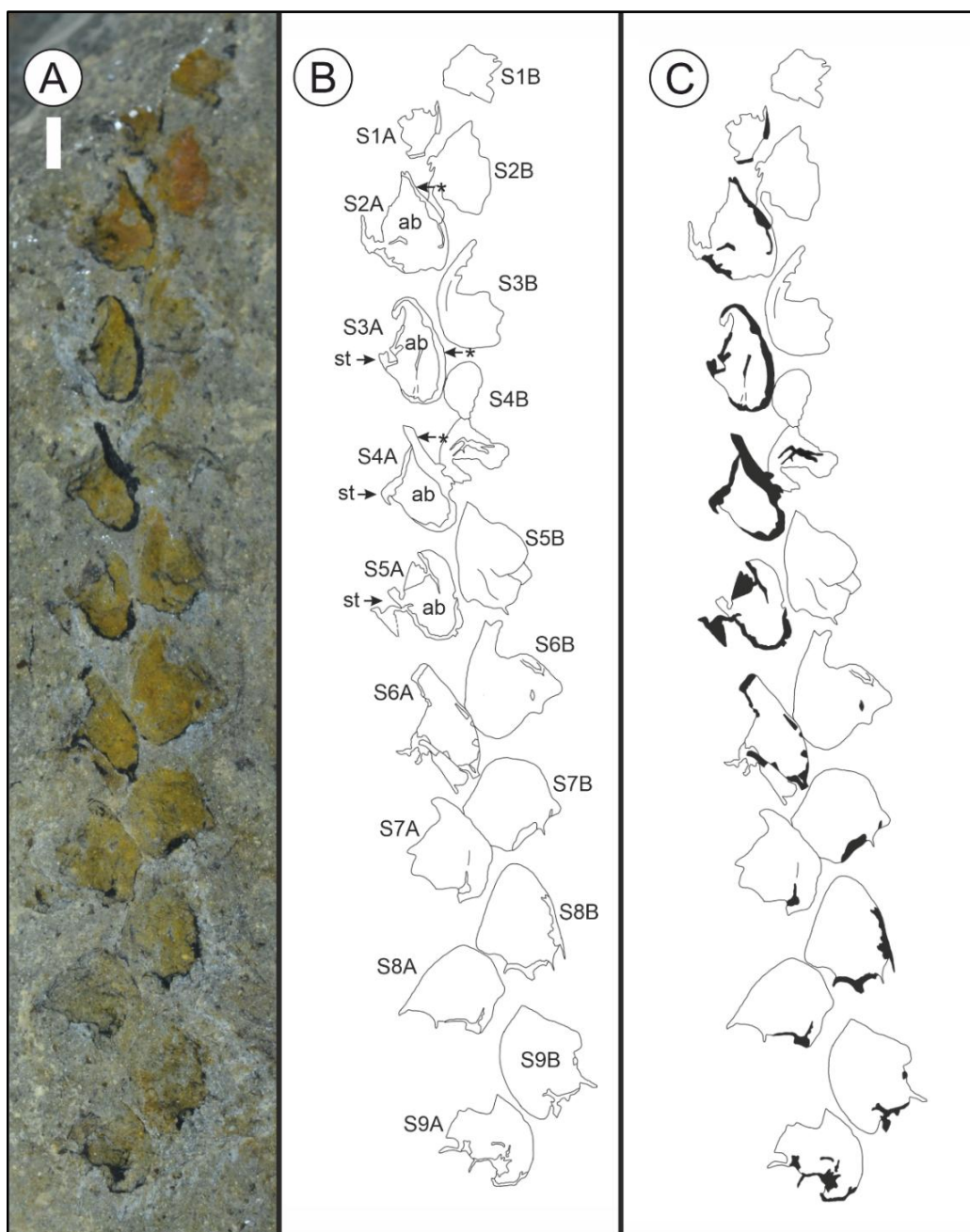
A faint carbonised margin occurs around several sporangia and may represent the dehiscence margin, best seen in S6B (Text Figure 6G; Text Figure 16B, *).



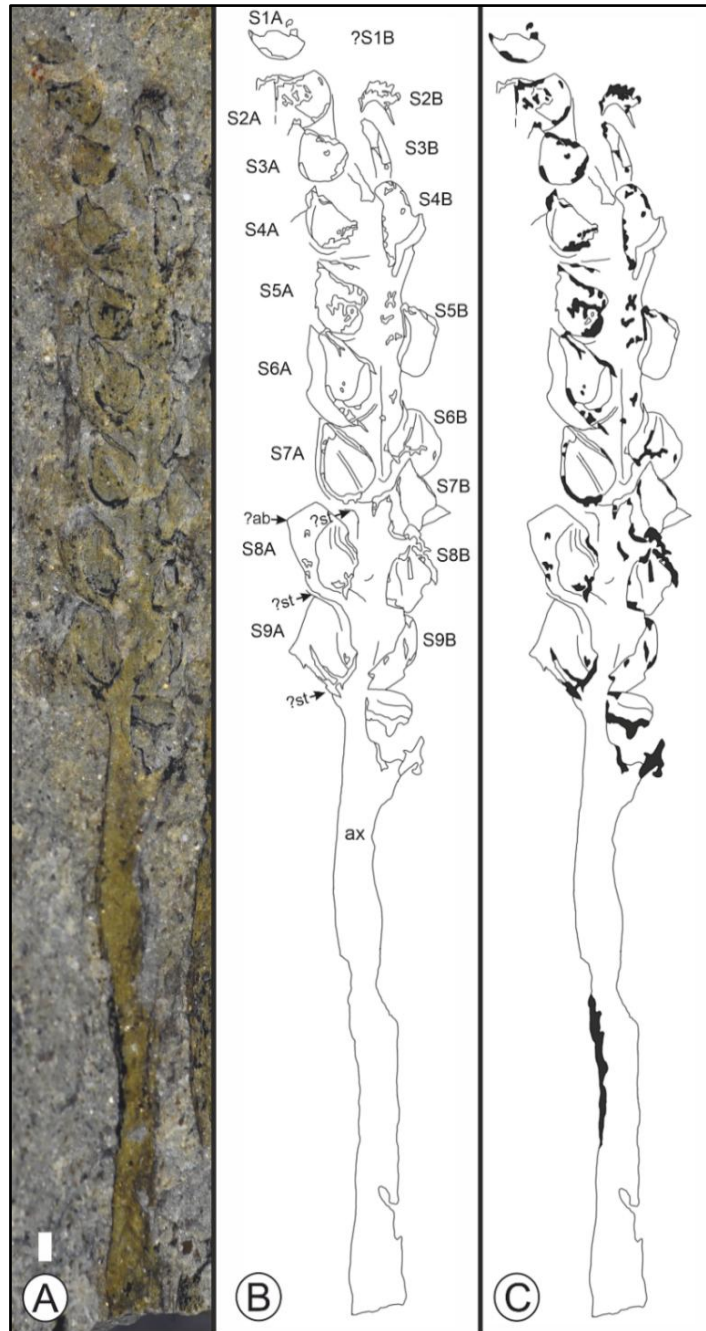
Text Figure 10. Moderately preserved spike, Buchananhalvøya (18-Spits-25-56B). Fourteen sporangial stalks have been preserved, with five poorly preserved sporangia on the right side of the axis. A. Photograph taken under polarised light to enhance contrast. B. Camera lucida interpretive drawing of sporangial stalk with labels. Each sporangial stalk has been labelled in Text Figure 6A.. Scale bar 1mm.



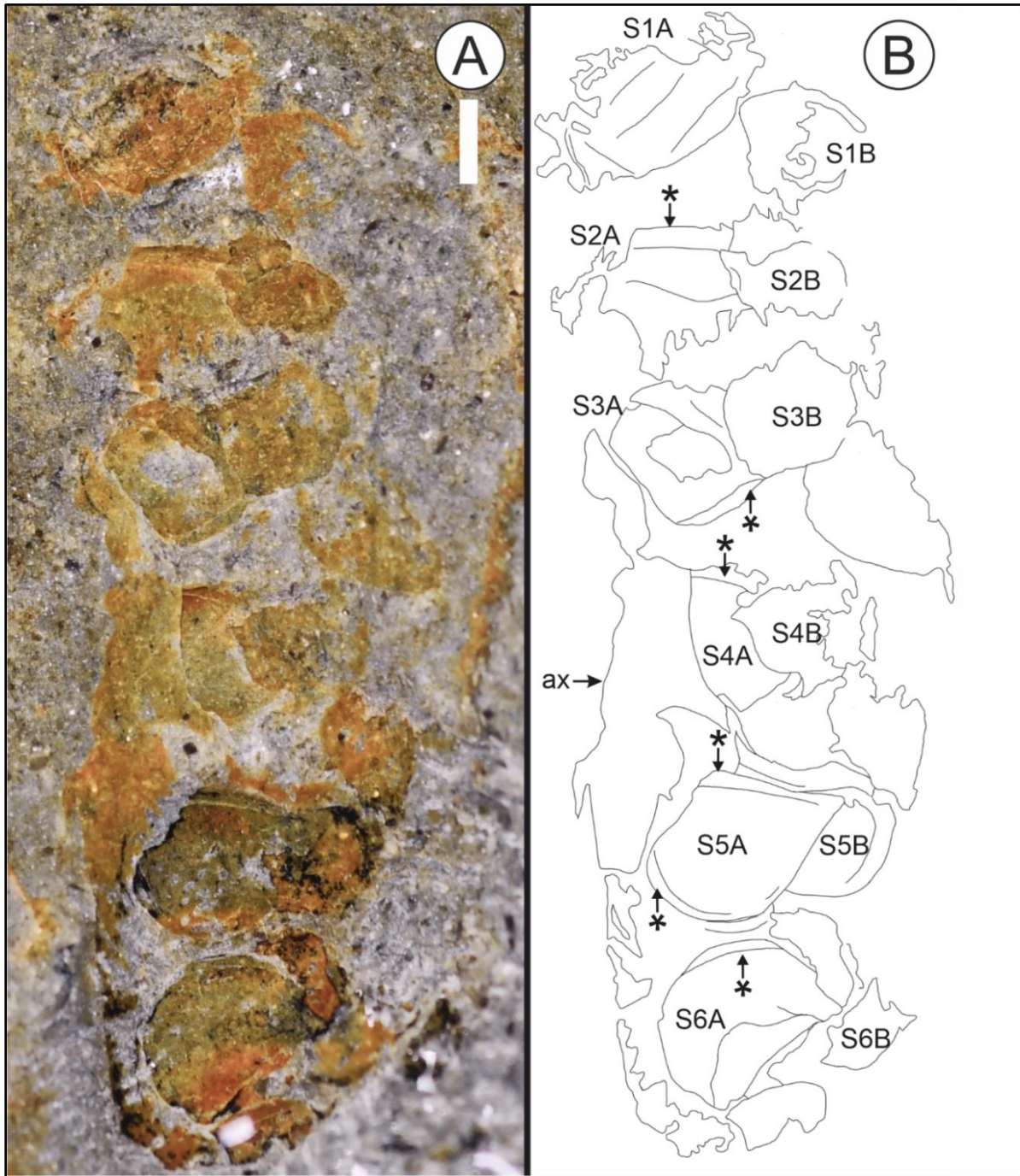
Text Figure 11. Moderately preserved spike, Buchananhalvøya (54R). Ten sporangia have been preserved in two rows. A. Photograph of spike, viewed under polarised light to enhance contrast. B. Camera lucida interpretative drawing of spike with labels. C. The same camera lucida interpretative drawing but with dark coloration where the carbonised material is left to aid with interpretation. Each sporangium has been labelled in Text Figure 6B. *st* denotes the presence of a sporangial stalk. * denotes the presence of carbonised dehiscence margin. ** denotes where the lateral edges of the abaxial valve has been folded under the sporangium. *ab* denotes the position of the abaxial valve. Scale bar 1mm.



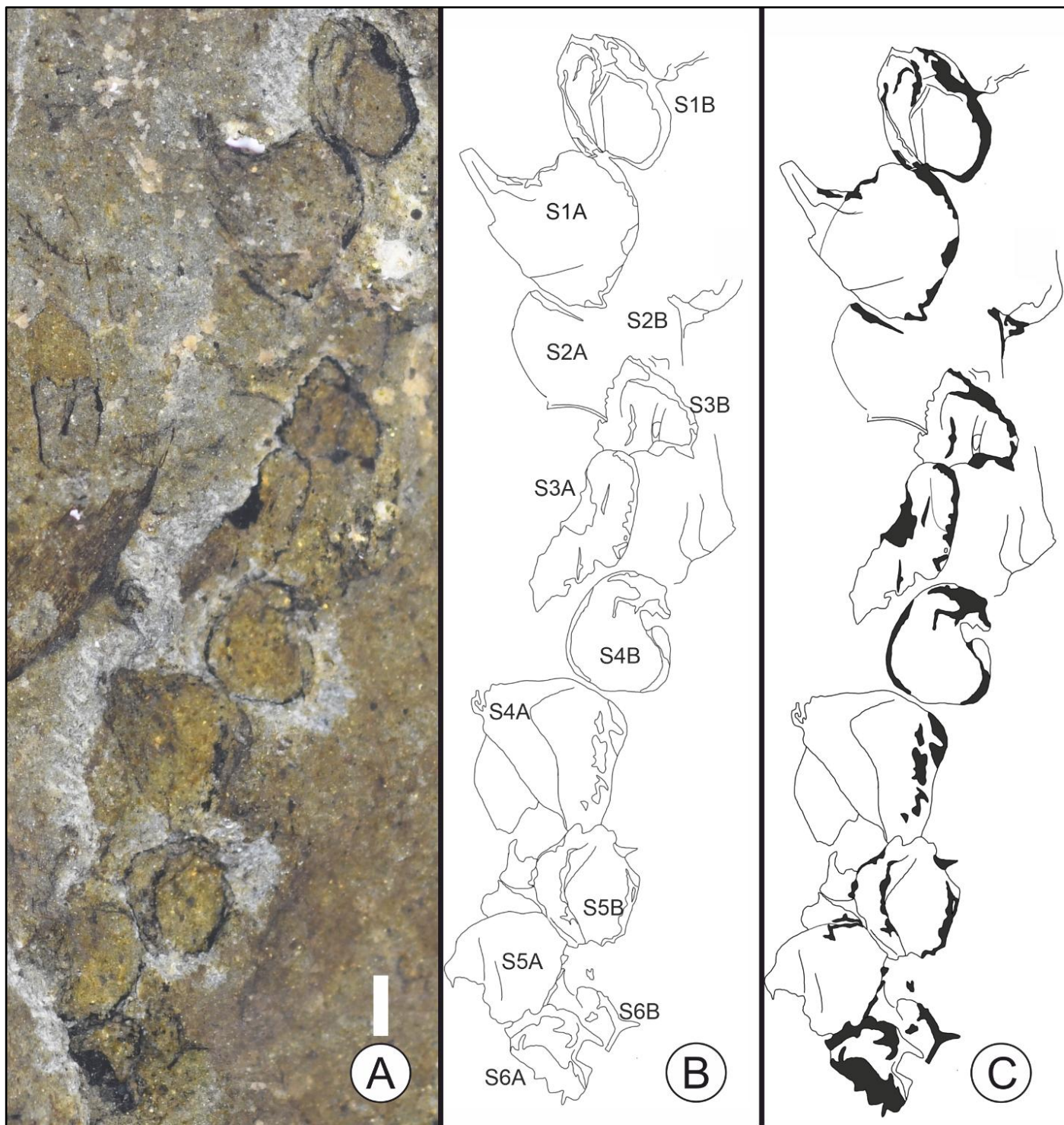
Text Figure 12. Moderately preserved spike, Buchananhalvøya (56C). There are 18 sporangia borne in two rows. A. Photograph of spike, viewed under polarised light to enhance contrast. B. Camera lucida interpretive drawing of spike with labels. C. The same camera lucida interpretative drawing but with dark coloration where the carbonised material is left within the specimen, to aid with interpretation. Each sporangium has been labelled (Text Figure 6D). *St* denotes where the horizontal limb of the sporangial stalk has been folded underneath the valve in sporangia in the left row. *ab* denotes the position of the abaxial valve. * denotes the position of the dehiscence margin surrounding sporangia the left row. Scale bar 1mm.



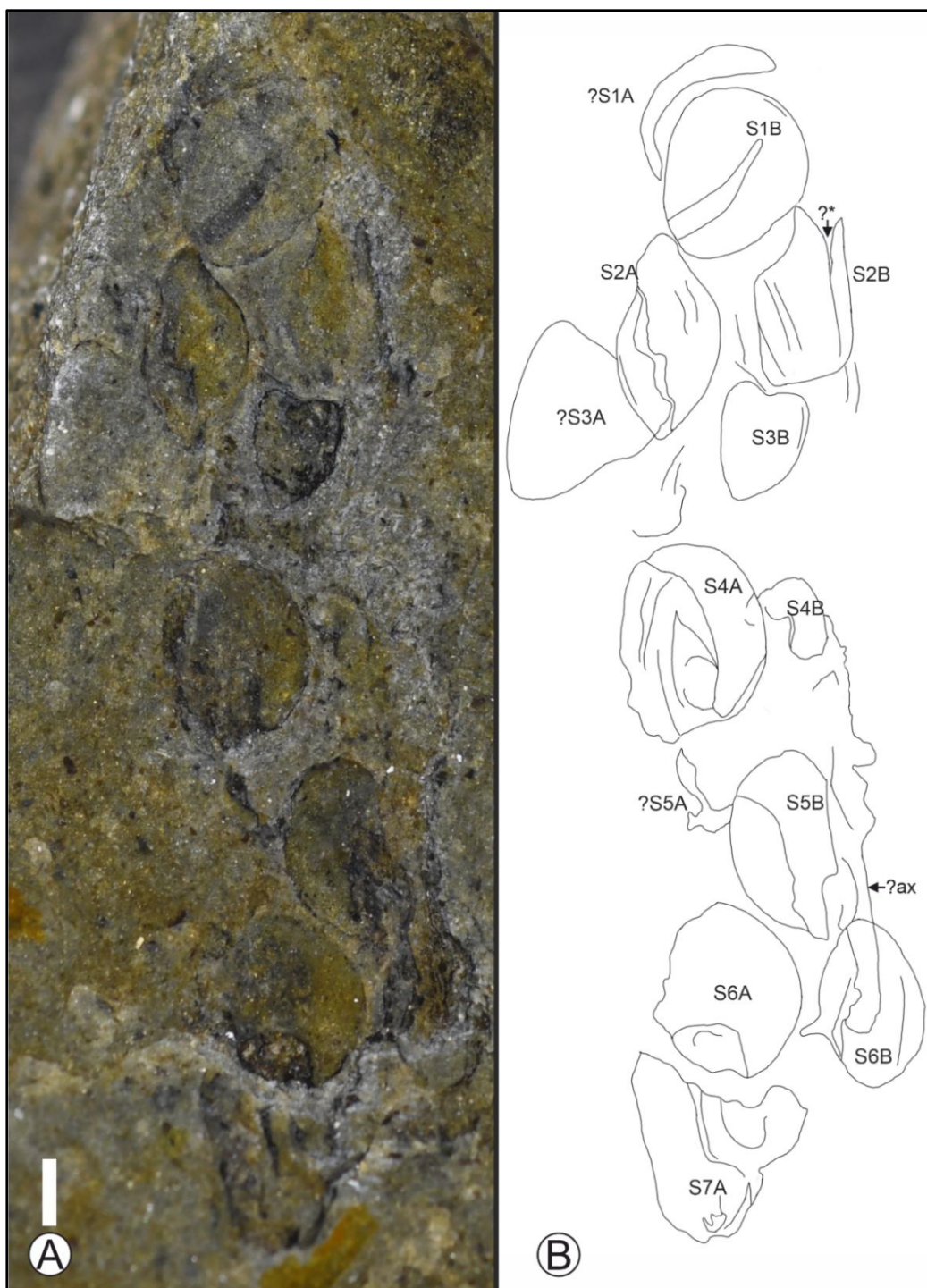
Text Figure 13. Moderately preserved spike, Buchananhavvøya (39-ii). 17 sporangia are preserved in two rows, with an overlaying axis. A. Macrophotograph taken with polarising light to enhance contrast. B. Camera lucida interpretative drawing of axis with labels. C The same camera lucida interpretative drawing but with dark coloration where the carbonised material is left within the specimen to aid interpretation. Each sporangium has been labelled (Text Figure 6C). ?st denotes the presence of a possible sporangial stalk, but preservation is not clear enough to say unequivocally. * denotes where there is a clearly defined margin around one of the valves in sporangium S7A. Ax denotes axis underneath spike. Scale bar 1mm.



Text Figure 14. Poorly preserved spike, Buchananhalvøya (12). Six pairs of sporangia have been exposed, underlying an axis. A. Macrophotograph of specimen after serial dégagement of two pairs of sporangia on the basal portion of the axis. B. Camera lucida interpretive line drawing of specimen after serial dégagement. Each sporangium has been labelled (Text Figure 6E). ax denotes overlying axis. * denotes dehiscence margin present around some exposed sporangia. Scale bar 1mm.



Text Figure 15. Poorly preserved spike, Buchananhelvøya (54L). A. Photograph of spike, taken with polarising light to enhance contrast. B. Camera lucida interpretative drawing of A. C. The same drawing as B but with black colouration to aid interpretation. Each sporangium has been labelled (Text Figure 6G). Scale bar 1mm.



Text Figure 16. Poorly preserved spike, Buchananhalvøya (29). At least ten sporangia in various planes of orientation have been preserved. A. Photograph of specimen viewed using polarised light to enhance contrast. B. Camera lucida interpretative drawing of specimen. Each sporangium has been labelled (Text Figure 6F). ?ax denotes the overlaying axis. ?* denotes an interpretation of where the two sporangial valves split. Scale bar is 1mm.

Sporangial measurements

Method

Measurements were taken only from specimens that exhibited sufficient preservation (Text Figure 6). Sporangial length was measured along the full extent of the sporangium. Stalk length was recorded only where the entire structure could be clearly defined (Text Figure 6A - red line), including both the horizontal limb emerging from the axis (Text Figure 8, black arrow) and the vertical limb attaching to the abaxial valve of the sporangium (Text Figure 8, grey arrow). Stalk width was measured at the base of the horizontal limb, immediately after it emerged from the axis (Text Figure 6A; blue line).

For spacing measurements, two parameters were defined. The *distance between individual sporangia* refers to the length of axis separating sporangia in alternating rows (e.g. between S4A and S4B; Text Figure 6). The *distance between sporangia in the same row* refers to the axis length separating consecutive sporangia within a single row (e.g. between S6B and S7B; Text Figure 6). In both cases, the axis length was measured from the base of each sporangium.

Sporangium Size

Across the seven fertile spikes examined, sporangia averaged 2.3 mm in length (range 1.5–3.7 mm; Text Figure 17A) and 1.6 mm in width (range 0.8–2.6 mm; Text Figure 17B). Specimen 54R bore the longest and widest sporangia (Text Figure 9), whereas specimen 12 had the shortest and specimen 56C the most slender (Text-figs 12A, 12B).

A statistically significant positive correlation was identified between sporangial length and width (Spearman's rank correlation coefficient, $r(57) = 0.62$, $p < 0.05$), indicating that width increases proportionally with length (Text Figure 18).

Sporangial Stalk Size

Stalk dimensions were measurable in two fertile spikes (56B: Text Figure 8; 54R: Text Figure 9). Mean stalk length was 2.1 mm (range 1.5–2.9 mm), with specimen 56B

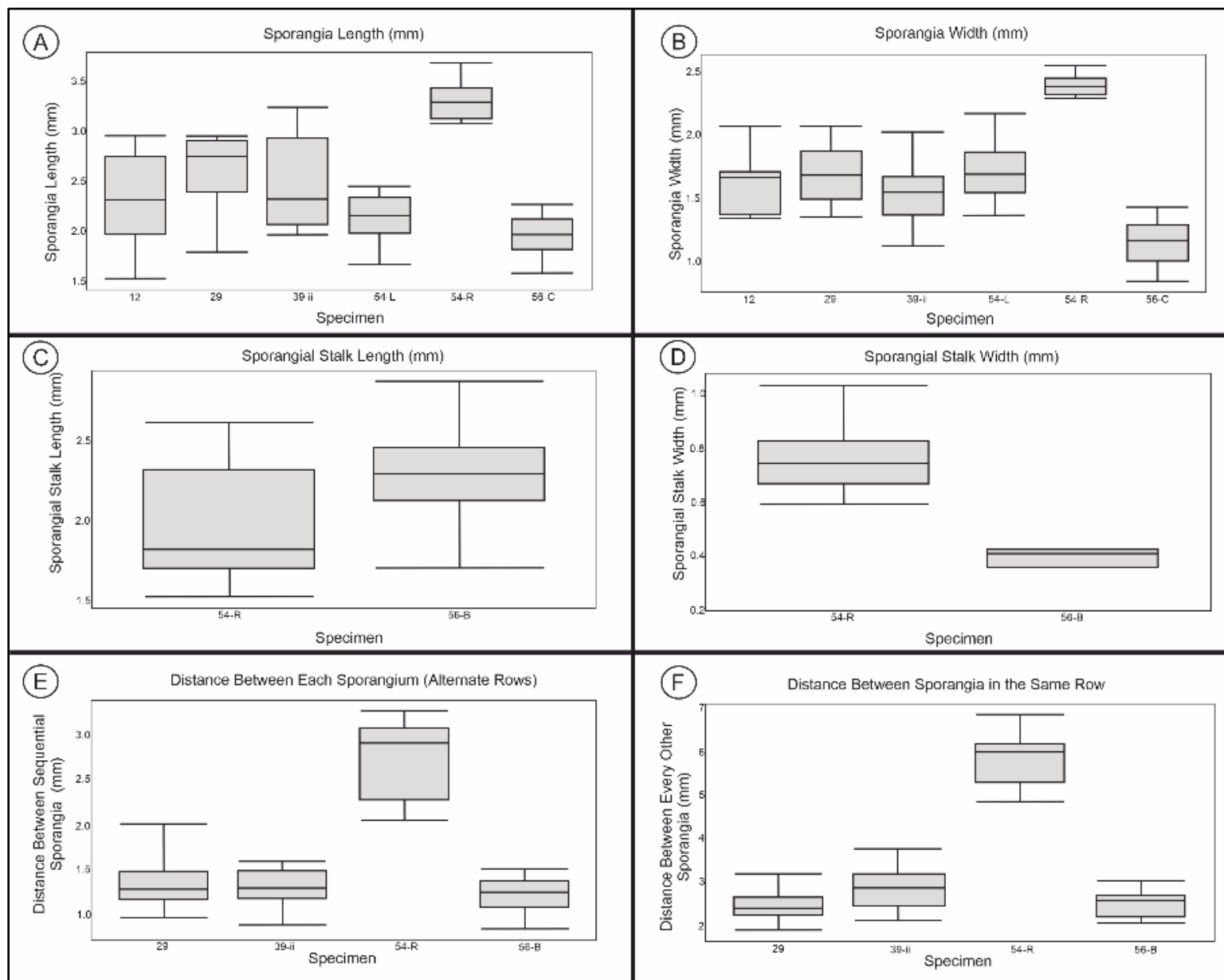
displaying longer stalks (Text Figure 17C) and specimen 54R exhibiting the widest (mean width = 0.6 mm; range 0.2–1.0 mm; Text Figure 17D).

Distance Between Sporangia

Distances between successive sporangia, measured from the base of one to the next, could be determined in four spikes where preservation permitted. The mean distance between adjacent sporangia was 1.2 mm (range 0.8–1.5 mm). Spikes 29, 39ii, and 56B exhibited similar spacing, whereas specimen 54R showed markedly greater separation (Text Figure 17E).

For sporangia within the same row, the mean spacing was 2.5 mm (range 2.1–3.0 mm), following a comparable pattern: specimens 29, 39ii, and 56B were consistent, while 54R displayed substantially wider spacing (Text Figure 17F).

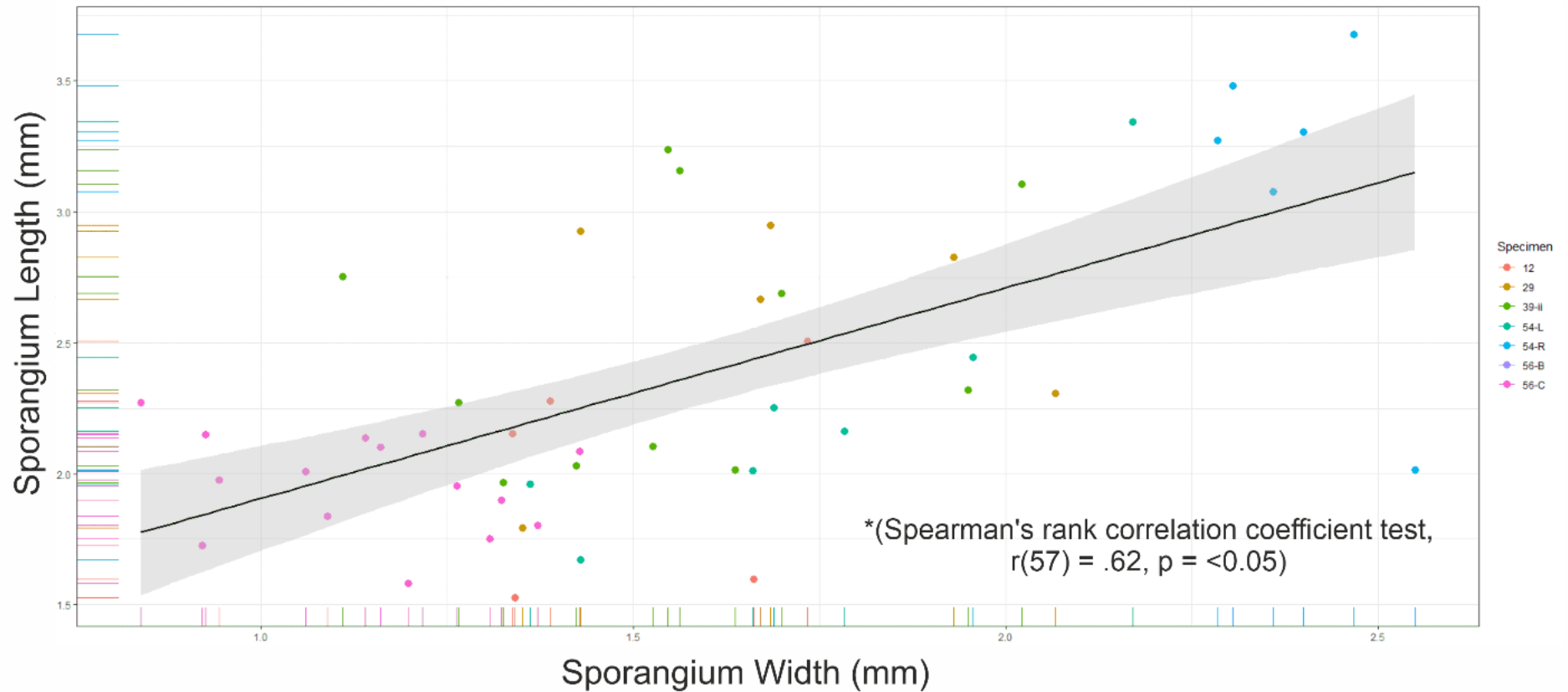
The measured variation among specimens reflects differences in preservation, orientation and degree of compression rather than substantial morphological disparity. No consistent basal-to-apical gradient in sporangial length is evident in the measured specimens, suggesting that the observed variation does not primarily reflect progressive apical development. Despite some variability, the dimensions, shape and organisation of the sporangia are consistent across the assemblage and indicate a single, coherent taxon. In all specimens, sporangia are borne alternately and appear arranged in two opposed rows in compression, each attached by a short stalk bent through $\sim 90^\circ$. This regular bilateral arrangement, together with the reniform valve shape and upright to slightly inclined orientation of the sporangia, is characteristic of *Zosterophyllum fertile* Leclercq, 1942. These features provide the basis for its systematic placement and for comparison with material described from other localities



Text Figure 17. Box and whisker plots depicting various morphological measurements in *Z. fertile*.

These box and whisker plots provide a visual representation of the average, spread, and presence of outliers in the data. A. Plot representing the length of sporangia. B. Plot depicting the sporangial width. C. Plot depicting the whole sporangial stalk length. D. Plot depicting sporangial stalk width. E. Box Plot depicting the distance between sequential sporangia in alternating rows. F. Plot depicting the distance between sporangia in the same row. Units are mm.

Scatterplot of Sporangium Length by Sporangium Width



Text Figure 18. XY scatter plot illustrating the relationship between sporangium length and width in *Zosterophyllum* sp. Each data point represents a single sporangium. Colour codes for individual specimens are on the right side of the graph. The x-axis represents sporangial width, and the y-axis represents sporangial length, units mm. Line of best fit and confidence interval are illustrated. *Results of the Spearman's rank correlational coefficient test.

Summary of Sporangial Features

Although the sporangia show some variation in form, including related to orientation and preservation as documented above, several features remain consistent across the assemblage

1. The sporangial stalk is divided into two distinct limbs: a horizontal limb that emerges from the axis at roughly 90° curving distally through 90° towards the apex of the spike.
2. The stalk measures between 1.5–2.9 mm in total length and 0.2–1.0 mm in width.
3. There is no clear boundary between the distal portion of the stalk (vertical limb) and the abaxial surface of the sporangium.
4. Sporangia sit upright to slightly inclined towards the axis distally and range from 1.5–3.7 mm in length and 0.8–2.6 mm in width.
5. The distance between alternating sporangia ranges from 0.8–1.5 mm whereas the spacing between those in the same row varies from 2.1–3.0 mm.
6. Sporangia are borne alternately and appear arranged in two opposed rows in compression, forming a compact, regular spike.
7. A possible dehiscence margin is visible in some specimens, measuring between 121–190 µm where preserved.
8. The abaxial valve is ovate to reniform in shape and its lateral margins are often folded underneath the sporangium.
9. There is no evidence that the valves were unequal; the adaxial valve was likely comparable in size and shape to the abaxial valve.

Systematic Palaeobotany

Subdivision: Zosterophyllophytina

Family: Zosterophyllaceae

Genus: *Zosterophyllum* Lang, 1927 (non Penhallow, 1892, nomen nudum)

Subgenus: *PlatyZosterophyllum* (Croft and Lang, 1942) Hao et Xue, 2013

Species: *Zosterophyllum fertile* Leclercq, 1942

Diagnosis: (translated from Leclercq, 1951).

Portion of a fertile axis forming a compact spike, approximately 3 cm long (or longer) and 3 mm wide. The axis is well differentiated and contains a thin woody strand composed of annular tracheids 30–33 µm in diameter. Eighteen sporangia are arranged in a regular spiral, forming two diametrically opposed rows. Each sporangium is attached to the axis by a short pedicel bent at a right angle. Sporangia are upright, reniform (2 mm high, 1.8–2 mm wide), orientated towards the axis, and show a dehiscence slit with a toothed margin along the upper convex edge. Sporangial walls are smooth; spores and sterile regions are unknown.

Holotype: NMV P50040.1 and P50040.2, Liège University.

The Buchananhalvøya assemblage, based on multiple fertile units rather than a single specimen, allows several features of the species to be refined, particularly the morphology of the sporangial stalk, the observed range in sporangial dimensions and the preserved arrangement of the sporangia. The sporangia appear in two opposed alternating rows in compression, although whether this reflects a strictly bilateral arrangement or a loose helix compressed into two rows remains uncertain. These observations suggest that Leclercq's diagnosis could be expanded, while the original concept of the species is broadly supported.

Discussion

Taxonomic determination

This plant is assigned to the genus *Zosterophyllum* on the basis of its naked, bifurcating vegetative axes and terminal fertile spikes bearing stalked sporangia. It is referable to the subgenus *PlatyZosterophyllum* in the sense of Croft and Lang (1942) because the sporangia are preserved in two regular alternating rows rather than showing an obvious multi-ranked helical arrangement around the axis, as in *EuZosterophyllum*. Croft and Lang used *PlatyZosterophyllum* for forms in which the sporangia appear organised in a bilateral, flattened arrangement, produced by the curvature of the stalks and the resulting presentation of the sporangia relative to the fertile axis. In the Buchananhalfvøya material, the sporangia are inserted alternately in two regular rows at approximately 180° around the axis, and their consistent bilateral organisation accords with this concept. However, because most species of *Zosterophyllum* are known from compression material rather than three-dimensionally preserved spikes, the spatial interpretation of this arrangement should be treated with some caution.

There are some morphological similarities of the sporangia described in this study to a number of *Zosterophyllum* species (Table 3). The sporangia of *Z. myretonianum*, the type genus for *Zosterophyllum*, are of a similar size and organization (Penhallow, 1892; Lang, 1927; Lele & Walton, 1961; Edwards 1972), but have more distinctively reniform shaped sporangia. Similarly, sporangia of *Z. australianum* are comparable in size but differ in shape and organization, being transversely elliptical and organized in very compact rows with significant overlap (Lang & Cookson, 1930; Hao, 1992). *Zosterophyllum sinense* has sporangia with similar size, but once again the overall sporangial morphology and insertion onto the axis differs considerably. *Z. sinense* has pear or fan shaped sporangia, which dehisce into very distinctive unequal valves (Li & Cai, 1977), whereas the sporangia in this study are clearly equivalve and inserted in two distinctive rows as opposed to helically inserted sporangia.

Similarly to specimens in this study, *Zosterophyllum llanoveranum* Croft and Lang (1942) has sporangia inserted in two distinctive rows, a feature which originally prompted the erection of the subgenus *PlatyZosterophyllum* Croft and Lang (1942), later emended by Hao and Xue (2013). This subgenus includes *Z. fertile* and *Z. artesianum*. Whilst the sporangia of *Z. llanoveranum* are of a comparable size, there are key differences in their overall shape, particularly in side profile, where they show an almost reniform morphology (Edwards, 1969a; fig. 4) with a distinctive protruding lip at the distal margin of the sporangial valve (Edwards, 1969a; figs 24–26).

The sporangia described here are remarkably similar in appearance, size and organization to *Zosterophyllum fertile* from Belgium (Leclercq, 1942), South Wales (Edwards, 1969b; Wellman, *et al.*, 2000), and Scotland (Edwards, 1972). There is one specimen collected from the Wilson Creek Shale in Australia which has been described as ‘cf. *Z. fertile*’ (McSweeney, 2022), but the preservation of the specimen is poor, and the sporangial morphology is difficult to elucidate. It is for this reason that it will not be included in any further discussion of the *Z. fertile* described in this study.

Comparisons with other specimens of *Z. fertile*

The dimensions of the spikes in this study are similar to the dimensions of the Belgian holotype and have a similar overall sporangial morphology. The holotype is 30 mm in length and 3 mm in width, the fertile spikes in this study range from 13 – 39 mm in length and 1.1 – 3.6 mm in width (Table 4). The largest specimens of *Z. fertile* was collected from Scotland (Edwards, 1972), with a total spike length of 72 mm. This is over double the length of the holotype spike and double the length of the longest specimen described in this study. The Welsh specimens of *Z. fertile* have a spike length which falls between the variation in length of specimens collected in this study, 20 mm (Wellman, *et al.* 2000) and 10 mm (Edwards, 1969b) respectively.

Across all published collections of *Zosterophyllum fertile*, only a small number of specimens have been described from each locality. Leclercq (1942) based the original description on a single, incomplete specimen from Nonceveux, Belgium (holotype). Edwards (1969b) described one incomplete specimen from the Brecon Beacons Quarry

in South Wales and later, Edwards (1972) illustrated a single bifurcating fertile axis from Forfar, Scotland. Wellman et al. (2000) recorded one specimen from the Brynglas Tunnels in Newport, South Wales. In comparison, the present study describes seven specimens from Buchananhalvøya, Svalbard, increasing the total number of known *Z. fertile* specimens from four to eleven.

The width of the spikes of *Z. fertile* is similar across all places where it has been collected, ranging from 3 – 4.7 mm (Table 4). This is a reduction of 44% from the widest to the slenderest of specimens.

All of the spikes described in this study are terminal and borne on a single, unbranched axis. Most of the specimens of *Z. fertile* are organised in this manner, apart from *Z. fertile* described from Scotland (Edwards, 1972; *Figure 1*) and Wales (Edwards, 1969b). This Scottish specimen represents a bifurcating axis with two separate terminal spikes, one of which contains 17 sporangia and the other 11. There are also two sporangia which are inserted below the bifurcation, a phenomenon also found in one of the Welsh specimens (Edwards, 1969b).

The number of sporangia borne on single spikes of *Z. fertile* range from 8-18 (Table 4), with specimens in this study accounting for all the variation in sporangia number across all collections of *Z. fertile*. Although it must be noted that all specimens, including ones in this study, have been described as containing an incomplete spike, with only four spikes ‘basally complete’ containing an axis beneath the spike (Edwards, 1969b, Plate 1; Wellman, et al. 2000, Plate VIII; Edwards, 1972, Plate 1; this study, Text Figure 17). As a result, it is unclear as to how many sporangia would have made up a complete spike but the range of 8-18 sporangia is in keeping with the number found in other species of *Zosterophyllum* (Hao, et al. 2007; McSweeney, 2022).

The increased number of specimens in this assemblage allows for a better understanding of intraspecific variation within *Z. fertile*. The variation in spike length and sporangial spacing may reflect different developmental stages, with larger sporangia and wider spacing representing more mature portions of the spike. Comparable

positional changes in sporangial size have been noted in other zosterophylls (Edwards, 1972; Hao et al. 2007), suggesting that the differences observed here are more likely developmental than taxonomic.

The incomplete nature of most spikes described from all localities suggests that the fertile portions were particularly fragile and prone to breakage before burial. The consistent absence of the basal portion in both the Welsh and Svalbard material supports the idea that disarticulation occurred during transport or deposition, which is common in zosterophyll preservation (Edwards, 1969b; Wellman et al., 2000). This may also explain the limited number of fully preserved fertile axes recorded globally.

Taken together, the material described here confirms the presence of *Z. fertile* in low-latitude Laurussian settings and adds to our understanding of how its morphology and preservation vary within near-shore fluvial environments typical of the Lower Devonian of Svalbard.

One specimen in this study has larger sporangia and wider spacing, which may reflect a more mature portion of the fertile system, although no consistent basal-to-apical gradient in sporangial size is evident across the assemblage. These observations show that preservation, orientation and possible growth stage can influence the appearance of *Z. fertile*, and caution is therefore needed when comparing incomplete material or using sporangial size alone to define species differences.

It is for the similarity in overall sporangial morphology described above that all specimens described in this study are placed in the taxon *Z. fertile* Leclercq, 1942. This work provides an important contribution to the descriptive morphology of the species and increases the sample size of this taxon from four to eleven specimens.

Table 3. Sporangial features of selected *Zosterophyllum* species that are comparable to the material described in this study. The table includes species name, sporangial morphology, interpretative drawing, age, locality and relevant references.

Species	Sporangia features	Image	Age	Location	Reference
<i>Zosterophyllum myretonianum</i>	Lateral, reniform sporangia arranged in two row. Sporangial stalks are inserted at the base of sporangia. Sporangia width between 2.3 – 2.7 mm and 2.5 – 3.8 mm in length).		Lochkovian	Scotland, United Kingdom	Penhallow, 1892 Lang, 1927 Lele & Walton, 1961 Edwards, 1972
<i>Zosterophyllum australianum</i>	Transversely elliptical, large sporangia (< 3 mm in width). Very compact rows, sporangia overlapping.		Emsian	Yunnan, China	Lang & Cookson, 1930 Hao, 1992
<i>Zosterophyllum sinense</i>	Pear-shaped or fan-shaped in face view and fusiform to oval in in lateral view. Helically inserted sporangia 2.4–4.7 mm high and 2.5–3.2 mm wide		Pragian - Emsian	Guangxi, China	Li & Cai, 1977 Wang, 2018
<i>Zosterophyllum llanoveranum</i>	Reniform to almost circular shape of sporangia in face view. On average 4mm high and 3.5 mm wide.		Pragian-Emsian	South Wales, United Kingdom	Edwards, 1969a
<i>Zosterophyllum fertile</i>	Sporangia with a wide variety of preservation forms: oval or reniform most common. Inserted in two distinctive rows. Length 1.6 – 3.8 mm, width 1.6 – 2.8 mm.		Lochkovian	Belgium South Wales, United Kingdom	Leclercq, 1942 Edwards, 1969 Edwards, 1972

Name	Reference	Location collected	Age	Spike dimension		Spike characteristics	Sporangia shape	Sporangial dimensions		Sporangial insertion	Stalk dimensions	
				Length	Width			Length	Width		Length	Width
Z. fertile	Leclercq, 1942	Nonceveux, Belgium	Lochkovian	30 mm (incomplete)	3 mm	18 sporangia inserted in two rows	Elongate – reniform	2 mm	1.8 – 2 mm	Stalks inserted 90° to the axes and recurves 90° so sporangia are borne upright	1 – 1.3 mm	0.3 – 0.4 mm
Z. cf. fertile	Edwards, 1969b	Brecon Beacons Quarry, South Wales	Pragian	10 mm (incomplete)	3 mm	8 sporangia inserted in two rows	Irregular or indeterminate owing to preservation	1.7 – 2.5 mm	1.6 – 2 mm	Stalks inserted 90° to the axis and recurve 90° so sporangia are borne upright	1 mm	0.4 mm
Z. fertile	Edwards, 1972	Forfar, Scotland	Lochkovian	72 mm (incomplete)	3 mm	Fertile axis bifurcates, producing two spikes with a total of 30 sporangia inserted in two rows	Oval – reniform	2.5 – 3.8 mm	2.3 – 2.7 mm	Stalks inserted 90° to the axis and recurve 90° so sporangia are borne upright. Stalk is inserted at midline of the sporangia valve		
Z. cf. fertile	Wellman, <i>et al.</i> 2000	Brynglas tunnels, Newport, South Wales	Lochkovian	20 mm (incomplete)	3.5 mm	11 sporangia inserted in two rows	Reniform – oblate	1.6 – 2.8 mm	2.3 – 2.8 mm	Stalks inserted ~60° to the axis and recurves 90°	1.8 mm	0.4 mm
Z. fertile	This study	Buchananhalvøya, Svalbard, Norway	Lochkovian	11 – 36 (?incomplete)	3.2 – 4.7 mm	8 – 18 sporangia inserted in two rows	Oval, but variable owing to preservation (see section 2.2.3.4.1)	1.5 – 3.7 mm	1.5 – 3.7 mm	Stalks inserted 90° to the axis and recurve 90° so sporangia are borne upright. In some specimens, stalks are inserted at the midline of the sporangia valve.	1.5 – 2.9 mm	0.2 – 1 mm

Table 4: Comparative table of features found in *Z. fertile* collected from the Lower Devonian of Belgium, Wales, Scotland and Norway. Includes details of taxonomic determinations, papers references, collection locations, age of specimen, dimensions of spike, characteristics of spike, shape of sporangia, dimensions of sporangia, insertion of sporangia relative to the stalk and dimensions of the sporangial stalk.

2.2.2 Frænkelryggen assemblage

Description of Collected Material

The new material described here consists of 34 slabs from the Lochkovian Frænkelryggen locality of the Frænkelryggen Formation, Red Bay Group, north-west Spitsbergen. The collection includes material from three separate sub-localities, as documented in Table 1. The first sub-locality, FR-A, yielded 22 slabs; FR-B yielded eight slabs; and FR-C yielded four slabs. The largest slab, FR-B-02, measures 195 mm in length and 115 mm in width. FR-B-08 is the best-preserved slab and contains a range of plant remains, from small axis fragments to larger carbonised masses (Text Figure 19).

All remains are preserved as highly coalified compressions. The assemblage also includes fragmentary fish remains, consistent with previous reports from the Red Bay Group that have contributed to dating of the strata (Blieck & Heintz, 1983; Ilyes et al., 1995). Plant preservation varies from poor to moderate, and in the most poorly preserved specimens taxonomic identification is not possible.

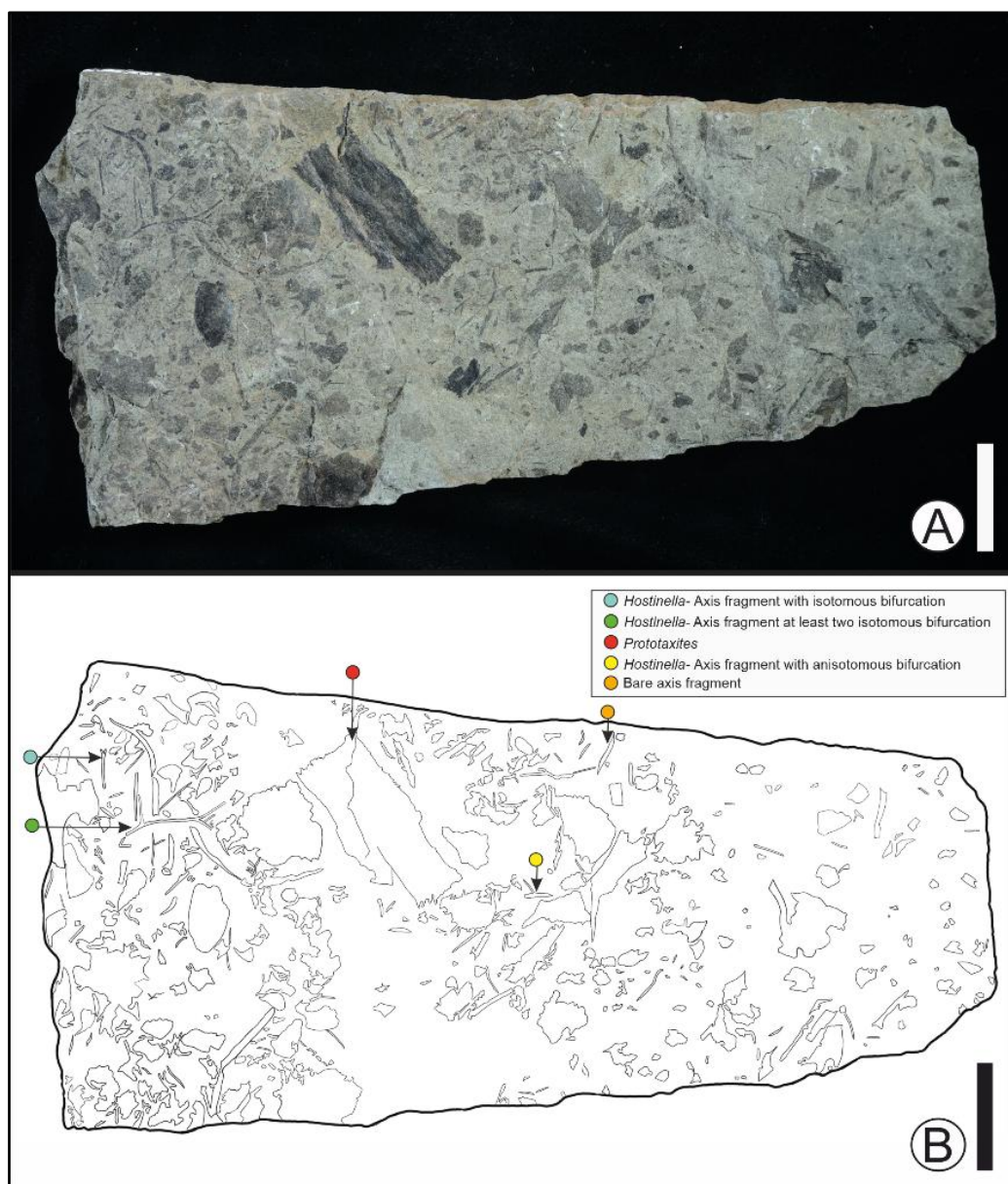
Because much of the Frænkelryggen material is fragmentary, sterile and poorly preserved, taxonomic assignments are used cautiously throughout this section. Where axes are bifurcating but lack reproductive organs or other diagnostic features, they are referred to the morphotaxon *Hostinella*. Unbranched sterile axes are treated as indeterminate axes rather than assigned to *Zosterophyllum*. Larger carbonised fragments and irregular carbonised masses are treated separately, as their relationship to *Prototaxites* or vascular plant axes cannot be demonstrated confidently. The names used in the headings therefore reflect the most conservative interpretation of the material rather than firm biological affinity.

The assemblage includes numerous small sterile axes, several bifurcating axes referred to *Hostinella*, at least two specimens of *Pachytheca*, larger carbonised fragments of uncertain affinity, irregular black carbonised material, and several isolated sporangia-like bodies. The total number and types of fossils found at this locality are presented in Table 5.

Bifurcating sterile axes: *Hostinella* sp.

The majority of plant remains collected from Frænkelryggen are small, fragmentary and mostly indeterminate (Plate 5). No sporangia or other reproductive structures are attached to the axis fragments, and many of the axes are extremely small, with some less than 1 mm wide. Some fragments show clear bifurcation, but preservation is often too poor to determine confidently whether the branching is isotomous or anisotomous. Because these remains lack diagnostic reproductive or anatomical features, the bifurcating sterile axes are referred to the morphotaxon *Hostinella*. This assignment is used here in a descriptive sense for sterile bifurcating axes and does not imply a secure biological affinity.

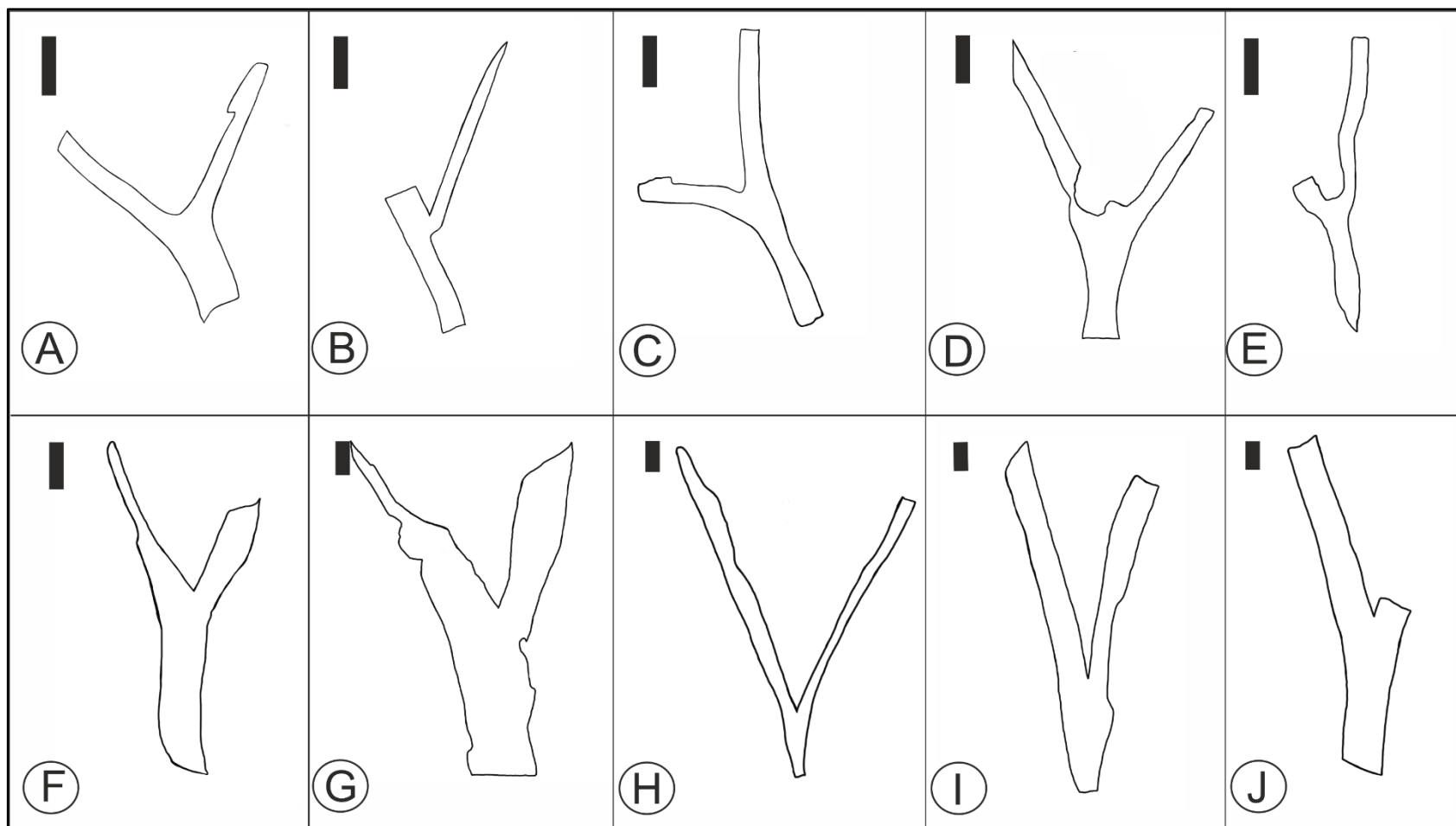
The length of these remains varies from 3-77mm, average 19mm (N=239). Axis width ranges from between 0.2 – 5.8 mm, average 1.5 mm (N= 103). Some of the axes are over 40mm long without bifurcation. Others are short but show a clear dichotomy. There is one axis fragment with at least two dichotomies along its length (Text Figure 21).



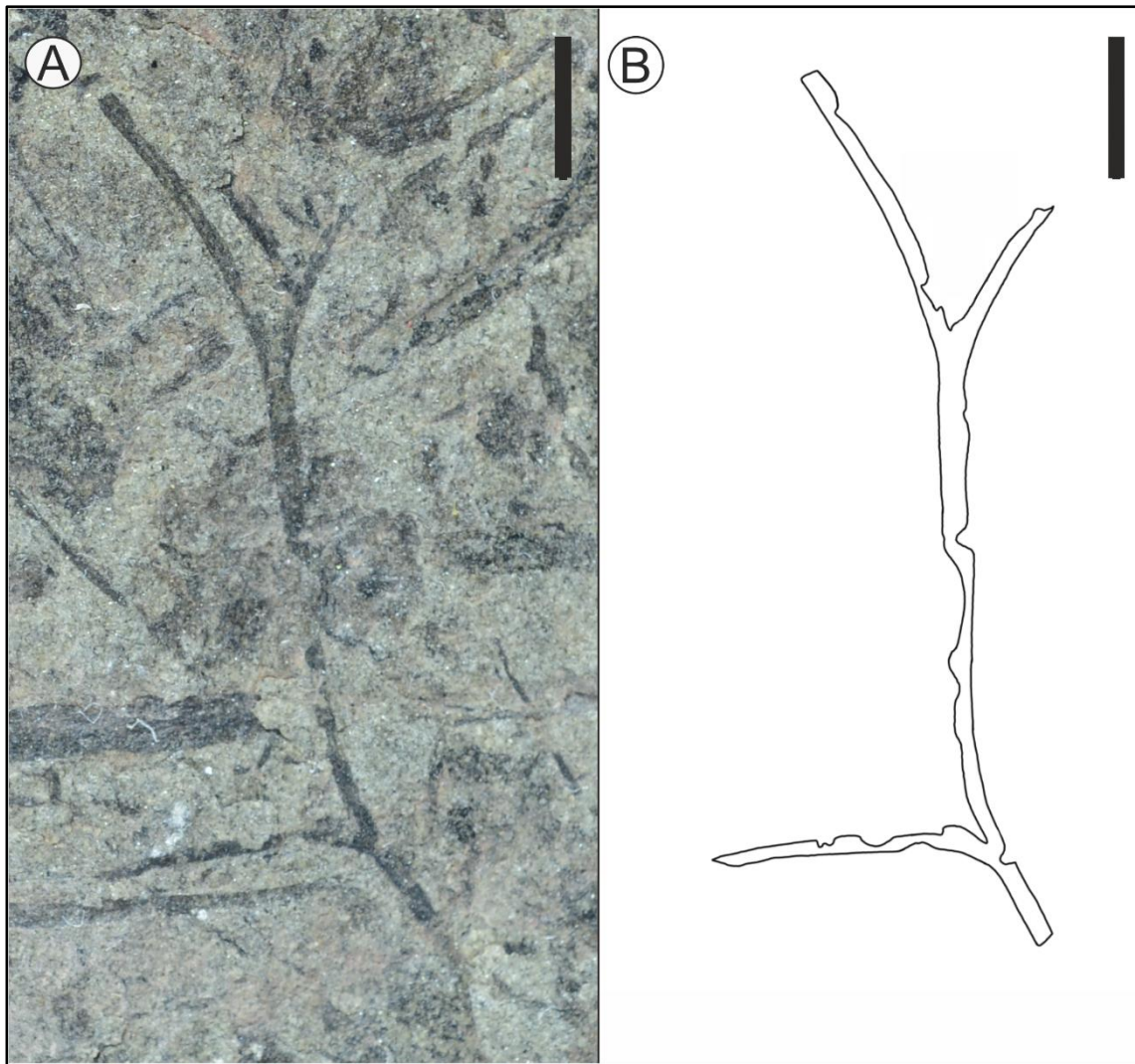
Text Figure 19. Plant megafossil assemblage, FR-B-08, Frænkelryggen, Andréebreen Fm. A. Macrophotograph of the most diverse set of megafossil remains from Frænkelryggen. B. A camera LUCIDA drawing of the assemblage at FR-B-08, enhanced with ProCreate for iPad. Scale bar is 30 mm.

Locality	Axes Fragment		Dichotomising Axis		Small axis (<1mm wide)	Large axis (>5mm wide)	Sporangia	<i>Prototaxites</i>	<i>Pachythea</i>
	Dichotomising	Single	Anisotomous	Isotomous			Isolated		
Frænkelryggen A	15	19	4	12	5	3	7	18	3
Frænkelryggen B	7	6	3	6	7	1	0	7	2
Frænkelryggen C	3	1	0	0	1	1	0	4	0

Table 5. A breakdown of all the characters found in the plant assemblage of the Frænkelryggen locality (FR-A, FR-B, FR-C).



Text Figure 20. Camera LUCIDA drawings of *Hostinella* axis fragments, Frænkelryggen. Enhanced with ProCreate for iPad **A.** Isotomous axis (FR-B-08). **B.** Anisotomous axis (FR-B-08). **C.** Isotomous axis (FR-B-08). **D.** Isotomous axis (FR-B-08). **E.** Anisotomous axis (FR-B-03). **F.** Anisotomous axis (FR-B-02). **F.** Isotomous axis (FR-B-02). **G.** Isotomous axis (FR-A-12). **H.** Anisotomous axis (FR-A-12). **I.** Isotomous axis (FR-A-10). Scale bar in all is 1mm.



Text Figure 21. Dichotomous axis fragment, Frænkelyggen. **A.** Macrophotograph (FR-B-08). **B.** A camera LUCIDA drawing of the same axis fragment, enhanced with ProCreate for iPad. Scale bar is 5mm.

Large Axis Fragments

From the three localities at Frænkelyggen, 8 slabs have distinctive, large (>5mm wide) carbonized material with well-defined margins that form an axis (Plate 6). It is unclear whether these fragments are plant remains or belong to *Prototaxites*, but the lack of distinctive features makes correct identification difficult. I refer to this material as axis fragments.

The remains varied between 23-101 mm in length, 58.5 mm on average (N=10). The width varied from 5.1-35 mm, with an average width of 14.3 mm (N=10). The most

well preserved large fragmentary axis (FR-B-08) was 52mm in length and 25.1mm in width (Plate 6A) with a distinctive three dimensional structure that displayed clear longitudinal striations. Although visible to the naked eye, these striations are difficult to photograph due to the highly coalified material. These longitudinal striations are present in other large axis fragments (Plate 6B-G) but due to the poor preservation they are much more difficult to see. In one of these axes, horizontal striations occur across the length of the axis (Plate 6G, upper).

Black, Carbonised, Indeterminate Material

In most of the slabs collected at Frænkelyggen (30/35), there are black, carbonised indeterminate masses (BCIM) scattered across the slab, which appears to be highly compressed (Plate 7A, White Arrows). There is no distinctive shape or structure and the area varies greatly, from small, scattered fragments $<9\text{mm}^2$ (Plate 7A white arrows) to much larger fragments which cover the entire surface of a slab $>5000\text{mm}^2$ (Plate 7B). The preservation varies, from very dark material that is easy to distinguish from the matrix (Plate 7D), to material that is much lighter in colour that is difficult to differentiate from the matrix (Plate 7C).

These BCIMs can be distinguished from the large axis fragments described in 1.2 because they have no distinctive margins to define the outer portion of the axis and don't have clear longitudinal striations. Whilst in some slabs there are fish remains that have been preserved these BCIMs show no evidence of fish scales or features associated with the preservation of fish.

In some specimens, there are circular impressions that either show up as a raised circular mark or a depressed indentation in the (Plate 7E- white arrows). These are only found in four specimens (FR-B-03, FR-B-07, FR-A-10, FR-A-14). The circular indentations are randomly distributed across the surface. Under a high powered microscope, undulations in the compressed carbon is sometimes observed which is often cracked or deformed in places where it is raised.

Pachythea sp.

In four slabs from two sub-localities (FR-A, FR-B), *Pachythea* is present. There are a small number of other occurrences that could possibly belong to *Pachythea*,

however the specimens are so poorly preserved that the typical features of *Pachythea* cannot be distinguished. For this reason I omit them from analysis. In the specimens positively identified as *Pachythea*, the preservation varies. Two of the specimens are very poorly preserved (FR-A-08, FR-A-10), two are relatively poorly preserved (FR-A-07, FR-B-03) and one is relatively well preserved (FR-B-08).

The two most poorly preserved specimens have a distorted (FR-A-08, FR-A-10), oval shape and part of the outer cortex has degraded, been destroyed or is not preserved (Text Figure 22A, B). The two specimens which have slightly better preservation (FR-A-07, FR-B-03) are also spherical, however the shape less distorted (Text Figure 22C, D).

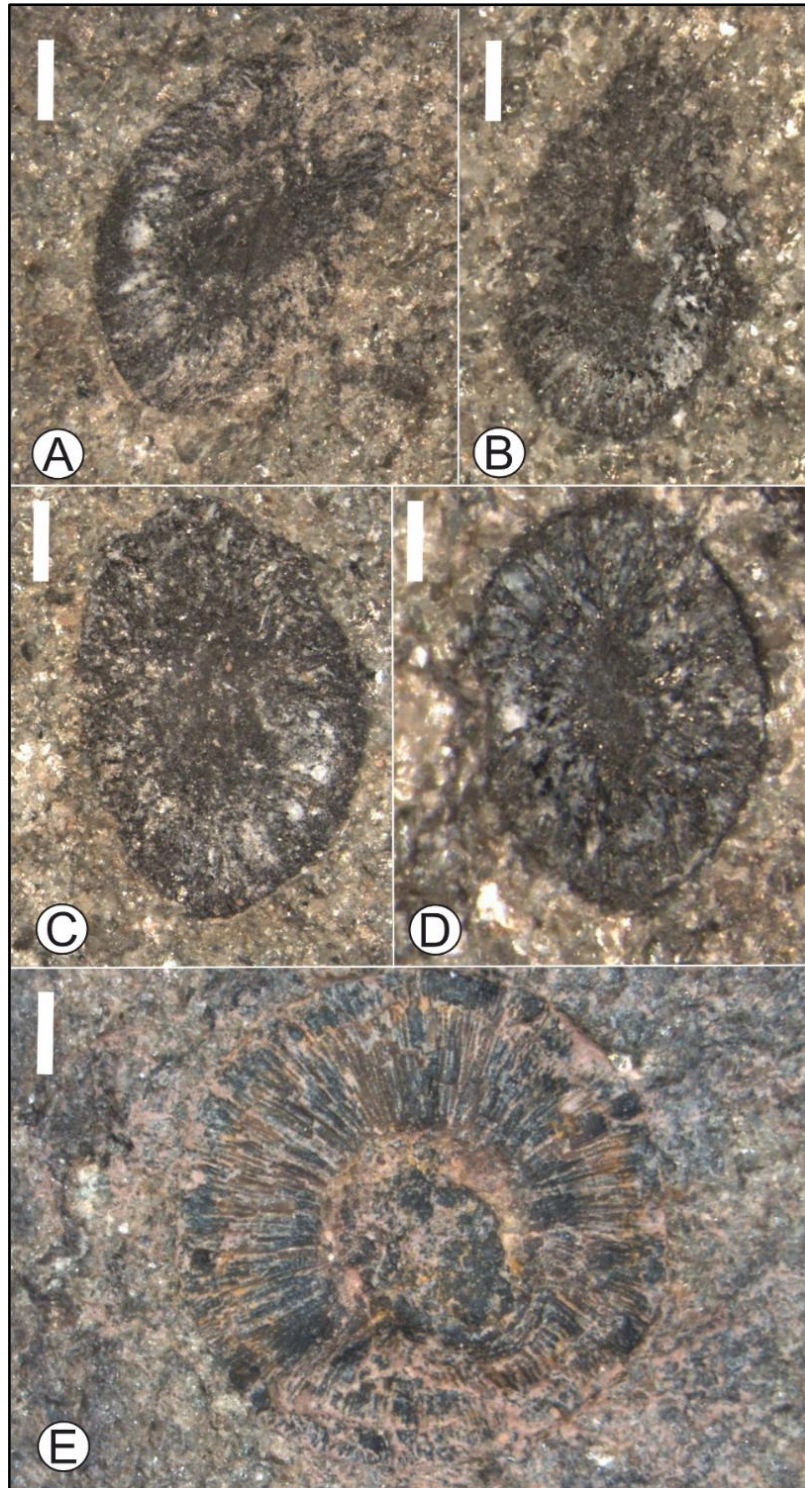
The best-preserved specimen is FR-B-08, which is approximately spherical in form and shows a well-defined outer cortical region (Text Figure 22E). The medulla is less clearly delimited, but remains visible. A small number of filaments can be identified within this region (N = 5), ranging from 63–95 μm in width, with a mean of 77 μm . Their preserved length could not be determined reliably. By contrast, the cortical region contains well-defined filaments extending from the medulla to the ensheathing layer. The average length of these cortical filaments, measured from the medulla to the ensheathing layer, is 0.89 mm (N = 48). The cortex is consistently more clearly preserved than the medulla in these coalified specimens, which may reflect

Specimen	Shape	Length	Width	Medulla Width	Medulla Height*	Ensheathing Layer width	Cortex Depth
FR-A-07	Oval	3.5	2.17	0.87	1.19	0.05	1.42
FR-A-10	Oval	3	1.77	0.76	1.1	N/A	0.59
FR-B-03	Oval	1.45	0.95	0.3	0.46	0.04	0.44
FR-B-08 (1)	Spherical	4.23	4.39	1.65	1.69	0.25	1.04
FR-A-08 (2)	Oval	3.57	2.52	1.39	1.3	N/A	0.81

Table 6. Measurements of *Pachythea* specimens from Frænkelryggen. All measurements are in mm. Apparent medulla dimensions vary according to specimen orientation and plane of fracture; medulla height should therefore be treated with caution.

differential preservation of the two regions. It is possible that the cortical filaments were originally surrounded by a mucilaginous coating, enhancing their preservation relative to the medullary region, although this interpretation remains tentative. The width of these filaments within the cortex varies from between 17-68 μm , average 37 μm (N =55).

Critical dimensions of the *Pachythea* specimens are given in Table 6. The relative proportions of the medulla and cortex vary among specimens, with some showing a broader apparent cortical zone and others a broader apparent medullary region. However, these differences should be treated cautiously, as the specimens are compressed and fractured, and the observed dimensions are likely to be influenced by orientation and plane of fracture rather than reflecting directly comparable medial sections.



Text Figure 22. Five specimens of *Pachytheca* sp. from Frænkelyggen. A, poorly preserved specimen in which part of the outer cortex has degraded during preservation, FR-B-08(2). B, poorly preserved specimen in which the cortex has degraded in the apical portion, FR-A-10. C, moderately preserved specimen, FR-A-07. D, moderately preserved specimen in which the outer ensheathing layer is clearly visible as a thick black band around the external portion, FR-B-03. E, best-preserved specimen; the medullary region, cortical region and outer ensheathing layer are clearly visible, FR-B-08(1). Scale bar in all = 1 mm.

Sporangia-like bodies

Five specimens from two sub-localities, FR-A and FR-B, contain isolated sporangia-like or reproductive bodies (FR-A-09, FR-A-11, FR-A-12, FR-A-14 and FR-B-03).

Three occur without any associated axis (FR-A-09; Plate 8A, B, E), one specimen contains a pair of adjacent bodies (FR-A-11; Plate 8C), one occurs close to an axis but without demonstrable attachment (FR-A-12; Plate 8G), one has a possible stalk-like extension (FR-A-14; Plate 8D), and one forms a three-dimensional ovate body protruding from the matrix (FR-B-03; Plate 8F). Preservation is variable and none of these specimens preserves enough detail for confident taxonomic assignment. They are therefore described here as sporangia-like bodies rather than assigned to a genus.

Preservation varies between specimens, and there is not enough detail for confident identification. Their size and ovate to globose outline are broadly comparable with some zosterophyll sporangia, but the absence of clear attachment, dehiscence features and diagnostic axes prevents confident assignment.

There were three separate sporangia on specimen FR-A-09. Sporangia S1 was the best preserved (Table 7) and comprises an oval impression. Inside, the coalified material, which makes up the sporangial wall, is cracked and slightly deformed (Plate 8A). The sporangium is ovate, 3.8 mm long, 2.5 mm wide. S3 (Plate 8B) has a similar overall morphology. The sporangium protrudes out of the rock matrix to form a positive, three dimensional structure. The preservation is moderate and the overall length is 3.95 mm and 3.0 mm wide. The third sporangium (S3) (Plate 8E) is permineralized and has a distinctive orange colour as compared with the coalified black of the other sporangia. This example is ovate, 3.95 mm in length by 2.45 mm maximum width.

In FR-A-11, a pair of sporangia was found situated next to one another, but not in association with any axis (Table 7, Plate 8C). Preservation is relatively poor, which makes identification of the shape and exact measurement difficult. A faint outline of the sporangial walls has been used to determine size. The sporangia are ovate-globose and measure 4.55 mm and 3.7 mm in length and 3.5 mm and 3.1 mm width, respectively.

The sporangium in FR-A-12 is relatively poorly preserved (S5, Table 7). There is an axis (Plate 8G - white arrow), however the lack of preservation and absence of any stalk from the axis to the sporangium make it difficult to prove association. The sporangium is ovate, 3.7 mm long and 2.3 mm wide. In the centre left there appears to be a large cavity which extends into the matrix. This could potentially be the site of attachment for a stalk.

The sporangium found in FR-A-14 is poorly preserved (S6, Plate 8D). Only the lower portion has been suitably preserved, but suggests that the shape is ovate. The sporangium is 3.5 mm length and 2.7 mm. On the lower portion there is a thin protrusion measuring 1.3 mm in length which emerges from the sporangia wall (Plate 8D). This could be a sporangial stalk which attaches to an axis, however the lack of any associated axis and the poor preservation of this structure make it impossible to say for certain.

The final sporangium (S8, specimen FR-B-03 - Plate 8F) is ovate and protrudes from the rock matrix to form a three dimensional structure. It has less round edges than S3 is very similar in size. The length is 3.8 mm, width 2.9 mm.

Identification	Specimen	Plate	Shape	Length(mm)	Width(mm)
Black cracked sporangia (S1)	FR-A-09	8A	Ovate	3.84	2.51
Orange, permineralized sporangia (S2)	FR-A-09	8E	Ovate - Globose	3.95	3.03
Black, 3D sporangia (S3)	FR-A-09	8B	Ovate	3.79	2.45
Double sporangia (S4)	FR-A-11	8C	Ovate - Globose	4.5	3.47
Possible sporangia with axis (S5)	FR-A-12	8G	Ovate	3.7	2.31
Possible sporangia with stalk (S6)	FR-A-14	8D	Ovate	3.48	2.7
Black, 3D sporangia 2 (S7)	FR-B-03	8F	Ovate	3.81	2.94

Table 7. Measurements of the sporangia from Frænkelryggen.

Discussion

Identity of Material and Comparison to other Frænkelryggen Collections

The first expedition to mention the 'Frænkelryggen' locality was an expedition to the North of Spitsbergen led by Isachsen, Hoel and Holtdahl in 1909 to collect Devonian fish (Stensio, 1918). The first palaeobotanical expedition to the Frænkelryggen locality was in 1928, led by Thorolf Vogt. This expedition led to the discovery of a plant bearing horizon in the Frænkelryggen by Strand and Størmer. Høeg described these plants (Høeg, 1942) and the same species were subsequently re-analysed by Schweitzer (1999). Taxonomic history is detailed in Table 2.

Hostinella sp.

The plant remains described are highly fragmented, incomplete and often preserved poorly, similar to those described by Høeg (1942). I have referred the small fragmentary axes that display bifurcations to the morphotaxon *Hostinella*.

Small, Indeterminate Axis Fragments

A variety of unornamented, unbranched axis fragments, some extremely narrow at less than 1 mm wide, cannot be placed in *Hostinella* because they lack bifurcation (Plate 5B–D, F, G). Høeg (1942) placed some comparable axes in *Zosterophyllum*, but Schweitzer (1999) later treated them as indeterminate axis fragments. I follow Schweitzer's interpretation here. Although some fragments may resemble zosterophyll axes, they lack attached sporangia, diagnostic branching systems or other features that would allow confident assignment to *Zosterophyllum*. They are therefore treated as indeterminate sterile axes.

Large Axis Fragments

Prototaxites remains are often reported as relatively indeterminate, black, carbonaceous masses of a relatively large size. They often have longitudinal striations or ridges, which have been assumed to represent the longitudinally orientated tubular matrix that makes

up the organism (Burgess & Edwards, 1988; Hueber, 2001; Edwards & Axe, 2011; Retallack, 2019).

In specimens collected from Frænkelryggen labelled 'Large Axes Fragments', there are clearly defined longitudinal striations which match those previously reported in *Prototaxites* (Plate 6A-G). The striations are most visible in specimen FR-B-08 (Plate 6A) and the specimen itself is preserved in three dimensions, so much so that you can see the rounded impression of the axis near the top (Plate 6A). Similar fragmentary remains that are highly coalified, three dimensionally preserved with rounded edges have often attributed to *Prototaxites* (Burgess & Edwards, 1988).

However, some of these fragments have clearly defined margins on both sides of the remains (Plate 6A, E–G), closely resembling the clean edges seen in highly carbonised compressed plant axes. These distinctive margins suggest that the fragments may represent discrete plant units that have been broken along a horizontal plane while retaining their full original width. However, this form may also be indicative of transport and fragmentation prior to burial, and caution is therefore needed in inferring the original morphology of the organism from these remains alone.

Although some specimens referred to *Prototaxites* have been interpreted as very large, trunk-like organisms (Hueber, 2001; Graham et al., 2010; Hobbie & Boyce, 2010), the Frænkelryggen material consists only of small fragmentary remains. It is therefore not possible to infer confidently whether these fragments derive from large individuals, small individuals, or particular regions of the parent organism. Branching has occasionally been reported in *Prototaxites* (Bahafzallah, 1981; Schweitzer, 1983; Retallack & Landing, 2013), although the interpretation of such structures remains controversial, particularly where supposed lateral branches are reconstructed from scars on otherwise unbranched axes.

Nonetheless, there is only a vague similarity between the remains described here and those attributed to *Prototaxites*. The parallel tubes which are often present in *Prototaxites* (Høeg, 1942, Plate IV. This text: Text Figure 2I-K) are not present or have not been preserved adequately. There are only vertical striations down the length of the

axis which do not display any recognisable three-dimensional structure. There is also a distinctive lack of features present for identification of these large axis fragments in the wider plant kingdom, so these remains will be attributed to *Incertae sedis* until the broader relationship of this taxon is elucidated.

Black, indeterminate carbonised mass

Highly compressed, carbonised material is scattered amongst the other fragmentary remains (Plate 7). There is no defined shape or size and there is a large variance in size. Remains similar to these have often hastily been applied to the genus *Prototaxites* (Burgess & Edwards, 1988), but unlike the remains discussed above (Section 2.3.2.4), these fragments of 'BCIM' do not have any longitudinal striations or parallel tubes typical of *Prototaxites*. Davies *et al.* (2021) attributes 'dark flecks of carbonaceous material between 1-5mm across' to the term 'comminuted debris' where taxonomic identification is not possible.

The only defining features of these structures is that they occasionally have circular impressions on the surface (Plate 6E, white arrows) which can either be indented or raised.

A wide diversity of fish remains have been collected from Frænkelryggen, including *Dinaspidae*, *Poraspis* spp, *Anglaspis*, *Phialaspis*, *Cephalaspis* spp, *Securiaspis* and *Ectinaspis*, (Kiær, 1932, Føyn & Heintz, 1943; Wängsjö 1952). At least some of the fragments of carbonised material may in part belong to fish remains, owing to the wide diversity of fish taxa which have been previously collected from here. I have identified fish remains within the slabs. These fish remains were clearly identifiable, owing to the 'bubbled' or 'raised' texture of fish plates. It's possible that at least some of these BCIM are the remains of very poorly preserved fish that were perhaps preserved in a very late state of decomposition

Pachytheca

Pachytheca is known from the Upper Silurian to the Early Devonian deposits from Western Europe, Canada and Australia (Hooker, 1889; Høeg, 1942; 1976; Abbott *et al.*,

1998). They have been described as small (1-6mm), spherical globular bodies with clearly defined tissue layers (Croft & Lang, 1942). Only one of the *Pachytheca* specimens found at Frænkelryggen (FR-B-08, Text Figure 22E) is well enough preserved to compare to other studied specimens.

Kidston & Lang (1924) described differences between the medullary and cortical regions of *Pachytheca*, including variation in filament dimensions and organisation. In the Frænkelryggen material, the cortex is more clearly preserved than the medullary region. Cortical filaments can be traced from the medulla towards the ensheathing layer and are generally narrower than the few filaments observed in the medulla. This difference may reflect original tissue organisation, but it may also be affected by compression, fracture plane and differential preservation. The clearer preservation of the cortex may indicate that the cortical filaments were originally surrounded by a mucilaginous coating, although this remains tentative.

Isolated Sporangia

Two of the sublocalities at Frænkelryggen (FR-A, FR-B) yielded seven potential sporangia (Plate 8). Unfortunately, the sporangia were preserved in isolation, only one has an axis potentially associated with it (Plate 8G) and this specimen is so poorly preserved that it is impossible to say for certain that the two structures are definitely associated.

The overall size and morphology of the sporangia are reminiscent of sporangia of *Zosterophyllum*, which can often be circular, ovoid or discoid in shape (Kenrick & Edwards, 1988; Hueber, 1992; Kotyk & Basinger, 2000; Jensen & Gensel, 2013). There is one specimen (FR-A-11, Plate 6C) where a pair of partially exposed sporangia have been preserved, albeit relatively poorly. A paired arrangement could be consistent with a zosterophyllalean affinity, but this remains uncertain because no subtending axis or clear attachment is preserved.

The size and ovate to globose shape of these bodies are broadly comparable with some zosterophyll sporangia, but the absence of clear attachment, dehiscence features and

diagnostic axes prevents confident assignment. Some may represent isolated reproductive structures, but alternative interpretations, including distorted or tightly coiled axes preserved at particular angles, cannot be excluded. For this reason, they are treated here as isolated sporangia-like bodies of uncertain affinity.

Drepanophycus, a genus of early lycopsids, have a similar circular-elliptical sporangial morphology (Li & Edwards, 1995), and have been collected from Lower Devonian deposits elsewhere, including Belgium (Fairon-Demaret, 1978), Luxembourg (Delsate, *et al.* 2003), China (Li & Edwards, 1995), Scotland (Rayner, 1984) and Canada (Hartman, 1981). However, no remains collected from this locality bear any resemblance to the easily identifiable *Drepanophycus* axis. The incomplete, fragmentary remains of axes collected could be attributed to the zosterophylls, specifically those species that have bare axes without any emergences or spines. However, without the presence of key zosterophyll features such as K or H branching, or spikes, it is impossible to say for certain.

Comparison with other Lochkovian Assemblages

The plant remains collected from this locality are incomplete, highly fragmented and largely indeterminate. This is unsurprising, given that the Frænkelryggen locality has been interpreted as representing braided alluvial floodplains. This type of depositional setting commonly results in highly fragmented plant remains. The fact that delicate material has been preserved at all suggests that the energy of the floodplain system was not especially high, that transport distances were relatively short, and thus that the remains were probably parautochthonous, or alternatively that some of the preserved plant material was relatively resistant to decay and breakage (Davies *et al.*, 2021). An interesting diversity of axes, including very small axes, hints at a greater floristic diversity, but the lack of connected fertile structures prevents more confident interpretation.

Only a small number of Lochkovian plant assemblages are available for comparison with Frænkelryggen, and in many of these the flora is preserved in lithologies and taphonomic settings more favourable to taxonomic resolution. In the Anglo-Welsh Basin,

Lochkovian floras occur in a range of continental to marine settings, including near-shore and shelf deposits, and are preserved in sandstone- and siltstone-hosted assemblages as coalified compressions and impressions; in some cases, charcoalfied mesofossils also preserve much finer anatomical detail (Edwards and Richardson, 2004; Morris and Edwards, 2014). Likewise, the Lochkovian flora of the Baviaanskloof Formation of South Africa was recovered from plant-bearing lenses and includes many complete or near-complete specimens, allowing identification to lower taxonomic levels (Gess and Prestianni, 2021). The Xitun flora of Yunnan is similarly represented by a diagnosable Lochkovian megafossil assemblage from the Xitun Formation (Xue, 2012). By contrast, the Frænkelryggen flora is preserved primarily as highly coalified, flattened and fragmentary compressions from shale- and sandstone-associated horizons, which greatly limits identification below morphotaxa. The apparently low diversity of the Frænkelryggen assemblage may therefore reflect preservational and lithological bias as much as genuine floristic impoverishment (Edwards and Richardson, 2004; Morris and Edwards, 2014; Gess and Prestianni, 2021; Xue, 2012).

2.3 Wood Bay Formation (Pragian/Emsian)

Stratigraphy and brief history of field work

The Wood Bay Formation forms the most extensive and intensively studied Devonian succession in northern Spitsbergen (Friend, 1961; Friend, 1966; Gee & Moody-Stuart, 1966; Friend & Moody-Stuart, 1970; Pernègre & Blicek, 2016; Davies et al., 2021). First defined by Høltedahl (1914), it represents the earliest Old Red Sandstone (ORS) unit to be formally described from Svalbard. Together with the Grey Hoek and Wijde Bay formations and the Mimerdalen Subgroup, it makes up the Andrée Land Group, which dominates much of northern Spitsbergen. The Andrée Land, Red Bay and Siktefjellet groups collectively comprise the Liefdefjorden Supergroup (ORS), which encompasses the Devonian basin across the archipelago (Harland 1974).

The formation extends over roughly 150 × 75 km and reaches a maximum thickness of around 3 km, making it the thickest Devonian succession in Svalbard (Friend & Moody-Stuart 1972). Its age is constrained to the Pragian–Emsian interval based on marine and terrestrial biostratigraphic evidence, including graptolites, conodonts, vertebrates, and palynomorphs (Friend 1966; Blomeier *et al.* 2003; Pernègre 2004; Pernègre & Goujet 2007; Pernègre & Blicek 2016).

Early work subdivided the succession into three faunal zones: Kapp Kjeldsen, Lykta and Stjørdalen, based on vertebrate assemblages (Føyn & Heintz 1943). Later stratigraphic studies identified inconsistencies between faunal and lithological boundaries (Friend, 1961), prompting several revisions before the integration of lithological and biostratigraphical data led to the three-fold division used today: the Austfjorden (lower), Dicksonfjorden (middle) and Verdalen (upper) members (Ørvig, 1969; Allen, 1973; Murašov & Mokin, 1979). Detailed sedimentological sections were later measured by Cambridge University expeditions, which also collected extensive vertebrate assemblages forming the basis of three informal time–rock divisions (Friend & Moody-Stuart, 1972). In 1939, two concurrent expeditions, the English–Norwegian–Scottish (ENS) Expedition collected fossil plants and vertebrates from Wood Bay and

surrounding areas. More recent fieldwork by Wellman *et al.* (2022) added new palaeobotanical and sedimentological material from Austfjorden.

Lithostratigraphy and sedimentary characteristics

The Wood Bay Formation records a progressive transition from semi-arid alluvial plains to more lacustrine and deltaic environments, reflecting a major phase in the progradation of the Old Red Sandstone basin across northern Laurussia (Friend & Moody-Stuart, 1970; Harland, 1997; Davies *et al.*, 2021). The succession comprises interbedded red, brown and green sandstones, siltstones and mudstones, locally containing calcareous or ferruginous nodules that formed under oxidising floodplain conditions (Friend, 1966; Pernègre & Blieck, 2016).

The lower Austfjorden Member is dominated by fine- to medium-grained sandstones with ripple marks, cross-bedding, mudcracks and thin siltstone partings, representing ephemeral fluvial channels and overbank deposits. The overlying Dicksonfjorden Member becomes more heterolithic, consisting of alternating grey siltstones, shales and fine sandstones that reflect meandering fluvial systems with floodplain lakes, crevasse splays and palaeosols (Friend & Moody-Stuart, 1970; Davies *et al.*, 2021). The upper Verdal Member comprises coarser, oxidised sandstones and conglomerates deposited by higher-energy, probably braided channels. Together, these members display upward-coarsening cycles generated by repeated avulsion and channel progradation, characteristic of continental Old Red Sandstone basins (Friend, 1966; Davies *et al.*, 2021).

Palaeoenvironmental and palaeogeographic context

During the Early Devonian, northern Spitsbergen occupied a near-equatorial position on the margin of Laurussia (Torsvik & Cocks, 2017; Wellman *et al.*, 2022), in agreement with broader Early Devonian palaeophytogeographic reconstructions. However, this low-latitude position does not necessarily indicate a humid tropical climate.

Sedimentological evidence suggests that the Red Bay and Wood Bay successions were deposited under seasonally dry to semi-arid conditions, with vegetation occupying intermittently wet floodplains, shallow channels and lake-margin settings (Boucot *et al.*,

2013; Davies et al., 2021). Despite this equatorial position, both megafossil and palynological records indicate a flora of relatively low diversity (Wellman et al., 2022). The Red Bay and Wood Bay successions therefore preserve some of the earliest low-latitude terrestrial ecosystems of the Old Red Sandstone continent.

Sedimentological evidence points to vegetated but weakly stabilised floodplains with shallow, ephemeral channels and lakes, lacking the deep rooting or bioturbation typical of younger, mid-Devonian deposits (Davies et al., 2021). The Wood Bay Formation therefore represents a thick, laterally extensive continental succession deposited in an equatorial, semi-arid fluvio-lacustrine setting. It marks the first significant expansion of terrestrial vegetation in Svalbard and provides the geological context for the Lower Devonian floras described below.

Description of Previously Reported Taxa

The Wood Bay Formation has been described previously by Nathorst (1884, 1894) and Høeg (1942), both of whom recorded a small number of fragmentary plant remains from northern Spitsbergen. These include indeterminate axes and petiole-like compressions from the west side of Klaas Billen Bay (Billefjorden) and Mimer Valley, and zosterophyll and rhyniophytoid axes from Buchananhalvøya and adjacent areas. Despite extensive collections made by several expeditions, few taxa were recognised, and most remains are too incomplete for confident identification.

Indeterminate leaf-stalk-like remains

Nathorst, 1894, Taf. I, Fig. 1–11; Taf. II, Fig. 5.

Nathorst described several indeterminate axis fragments from the west side of Klaas Billen Bay associated with *Porolepis* and *Leperditia isochiinooides*. The specimens vary from smooth axes to irregular spindle-shaped fragments with faint secondary projections. Although compared to *Psilophyton robustius*, Nathorst considered them to be fern petioles or fern spindle-like remains. The material represents a mixture of axes comparable to those referred to *Psilophyrites* and *Aphylopteris*

Indeterminate impressions

Nathorst, 1894, Taf. II, Fig. 3.

Collected from Mimer Valley, these wedge-shaped impressions with radiating grooves were compared to *Psilophyton*-like twigs. They lack diagnostic features and are regarded as indeterminate.

***Cyclopteris* sp. (Upper Devonian)**

Nathorst, 1894, Taf. I, Fig. 12.

A large, fan-shaped leaflet originally described as *Cyclopteris* sp. from the west side of Billefjorden was later shown by Stensiö (1918) to derive from Upper Devonian fish-bearing beds at Mimerdalen. It is therefore excluded from the Lower Devonian assemblage.

Unpublished Nathorst material

Unpublished specimens housed in the Swedish Museum of Natural History (Stockholm) contain additional compressions from the same localities. These are treated separately (see Section appendix).

***Hostinella strictissima* Høeg 1942**

Høeg, 1942, Pl. XX, figs. 1–4.

Slender, axes with small transverse ribs and possibly slightly anisotomous branching were described by Høeg as *Hostinella* (*Hostimella*) *strictissima*. The material is incomplete and probably represents indeterminate vegetative axes, although the characteristics are recognisable. West side Billefjorden.

***Hostinella* sp. Høeg, 1942**

Høeg, 1942, Pl. XIX, figs. 6–7.

Høeg described a slender, dichotomously branching axis with small axillary swellings, comparable to *Hostinella* from other Old Red Sandstone floras.

Bucheria longa Høeg 1942 (= Zosterophyllum longum)

Høeg 1942, Pl. XIX, figs. 8–9.

Originally described as *Bucheria longa* and later reassigned to *Zosterophyllum longum* by Schweitzer (1999), this material comprises bifurcating fertile spikes with reniform sporangia arranged in two rows along the axis. In this general organisation it is comparable to *Z. fertile*, but the sporangia appear larger and less erect, and differ in overall form. On this basis, it is better regarded as a distinct zosterophyll taxon rather than closely comparable to *Z. fertile*. West side Billefjorden.

Psilophyton sp. (cf. Psilophytites sp.)

Høeg 1942, Pl. XIX, figs. 4–5.

A single dichotomous axis described as *Psilophyton* sp. lacks diagnostic characters but closely resembles *Psilophytites*. It is therefore treated here as *Psilophytites* sp. indet. West side Billefjorden.

Barinophyton sp. Høeg 1942 (cf. Serrulacaulis sp.)

Høeg 1942, Pl. XX, figs. 5–8.

A poorly preserved axis attributed to *Barinophyton* lacks diagnostic features. The surface striations and lateral projections (enations) are more consistent with *Serrulacaulis*-type axes recorded from ENS material. West side Billefjorden.

Summary

The combined collections of Nathorst (1884, 1894) and Høeg (1942) represent the only previously recorded Lower Devonian flora from Wood Bay. The assemblage comprises fragmentary zosterophyll and euphyllophyte axes with few diagnostic features.

Historical Collections and Undescribed Material

In 1939 two separate expeditions collected Lower Devonian plant material from Svalbard: the English–Norwegian–Scottish (ENS) expedition and Høeg's Norwegian expedition. The ENS material is primarily housed at the Naturhistoriska Riksmuseet in Stockholm, with a smaller subset curated at the Natural History Museum, London. Høeg's material remains largely uncatalogued at the Natural History Museum in Oslo.

Several hundred specimens from the ENS collection were examined under a SYNTHESYS grant. The majority are fragmentary and vegetative, with simple morphologies and no preserved fertile organs or anatomy. Most can be assigned to the morphotaxa *Aphylopteris*, *Hostinella*, and *Psilophytites*, which dominate the assemblage across all localities. Less common but significant forms include cf. *Drepanophycus* and cf. *Serrulacaulis*, suggesting the presence of zosterophyll-grade and lycophyte-like plants. The Oslo material is less fragmentary, though not well preserved, and includes the most notable examples of *Zosterophyllum*, although none are complete enough for confident species-level identification.

The Stockholm material has been described and catalogued as part of the SYNTHESYS project and is included in Appendix A, while the Oslo material is summarised in Appendix B. Despite extensive investigation of several hundred specimens across both collections, the fragmentary and morphologically simple nature of the material limits further taxonomic resolution. Capel et al.'s statement (2023), that the Laurussian record which includes Svalbard, is dominated by incomplete form taxa and under-sampled localities, constraining our ability to refine palaeofloristic interpretations, seems to be confirmed. Consequently, this reassessment does not expand upon the known Lower Devonian flora beyond that already recognised by Capel, but it provides essential context for understanding the composition and preservational bias of these historical collections.

2.3.3 Description of New Taxa: *Psilophytites svalbardensis*

Description of Material Collected at Type Locality: Kapp Petermann

The assemblage comprises approximately twenty slabs collected in 2018 by Wellman and colleagues from the Pragian Kapp Petermann locality, situated within the Austfjorden Member of the Wood Bay Formation. A detailed account of the locality and its sedimentology is provided by Davies et al. (2021, fig. 5, p. 8). The site coordinates are UTM Zone 33X, 0515584 E, 8785149 N. All specimens are catalogued under the prefix PMF-, followed by their individual specimen number; for brevity, only the specimen number is used in the following descriptions.

The fossils are preserved in a medium- to fine-grained, light–mid grey sandstone containing abundant mica flakes. Preservation is variable, ranging from partial limonitic permineralisations to coalified compressions and impressions, in some cases combining more than one mode of preservation. The largest slab (PMF 19; Text-fig. 23) measures 34 cm in length, 19 cm in width, and approximately 5 cm in thickness, and contains around twelve axis fragments distributed across the surface. No sporangia were observed on any specimen.

Although the material from the type locality at Kapp Petermann forms the basis of the description and the definition of diagnostic characters, additional material from other localities provides supplementary morphological information. The primary description focuses on the Kapp Petermann specimens, with features from other sites incorporated subsequently to broaden the interpretation of overall morphology.

Other Material

E.N.S. Expedition, 1939

Material collected during the E.N.S. Expedition of 1939 is housed in the Swedish Museum of Natural History (Naturhistoriska riksmuseet), Stockholm. These specimens were obtained primarily from north-western Spitsbergen, with additional material from

the Isfjorden area. One specimen from Jakobsenbukta (S017435; Text-fig. 27, Pl. 12A) provides supplementary details of overall morphology and is discussed at the end of this description.

It should be noted that additional localities yielded fragmentary plant remains exhibiting similar morphology, but preservation quality and diagnostic completeness were insufficient for confident identification. Specimens attributed tentatively to this taxon but not contributing directly to the species description are included in the relevant sections detailing morphotypes from other Lower Devonian localities (Appendix A, B).

Jakobsenbukta. The material is preserved in light grey, fine-grained sandstone. Three specimens have been identified as *P. svalbardensis* sp. nov. (S017433, S017434, S017435). Axes range from 21 to 45 mm in length and occur as compressions and impressions.

Jørgensendalen. Specimens are preserved as coalified compressions within yellowish, coarse grey sandstone. Three slabs (S017437, S017438, S017439) contain fragments assignable to *P. svalbardensis* sp. nov.

Sørlieljellet. Material is preserved as coalified compressions and partial permineralisations, with frequent limonite inclusions, within yellowish coarse grey sandstone. Seven slabs contain *P. svalbardensis* sp. nov. (S017575, S017576, S017579, S017580, S017581, S017583, S017587). One specimen (S017587) is fragmented into seven pieces, each bearing limonitic inclusions.

Høeg Expedition, 1939

Additional material was collected during the 1939 expedition involving Ove Høeg, Reidar Jørgensen and Jakob Vague. This collection is housed in the Natural History Museum, Oslo (Naturhistorisk museum). All specimens originate from the western side of Klaas Billen Bay (Billefjorden), within the Dicksonfjorden Member of the Wood Bay Formation. One slab (PMO.250.125) contains remains attributable to *P. svalbardensis*, exhibiting features that contribute to the species description presented below.

Description – *P. svalbardensis* sp. nov.

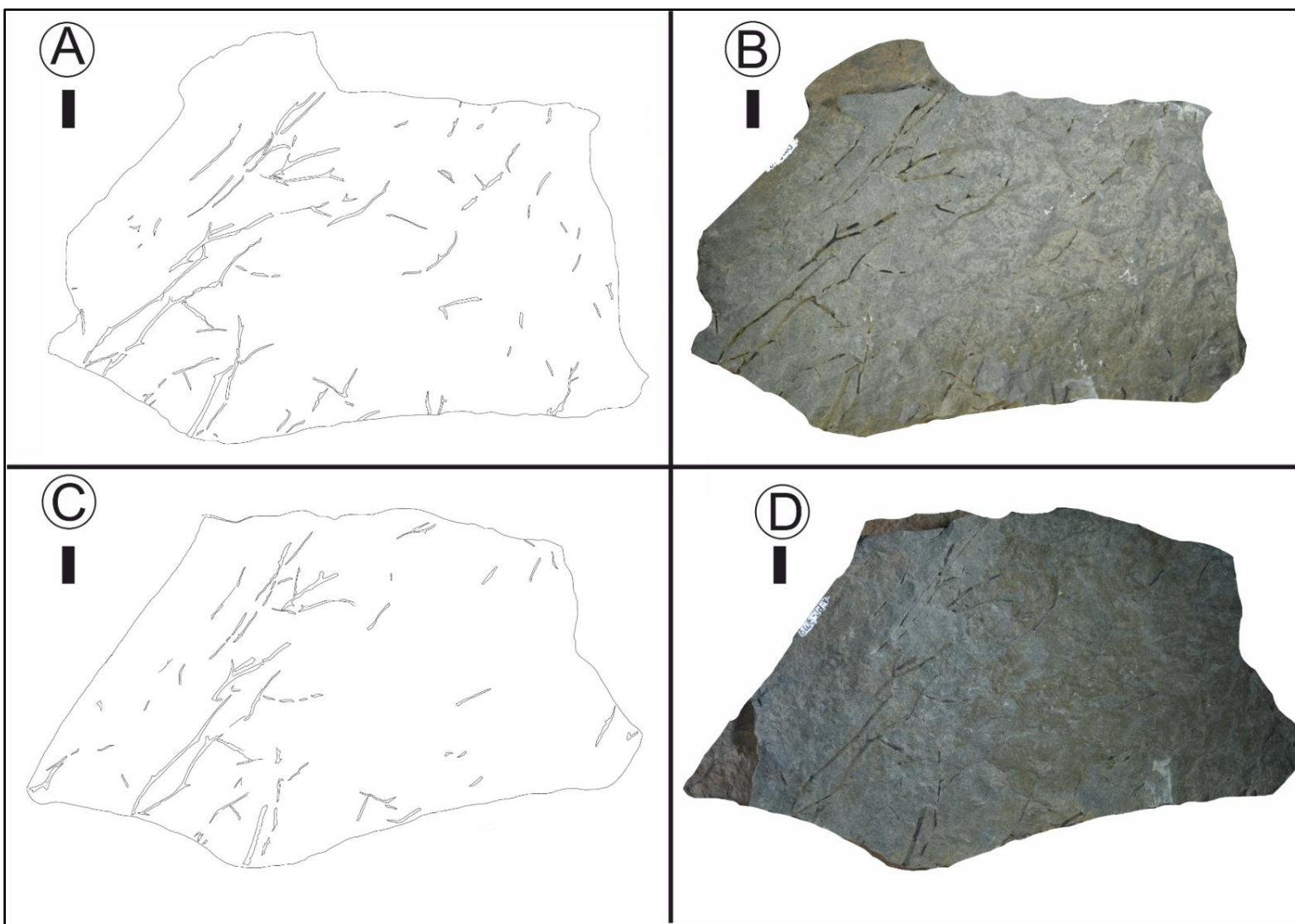
General Features of Fossils

The plant remains are fragmentary and represent portions of a larger plant of probable greater stature. Primary axes average 56 mm in length (range 16–133 mm, $n = 80$) and 2.1 mm in width (range 0.9–3.6 mm). Axis length and width are positively correlated, with longer axes generally exhibiting greater diameters. Internode length follows the same trend, with the widest axes showing the longest intervals between bifurcations.

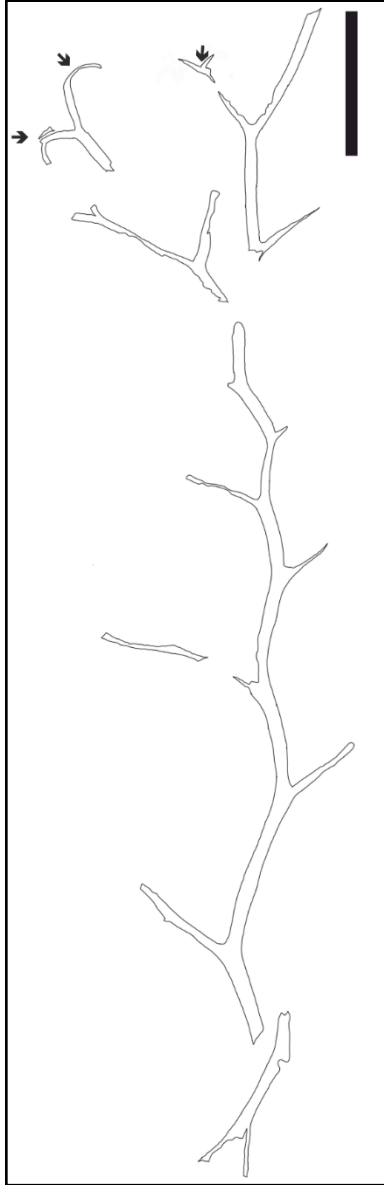
In most specimens, a dominant primary axis bears smaller lateral branches that diverge alternately, each showing a slight deflection away from the parent axis. This organisation produces a pseudomonopodial branching pattern (Text Figure 24). In some cases, a small raised axillary tubercle is visible at the point of lateral divergence (Plate 10B-D - white arrow).

Isotomous branching is relatively uncommon and where present, is restricted to secondary axes after separation from the primary axis. It is not observed on the main axis itself and generally occurs only in larger fragments that preserve distal portions of secondary branches (Plate 9A - black arrow; Plate 13C, F - white arrow). These examples are preserved in different modes, including an iron-stained impression in Plate 13C and better-preserved compressions in other specimens. Isotomous branching also occurs terminally in a few specimens, forming recurved distal tips.

Spines or spine bases are evident on most axes, although their expression varies with the mode of preservation. In compressions, slender, elongate spines are typically retained (Plate 9G; Plate 11A, E, F; Plate 13D). Where the coalified layer has been lost, only the impressions of spine bases remain (Plate 9F, Plate 10A, Plate 11D; Plate 12B, D; Plate 13F). In specimens where the epidermis has been compacted, a distinct marginal border is often visible along either side of the axis, forming a characteristic narrow ridge or margin (Plate 9F; Plate 10A; Plate 12B, D; Plate 13F).



Text Figure 23: Interpretative line drawing and photographs of *P. svalbardensis* axes from largest slab collected from Kapp Petermann. Part PMF-18 and counterpart PMF-19. Scale bar 2 cm.



Text Figure 24. Interpretative line drawing of type specimen of *P. svalbardensis*. Black arrows show probable position of recurved tips at the distal portion of the axes. PMF-13, Plate 9A. Scale bar 50 mm.

Branching patterns

First- and Second-Order Branching

The larger axis fragments show a dominant primary axis from which lateral secondary axes emerge (Plate 9A, Plate 10A), forming the upright stem of the plant (Plate 9A, B; Text Figure 25G–H). Most bifurcations from the primary axis are anisotomous (Plate 9A, B; Plate 10A–D; Plate 11B; Plate 12A, D; Plate 13C, F). The secondary axes are

markedly smaller than the primary axis, in some cases up to three times narrower (Plate 10A, D).

The main axis branches regularly. At each branching point, the axis bifurcates anisotomously in an apparently alternate arrangement (Text Figures 24, 25). When the lateral axis emerges on the left side, the main axis changes direction and subsequently bifurcates to the right at the next branching point. When the lateral axis emerges on the right, the subsequent bifurcation occurs to the left. In the best-preserved and more completely exposed axes, this alternating pattern of lateral emergence produces a weak to distinct zig-zag architecture. The pattern is less obvious in lower-magnification slab photographs and in larger or more incomplete fragments, where only one or two branching points are visible.

Smaller axis fragments exhibit a more exaggerated zig-zag effect, resulting from the progressive shortening of the intervals between successive bifurcations distally. In the type specimen (Text Figure 24; Text Figure 25G–H; Plate 9A), the length of the axis between branching points decreases from 21.3 mm proximally to 7.3 mm distally, a 67% reduction. Axis width also decreases from 2.9 mm at the base to 1.0 mm at the distal tip, a 64% reduction.

In some specimens the zig-zag pattern is less pronounced. This occurs in larger axes where the interval between bifurcations is longer, or where preservation is incomplete and only a single bifurcation is visible along the exposed length (Text Figure 25A–F), or absent altogether (Text Figure 28B; Plate 9G; Plate 13D). Medium-sized axis fragments typically retain a weaker zig-zag pattern (Text Figure 25L, N, P; Plate 13A, B, E) compared with smaller axes (Text Figure 25A–B, I–J; Plate 25B; Plate 10A; Plate 13F).

Third-Order Branches

In most specimens, lateral axes terminate near their point of origin from the primary axis (Plates 9A, B; 10A; 11B; 13A, B), suggesting breakage. A small number of specimens show dichotomy of the secondary axes, usually isotomous, producing third-order branches (Text Figure 25A–D; Plate 13C - white arrow; Plate 13E, F - white arrows).

These occur mainly in smaller axis fragments, whereas larger fragments typically preserve secondary axes without visible bifurcation (Text Figure 25E).

Apparent Trifurcate Branching

The primary axis extends 6.8 mm beyond the upper branching point before terminating. At least one specimen gives the appearance of trifurcation in the primary axis (PMF-5: Text Figure 26; Plate 9C, D). Serial *dégagement*, however, suggests that this configuration is better interpreted as two closely spaced lateral axes arising from the primary axis in rapid succession, rather than as a true three-way division. The lower lateral axis (Text Figure 26A–E, green axis; Plate 9D, black arrow) diverges from the main axis (Text Figure 26A–J, yellow axis) at an angle of 61° and extends 5 mm into the matrix before terminating. The upper lateral axis is only partly visible on the part, where the first 2 mm diverges from the primary axis at an angle of 91° (Text Figure 26A–C, red axis; Plate 9D, white arrow). The remainder is exposed on the counterpart (Text Figure 26F–J, red axis).

The upper lateral axis measures 0.9 mm in width at its point of emergence from the primary axis. Serial *dégagement* shows that it extends 7 mm into the counterpart matrix before bending. After the bend, the axis widens to 1.5 mm (Plate 13C; Text Figure 26F–J, red axis). Beyond this point, it continues for 12 mm into the matrix before bifurcating isotomously at an angle of 45° (Plate 9C, black arrow). The daughter axes extend for 1.7 mm and 1.4 mm, respectively, before reaching the opposite edge of the slab.

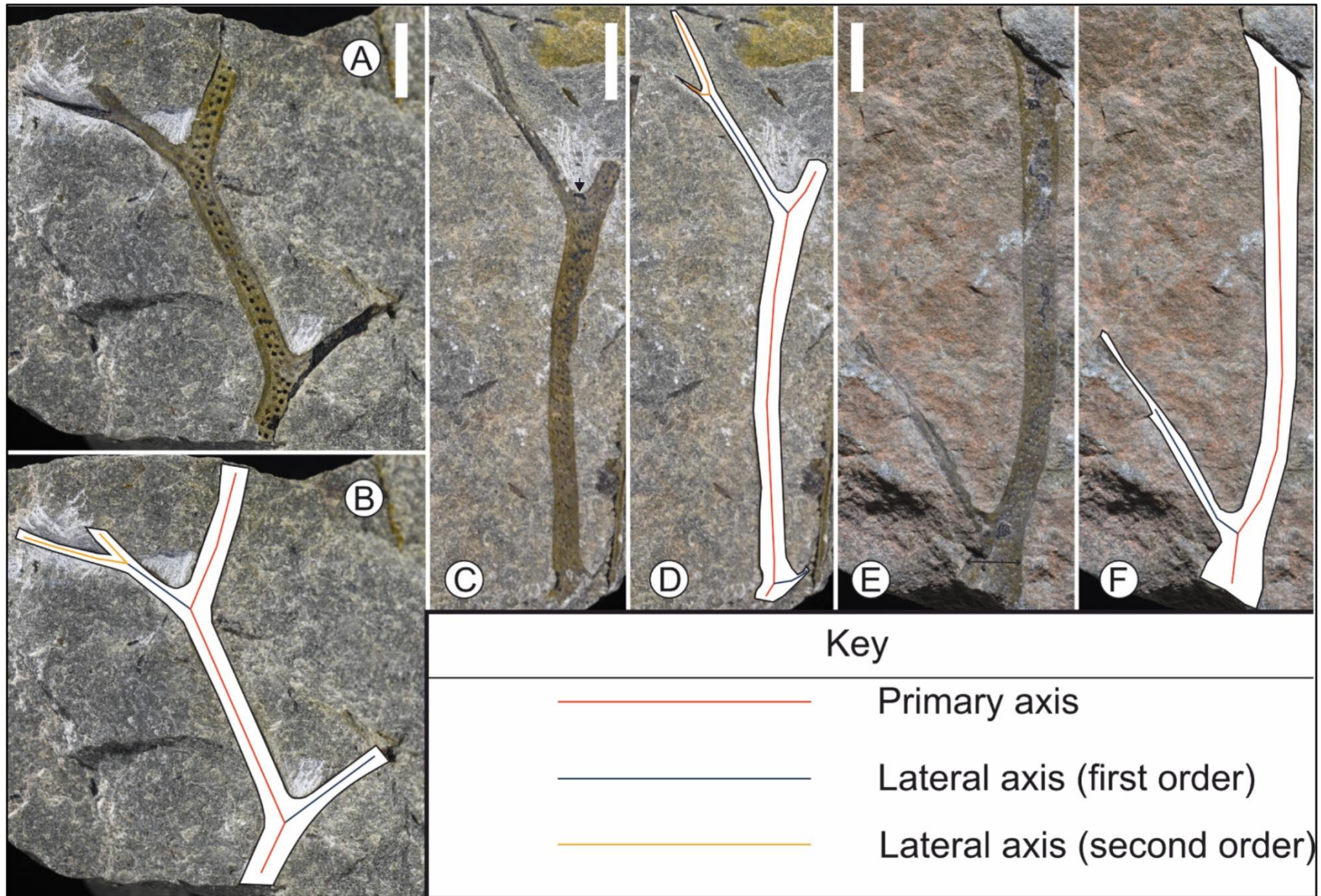
A specimen from Jakobsenbukta shows a similar arrangement (Text Figure 27; Plate 12A). Here, two lateral axes arise in close proximity from a single primary axis, again producing an apparent trifurcate configuration. The primary axis measures 21 mm in length. The first lateral axis emerges from the left side (Text Figure 27B, black arrow), while the second emerges from the right (Text Figure 27B, white arrow). The lower axis diverges at 23° anticlockwise from the primary growth direction, while the upper axis diverges at 73° clockwise (Plate 12A). The primary axis extends 6.8 mm beyond the upper branching point before terminating.

Similar apparent trifurcate arrangements have been described in other Early Devonian plants, particularly *Pertica*-type euphyllophytes. In these plants, an apparent three-way division may result from an axis dichotomising, followed by one daughter axis dividing again just above the first division, rather than from a true simultaneous trichotomy (Banks et al., 1975; Doran et al., 1978; Gensel, 2022). The Svalbard material is interpreted in the same cautious way. The specimens show closely spaced lateral branches produced within a short interval, but they do not provide clear evidence for a true three-way division from a single point.

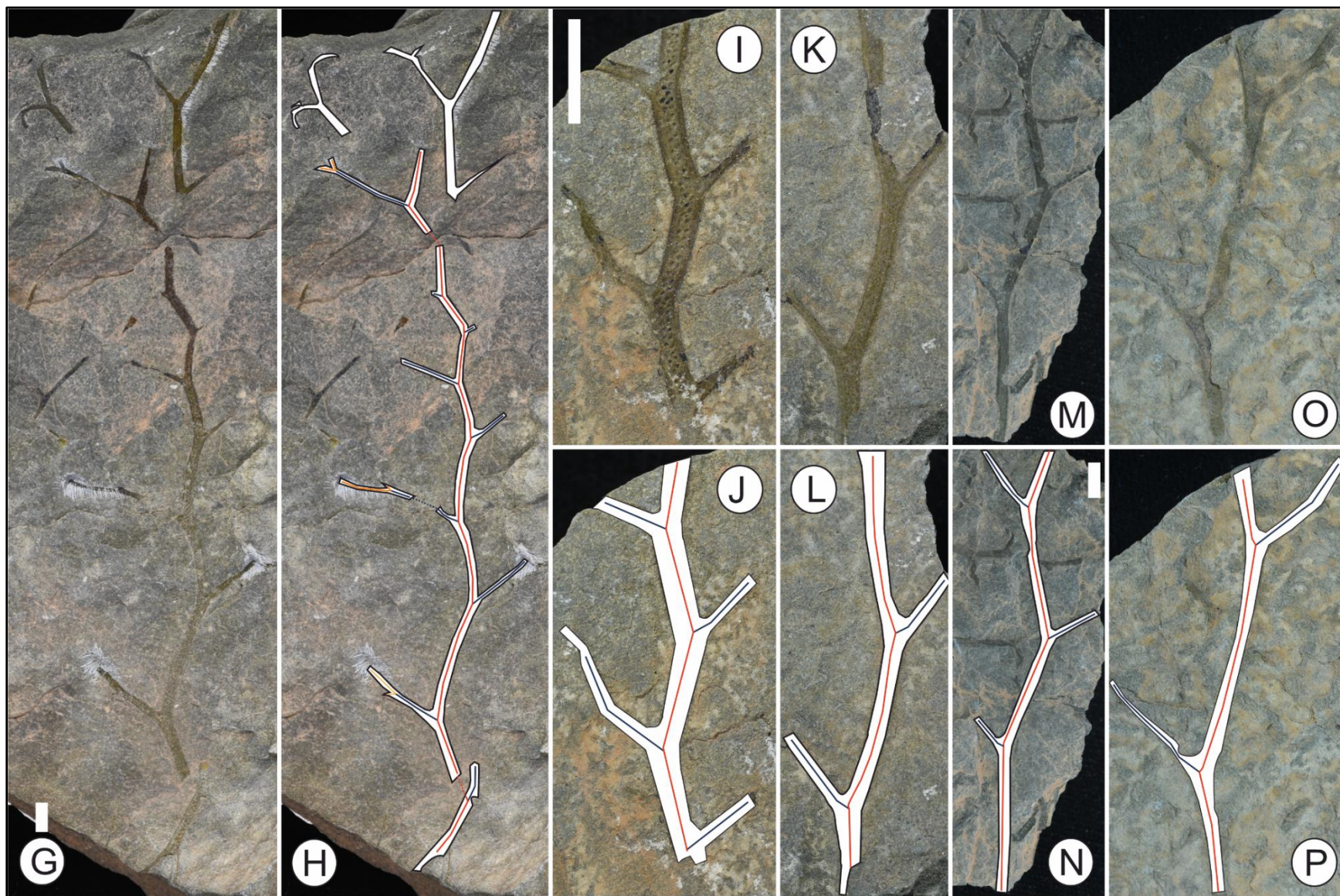
These specimens indicate that the primary axis was capable of producing two lateral axes within a very short developmental interval. Although this gives a trifurcate appearance, the branching is more parsimoniously interpreted as closely successive lateral branch production than true trichotomy. This apparent trifurcate arrangement is rare in the material and has been observed clearly in only two specimens, PMF-5 and S017435, although similar branching may be obscured in more fragmentary axes.

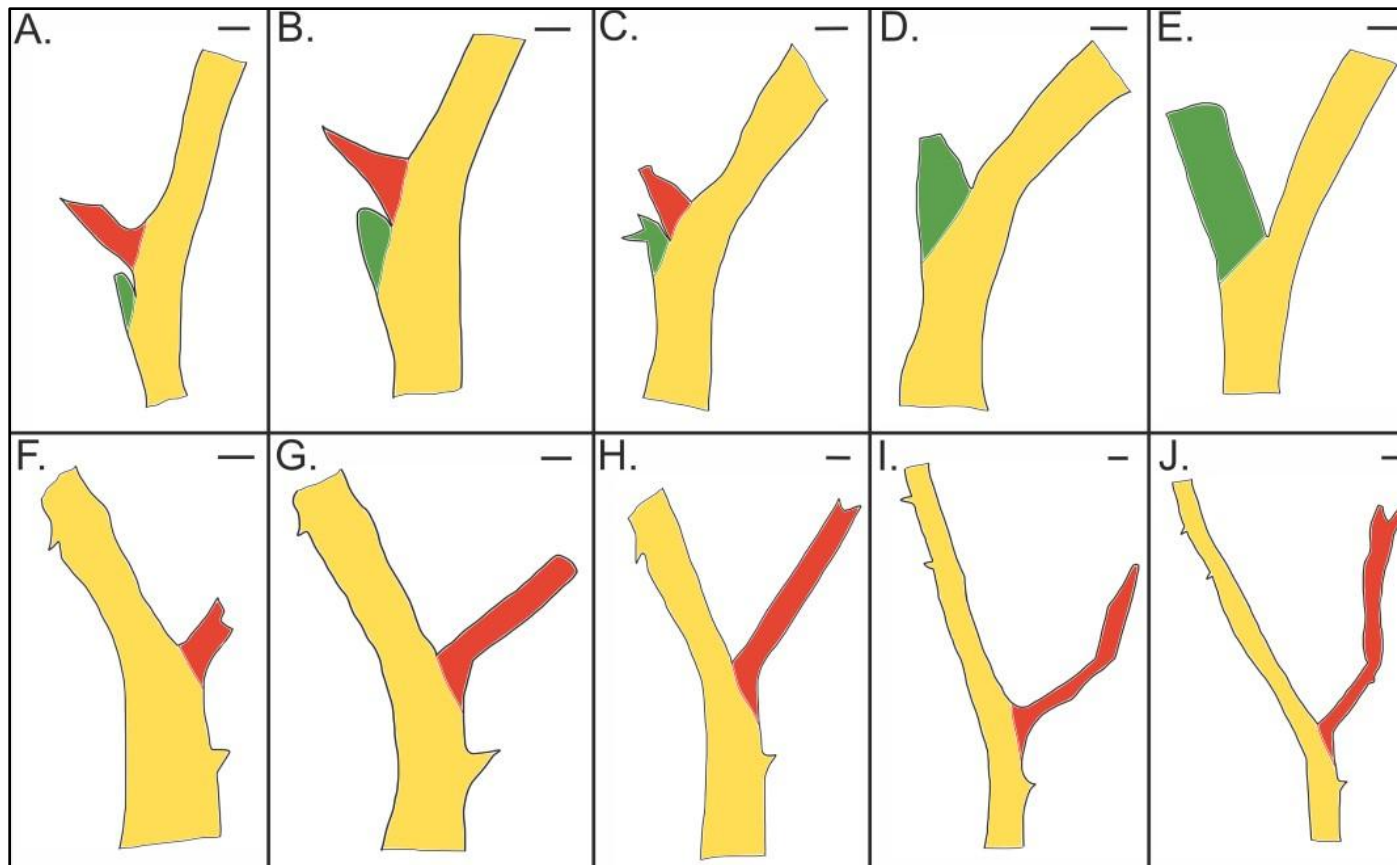
Text Figure 25. Branching architecture in *P. svalbardensis* A. Primary axis (PMF-14) showing two anisotomous divisions producing paired first-order laterals (blue line seen in B), one of which bifurcates isotomously to form second-order laterals (yellow line seen in B). B. Line drawing of A seen with coloured lines to denote type of axes present. C. Large primary axis fragment (PMF-14) with anisotomous branching. Black arrow shows axillary tubercle. D. line drawing of C. E. Basal fragment (PMF-19) with a single anisotomous bifurcation. F. Line drawing of E. G. Type specimen (PMF-13) showing a robust primary axis with multiple first-order laterals, some dividing into second-order branches. H. line drawing of G. I. Smaller fragment with four first-order laterals arising alternately from the main axis. J. line drawing of I. K. Axis fragment (PMF-9) with two opposite first-order laterals. L. Line drawing of K. M. Specimen (PMF-6) showing three successive anisotomous divisions. N. Line drawing of M. O. Specimen (PMF-13) with two anisotomous bifurcations of the primary axis. P. Line drawing of O. Interpretative drawings (B, D, F, H, J, L, N, P) illustrate branching organization; coloured lines denote branching order. Scale bar = 5 mm.

Text Figure 25A

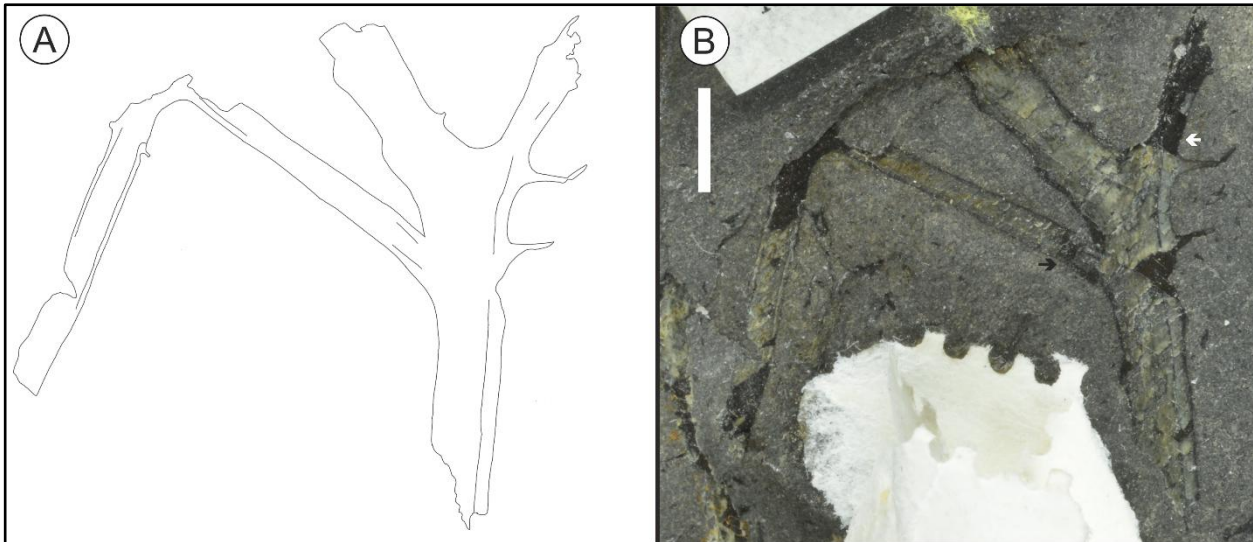


Text Figure 25B





Text Figure 26. Step-by-step camera lucida drawings showing serial *dégagement* of PMF-5 (Kapp Petermann), highlighting an apparent trifurcate arrangement produced by two closely spaced lateral axes. The green axis represents the lower secondary axis, and the red axis the upper secondary axis; together these produce an apparent trifurcate arrangement. The yellow axis represents the primary main axis. **A–E** show the *dégagement* steps on the part of the specimen, whereas **F–J** show the *dégagement* steps on the counterpart. In **A–C**, both the lower and upper secondary axes are present on the part, whereas in **D–E** the upper secondary axis has been removed to expose the full length of the lower secondary axis. In **F–J**, on the counterpart, only the main axis and upper secondary axis are present. In **A–H**, camera lucida drawings were completed at $\times 16$ magnification, and in **I–J** at $\times 4$ magnification. Scale bar in all drawings = 2 mm. B



Text Figure 27. Apparent trifurcate branching in *Psilophytites svalbardensis* from Jakobsenbukta. The arrangement is interpreted as two closely spaced lateral axes diverging from the primary axis rather than a true three-way division. A. Camera lucida drawing of the axis, enhanced with ProCreate for iPad. B. Macrophotograph of the same specimen. The black arrow marks the lower lateral axis diverging from the left side of the primary axis; the white arrow marks the upper lateral axis diverging from the right side. Scale bar = 5 mm. Specimen S017435, Naturhistoriska riksmuseet, Stockholm.

Plant features

Epidermal margins

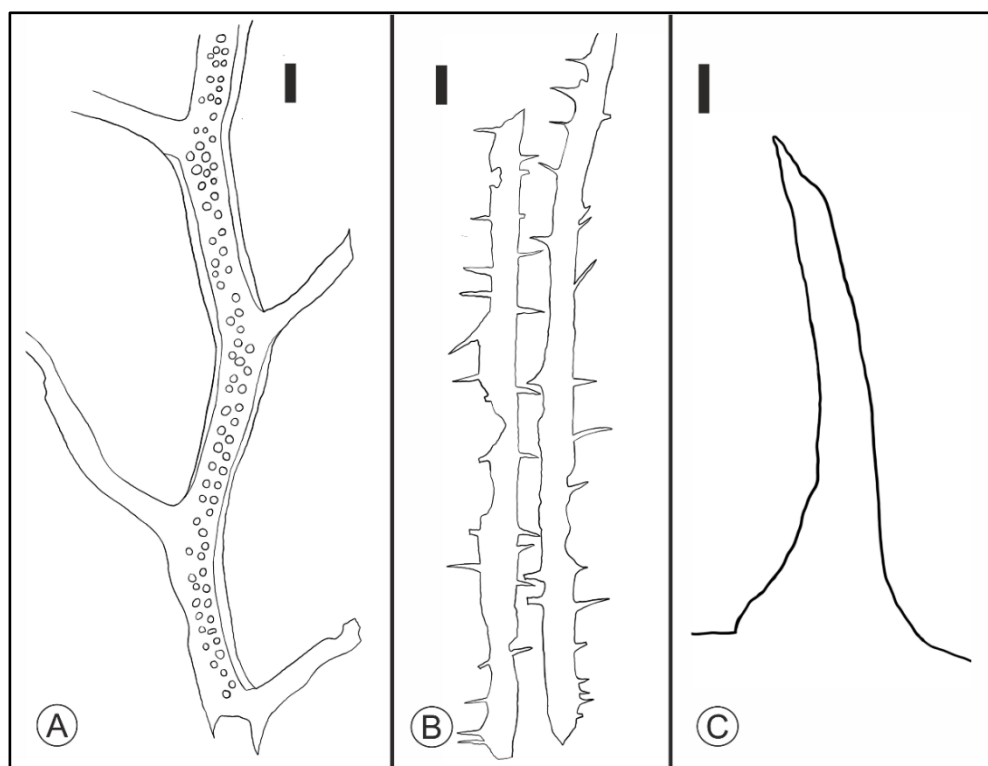
In some types of preservation, there is often a very distinctive margin running down one or both sides of the axis (Text Figure 28A; Plates 9F, 10A, 11D). This margin is between 0.2-0.7 mm in width. In some cases, this margin has been associated with the spine like emergences discussed in section 3.2.1.3.1, with the spines and the epidermal margin appearing continuous down the length of the axis (Plate 12A-white arrow).

In S017435, the epidermal margin is present on the right hand side of the primary axis and left side of the emerging lateral axis (Text Figure 27A), in addition to both sides of the lateral axis on the left hand side (Text Figure 27A). In some specimens (Plate 9E) this feature is not visible.

Spines

Specimens have spine-like protrusions on the surface of the axis (Text Figure 28; Plate 9E, F, G; Plate 11). Depending on the type of preservation, different aspects of the spine morphology are preserved. In specimens which have been preserved as coalified compressions, the full length of the spine from the base to the tip is sometimes visible (Plates 9G, 11E; Text Figure 28B, C;). The quality of spines preserved in this way vary greatly, the majority have been snapped off at the base or broken along their length (Plate 11A, F). Where the full length of the spine is visible, it tapers from a wide base to a fine, hair like tip (Text Figure 28C). The shortest spine is 0.8 mm, the longest 3.3 mm and the average 1.45 mm. The majority of lateral axis did not show any spines, however there were a small number of lateral axis that did show spine bases (Plate 12C) although they were not as dense as those on the primary axis.

In specimens that have been preserved as impressions, where the compressed coalified material has been removed, the base of the spines is visible but the three-dimensional structure of the spines is rarely preserved (Plate 9F; Text Figure 28A; Plate 11B, D). This type of preservation is most common in specimens collected at the Kapp Petermann locality. The width of the spine bases varies from 0.5-0.17 and on average were 0.29 mm (N= 139). Where the plants have been preserved with the



Text Figure 28. Camera lucida drawings, enhanced with ProCreate, of spiny protrusions in *P. svalbardensis*, Kapp Petermann. A. Remains of an impression fossil where the spine bases are visible in the epidermal layer. Scale bar = 2 mm. Specimen PMF-4. B. Plant remains preserved as coalified plant compressions, present are two axes where multiple spines are present on each. Scale bar = 2 mm. Specimen PMF-13. C. Close up of one of the spines present. The base of the spine tapers towards a point. Scale bar is 0.125 mm. Specimen PMF-6.

inclusion of limonite, the bases of the spines are visible but not the overall 3D structure of the spines (Plates 9E, 11C).

The density of spines on the axis surface is variable according to the overall size of the axis. On the most complete axis (PMF-13; 1.4 mm width, 133 mm in length) the density of spine bases found was 6 per mm². On a smaller axis (PMF3- 1.1 mm width, 54 mm in length), the density was 3 spines per mm². The density of spines found on different axis varied from between 3-7 spines per mm², with an average of 5 spines per mm² (N=55).

The distribution of the spine bases is also of interest. In some specimens, particularly that illustrated in Text Figure 25A, the bases appear to be concentrated within a central strip of the main axis, while the margins are comparatively smooth and the lateral axes do not show an equivalent distribution. Although this pattern may in part reflect preservation or the plane of exposure, it suggests that the spines were not uniformly distributed across the axis surface. Instead, they may have been positionally restricted on the primary axis, adding a further distinctive feature to the morphology of *Psilophytites svalbardensis*.

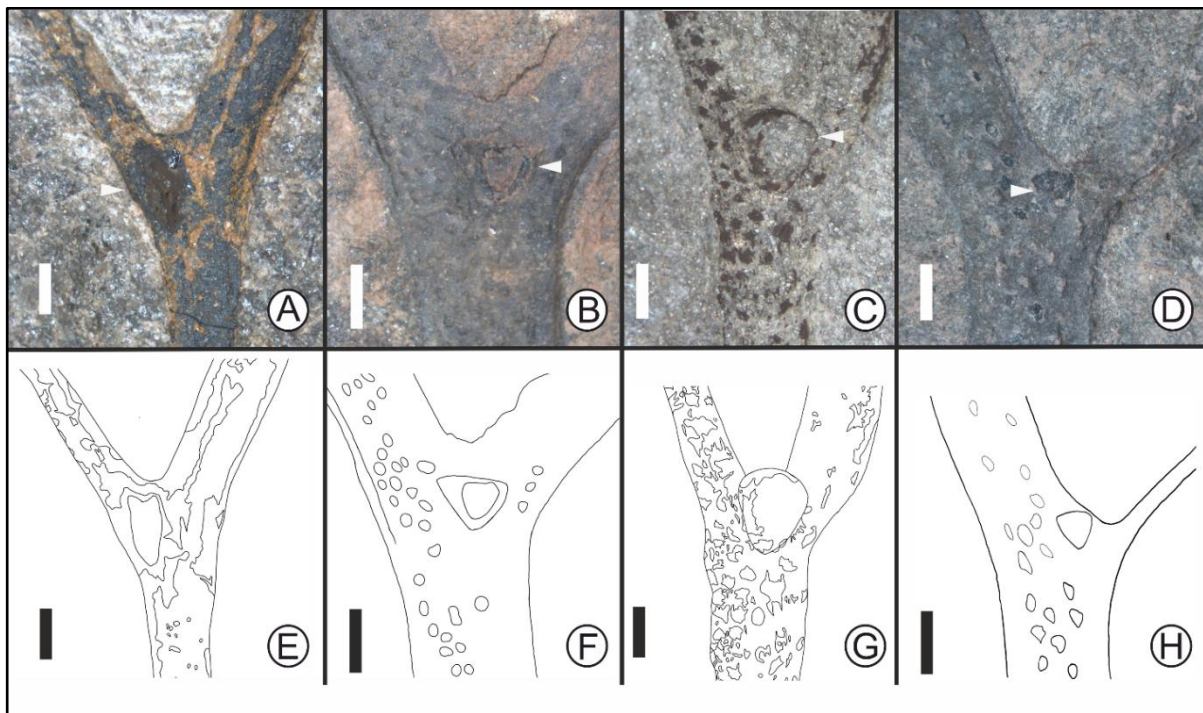
Axillary Tubercles

In this study, the term “axillary tubercle” is retained as a descriptive term for the small outgrowths associated with branching points. In some specimens, the tubercle appears to lie within the axil of the lateral branch, whereas in others it is positioned beside or slightly below the axil. This variation may reflect preservation, exposure during dégagement, or the orientation of the branch in the matrix. The term is therefore used here in a broad descriptive sense to refer to branch-associated tubercles, rather than to imply a consistently precise axillary position.

At least seven specimens preserve an axillary tubercle, expressed as a raised or sunken structure at the point of dichotomy (Text Figure 29). This is commonly associated with the smaller lateral axis that diverges from the larger primary axis (Text Figure 29A, D; Plate 10B–D). However, in some slightly wider axes that appear to bifurcate more isotomously, the axillary tubercle is positioned centrally between the two daughter axes (Text Figure 29B, C). Axillary tubercles have not been observed in any axis shown to exhibit trifurcate branching.

There is considerable variation in the appearance of the axillary tubercles among specimens, reflecting both preservational differences and possible original morphological variation (Text Figure 29). In some specimens, the tubercle is preserved as a three-dimensional, rounded triangular structure (Text Figure 29C), whereas in others it appears as a thinner ovate- to triangular-shaped impression (Text Figure 29B). A few specimens preserve only a two-dimensional carbonaceous film at the site of the tubercle, retaining little more than its outline (Text Figure 29A). In specimens showing mixed modes of preservation (Text Figure 29D), more than one of these forms may occur within a single axis. Although some of this variation is clearly taphonomic, it is not possible to determine whether the observed differences represent distinct preservational states alone or also reflect genuine morphological variation within the plant.

The repeated occurrence of developed axillary tubercles is a notable feature of the material. These structures are not confined to a single specimen, but recur in several examples, including the material illustrated in Text Figures 26 and 27. Their consistent association with branching points suggests that they represent a genuine morphological character rather than an isolated preservational artefact. This feature is of particular interest because comparable structures are only rarely documented in other zosterophyll-like taxa such as *Gosslingia*.



Text Figure 29. Modes of preservation of axillary tubercles in *Psilophyites svalbardensis*. A-D Images of axillary tubercle in different modes of preservation. E-H show camera lucida drawings (enhanced with ProCreate for iPad) of the same specimens. A and E show an axillary tubercle and axis preserved as a coalified compression. B and F show an axillary tubercle preserved as an impression. C and G show a poorly preserved axis and axillary tubercle as an impression, with inclusions of limonite. D and H show an axillary tubercle and axis with a mixture of preservation types, the axillary tubercle is more closely associated with the smaller lateral axis. White arrows in all images highlight the presence of the axillary tubercle. Scale bar is 1 mm.

Recurved Tips or Protrusions

In the most complete specimen from Kapp Petermann (PMF-13), serial *dégagement* of the distal portion of the axis revealed two pairs of recurved tips, each projecting from opposing lateral axes (Text Figure 24; black arrows). These recurved tips likely occur in pairs at the termini of two isotomous axes, producing four tips in total. In the best-preserved axis (Text Figure 24 - right black arrow), only three recurved tips are visible, the fourth having presumably broken away.

Microscopic examination also revealed singular pairs of recurved tips projecting laterally from the external surface of the axis in two additional specimens from Kapp Petermann (PMF-16, PMF-6). Preservation was insufficient for photography, but

some observations were noted. Each recurved tip measures 1.1 mm in width and 1.5 mm in length, diverging at approximately 45° from the left-hand side of the primary axis.

Anatomy of *P. svalbardensis*

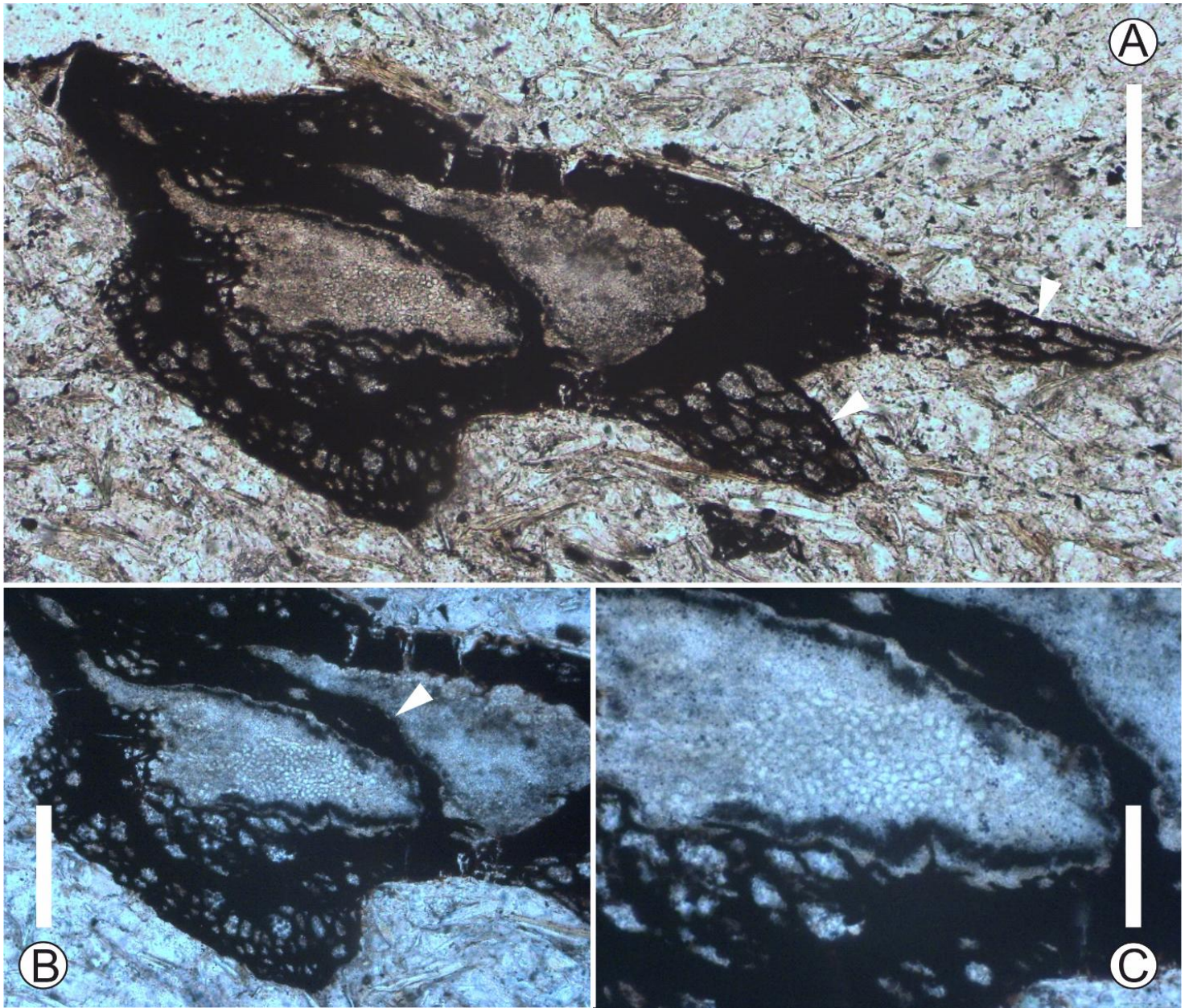
Although over fifty thin sections and peel preparations were made using the method described by Stein et al. (1982), only a small number preserved sufficient cellular detail to yield useful anatomical information (Text Figure 30). One transverse section in particular (Text Figure 30A) shows a well-defined outer cortex and epidermal region, providing insight into the tissue organisation of the axes.

The axis measures approximately 200 μm by 625 μm , with a conspicuous, darkly carbonised outer rim forming a sterome approximately 120 μm thick. Because the section is small, it may represent a distal portion of a primary axis or a lateral branch rather than the main axis. The sterome is composed of thick-walled, polygonal to slightly elongate cells (Text Figure 30C), ranging from 12–20 μm in diameter. The thickness of the cell walls and the high degree of carbonisation suggest a mechanically strengthened tissue that resisted decay, accounting for the sharp black border frequently observed in compression specimens. Externally, a thin epidermal layer is locally preserved as a single row of flattened cells, from which arise small multicellular spines up to 200 μm in length, composed of a few (2–4) layers of elongated cells. These spines project outward from the epidermal surface and are continuous with the outer tissue layers (Text Figure 30A, white arrows), indicating a superficial origin rather than deep cortical extensions. Two of the spines are preserved in moderate detail, whereas one has been compressed into the epidermis.

The interior of the axis is largely degraded and replaced by matrix, but a faint median partition of darker tissue divides the axis into two halves (Text Figure 30B, white arrow) and may mark the position of a central strand compressed during preservation. However, a taphonomic origin linked to collapse of the inner tissues cannot be excluded. No differentiated conducting tissue can be recognised, suggesting that decay of the inner cortex and stele occurred prior to mineral infiltration.

The anatomical evidence also supports the interpretation of the spinose emergences as genuine features of the plant rather than superficial preservational irregularities. In the best-preserved material (Text Figure 30), the axis shows a well-defined outer cortex and sterome, with the bases of the emergent structures visible in association with the epidermal region. This suggests that the spines formed part of the original external morphology and were supported by a mechanically strengthened outer tissue.

In summary, *P. svalbardensis* exhibits a distinct outer sterome composed of thick-walled supportive cells, an outer epidermal region bearing spine bases, and an incompletely preserved central region. Spine-base density varies between specimens, ranging from 3–7 per mm² and averaging 5 per mm² (N = 55). In the best-preserved material, the spine bases appear to be more strongly developed on the primary axes, whereas lateral axes may be smoother and show fewer or no comparable spine bases. The well-developed sterome likely conferred rigidity to these slender axes, while its thick-walled nature explains the carbonised border often observed in compression fossils.



Text Figure 30. Anatomical section of *P. svalbardensis* sp. nov. A. Transverse section of axis with well-defined sterome and epidermal cells which include spines (white arrows). B. Transverse section as the same as in A showing details of central strand in the centre of the axis. C. Close up of thick walled cells of the sterome. Scale bar = 100 μ m.

Discussion

Most plant material described here comes from the Ausfjorden Member of the Wood Bay Formation, with the remainder from the Dicksonfjorden Member. The remains are abundant but fragmentary, with dozens of axes collected from several localities across the Lower Devonian basin of north-west Spitsbergen. The fossils consist of narrow, spinose axes that branch isotomously and anisotomously, with rare apparent trifurcate arrangements produced by two closely spaced lateral axes. Spines are concentrated mainly on the primary axes and occur less frequently on lateral axes. Some specimens show these closely spaced paired laterals, and small axillary tubercles are occasionally present between primary and secondary axes. All material is sterile, and no sporangia have been identified.

The spinose emergences of *Psilophytites svalbardensis* invite comparison with other early tracheophytes bearing similar appendages, particularly *Sawdonia*. However, the Svalbard material differs in that the spine bases are not simply expressed as uniformly distributed emergences on all axes. Instead, they appear in some specimens to be concentrated on the primary axis, while the lateral axes may be smoother and less consistently spinose. In addition, the repeated presence of axillary tubercles associated with branching points distinguishes the material from many superficially similar forms. Together, the combination of anisotomous to pseudomonopodial branching, fine spinose emergences, rare apparent trifurcate arrangements produced by closely spaced lateral axes, and developed axillary tubercles supports the interpretation of *P. svalbardensis* as a distinctive morphotype within these early tracheophyte assemblages.

In transverse section, a small number of specimens show limited anatomical preservation. The axes contain a narrow zone of thick-walled cortical cells forming a distinct sterome up to about 120 µm thick. The central region has not been preserved. This sterome suggests a mechanically strengthened outer cortex, comparable to that seen in some other early tracheophytes.

The Kapp Petermann material therefore combines a set of features: spiny axes, closely spaced paired lateral branching giving an apparent trifurcate form, axillary tubercles and a cortical sterome, that have not previously been recorded together. It provides a valuable opportunity to reconsider the morphology and affinities of these early spiny plants within the wider Laurussian flora. The following discussion examines these characteristics in relation to known Early Devonian taxa and considers their anatomical, palaeogeographic and evolutionary context.

The enclosing matrix is fine grained, and several specimens are preserved with limonitic inclusions, indicating rapid burial within a quiet overbank or floodplain setting. Such environments accumulate fine suspended sediment during short flood events, promoting rapid burial of plant debris and early iron-oxide mineralisation around decaying tissues (Davies et al., 2021; Wellman et al., 2022). These conditions favour abundant preservation, but they are also selective, promoting survival of the more resistant cortical tissues and spine bases, while finer distal axes and fragile appendages are more likely to be lost before burial. This preservational pattern is consistent with that seen in other Lower Devonian assemblages from Laurussia (Gerienne, 1992; Capel et al., 2024).

Taxonomic Justification: Assignment to *P. svalbardensis* sp. nov.

Given the absence of reproductive organs and the limited anatomical detail that could provide taxonomic clarification, the new plant is referred to the morphotaxon *Psilophytites*, as *Psilophytites svalbardensis* sp. nov., rather than to a whole-plant genus such as *Psilophyton*. *Psilophytites* is an incertae sedis morphotaxon erected by Høeg (1952) to include fragmentary Devonian plant axes that show general psilophyte-like characters, including spines, but lack diagnostic fertile or anatomical features.

Many Early Devonian plants were historically placed within *Psilophyton*, a genus first defined by Dawson in 1859 and later used for leafless, dichotomously branched, spiny plants. However, such assignments are only appropriate where critical characters, particularly sporangial morphology and vascular anatomy, are known. *Psilophyton* is a natural genus defined by paired terminal sporangia on ultimate branches and a centrarch protostele. In the type species, *P. princeps*, the axes also bear fine, non-swollen spines of probable glandular origin (Hueber & Banks, 1967; Banks, 1975). In contrast, the Svalbard specimens show no evidence of sporangial attachment or preserved xylem, and their relationship to any specific natural genus cannot currently be demonstrated.

This follows Høeg's original reasoning that it is "incorrect and unsatisfactory to burden a fairly well-defined, natural genus like *Psilophyton* with 'species' of such uncertain affinities" (Høeg, 1952, p. 213). It is therefore more appropriate to assign

the material to *Psilophytites*, an artificial but conservative repository for indeterminate spiny axes of psilophyte-like habit.

The distinction between sterile spinose euphyllophyte-like axes and zosterophyllalean axes is difficult in the absence of fertile organs. Spines, a strengthened outer cortex or sterome, and anisotomous branching occur in several Early Devonian groups, including species assigned to *Psilophyton* and some zosterophylls. For this reason, the Svalbard material is not assigned to *Psilophyton* or to a zosterophyll genus. Instead, it is retained in *Psilophytites* as a conservative morphotaxonomic placement for sterile spinose axes of uncertain affinity. This cautious approach is consistent with broader discussions of Early Devonian plant morphology, where sterile axes are difficult to assign confidently to natural genera without fertile organs or well-preserved anatomy (Gensel & Berry, 2016).

In Devonian palaeobotany, morphotaxa play an essential role in documenting plant diversity without extending the limits of natural genera. Høeg (1952) recognised this when he established *Psilophytites* as a morphotaxon for sterile, spiny axes lacking fertile organs, noting that his earlier *Psilophyton rectissimum* would more appropriately belong there. Similarly, Gerrienne (1990) suggested that *Psilophyton arcticum* Høeg 1942, another high latitude spinose plant known only from vegetative remains, should also be referred to *Psilophytites* owing to the absence of sporangia or anatomical information.

The assignment of the Svalbard material to *Psilophytites* is therefore a conservative placement, reflecting a common difficulty in early land plant studies where sterile fragmentary axes cannot be confidently linked to natural genera. Many Devonian fossils are morphologically distinctive yet lack the characters required for confident placement within natural genera. Referring the material to *P. svalbardensis* conveys this uncertainty while acknowledging its psilophyte-like habit of leafless, dichotomously branched, spinose axes. This approach provides a consistent framework for comparison with other *Psilophytites* species and related taxa and leaves scope for future reassessment should fertile or anatomically preserved material become available.

Recent revisions of Early Devonian floras from Laurussia illustrate a long-recognised taxonomic difficulty rather than a newly identified problem. In the Rebreuve

assemblage, re-examination of vegetative remains previously described as *Psilophyton* led to the recognition of fertile structures that allowed some specimens to be referred instead to *Sawdonia* (Capel et al., 2022). Likewise, the Consthun flora highlights the continuing difficulty of identifying sterile Early Devonian axes and the need for caution when dealing with fragmentary material (Capel et al., 2024). These studies therefore provide further examples of the longstanding uncertainty surrounding sterile spinose axes, rather than rewriting the earlier taxonomic history of such plants. In this context, the use of *Psilophytites* for the Svalbard material remains the most conservative and appropriate course until fertile or more informative anatomically preserved specimens become available.

Comparison with *Psilophytites rectissimus* and *P. gileppensis*

P. svalbardensis is best compared with the few named species of *Psilophytites*, particularly *P. rectissimus* (Høeg, 1945) and *P. gileppensis* (Gerrienne, 1992).

Psilophytites rectissimus, originally described by Høeg (1945, p. 33) as *Psilophyton rectissimum* from the Lower Devonian of Ringerike in southern Norway, shares with the *P. svalbardensis* the traits of spiny, robust axes with sparse lateral branches. Both show dichotomous to pseudomonopodial branching and similar surface preservation. However, the Norwegian plant, was larger, with axes 4–7 mm wide compared with 1–3.6 mm in *P. svalbardensis*. Branching in *P. rectissimus* was rare and clearly anisotomous whereas the *P. svalbardensis* material shows more frequent division and apparent trichotomies. Axillary swellings are common in the *P. svalbardensis* material but were not described in *P. rectissimus*. Its straight, rigid spines match the *P. svalbardensis* emergences in form, though they appear slightly less regular. In overall aspect the two are closely allied, differing mainly in scale, branching frequency and the presence of axillary tubercles.

Psilophytites gileppensis from the upper Lochkovian to lower Pragian of Belgium provides a closer match. Its axes (1.2–3.8 mm wide) overlap the Svalbard range and show both isotomous and anisotomous branching. A defining feature is the spiny axillary organ, 0.6–1.0 mm thick and up to 10 mm long, which arises between primary and lateral branches. The *P. svalbardensis* specimens possess smaller, non-elongate tubercles in the same position, suggesting a homologous structure that

could be reduced in form. Spine morphology is comparable, *P. gileppensis* bears fine, slightly curved emergences 1.6–4 mm long, whereas the Svalbard plant's spines are straight to faintly recurved and preserved mostly as bases. In both, the emergences are slender and non-swollen, consistent with Høeg's (1942) description of *Psilophyton*-type spines.

P. svalbardensis also shows a distinctive alternating anisotomous, or “zig-zag,” branching pattern not documented in either *P. rectissimus* or *P. gileppensis*. These consistent differences in size, branching architecture and axillary morphology justify recognition of the Svalbard material as a distinct species within *Psilophytites*.

Comparison with other spinose Early Devonian taxa

A wider comparison is needed because several Early Devonian plants have similar combinations of spiny axes, anisotomous branching and small outgrowths close to branch points. *Anisophyton* is a useful comparison because some species have spines and structures associated with the branch angles. However, the Svalbard material differs in several ways. The tubercles are small and do not form the more organised angle organs described in *Anisophyton*. The branching pattern is also different, with repeated alternating lateral branches producing a pseudomonopodial habit. No fertile material has been found, so the plant cannot be confidently linked to *Anisophyton* or any other natural genus.

Margophyton is another useful comparison because it has slender axes and subaxillary tubercles, and has also been discussed as a possible zosterophyll-like plant. However, the Svalbard specimens differ in the combination of dense spine bases, repeated branch-associated tubercles and rare apparent trifurcate arrangements. These features occur together across the material and support treating the Svalbard plant as a distinct species of *Psilophytites*, rather than assigning it to another genus without fertile or better anatomical evidence.

Axillary Tubercles: Morphology and Interpretation

One of the most distinctive features of *P. svalbardensis* is the presence of axillary tubercles at many branching points. These appear as small, rounded protuberances between a primary axis and its lateral branch, or centrally positioned in near-isotomous forks in the axis. They measure 0.5–1 mm across and occur in at least seven well-preserved specimens. The tubercle is consistently associated with the

smaller branch in anisotomous divisions, indicating a close association with the branching process. In trifurcate axes the tubercle is absent, but this does not demonstrate directly that it developed into a third branch, as it may equally have been lost during growth, shed, or not preserved. The safest interpretation is therefore that the tubercle represents a recurrent branch-associated structure, probably representing a localised feature associated with lateral branch initiation. This interpretation is more consistent with comparisons to taxa such as *Gosslingia*, in which subaxillary tubercles are associated with a weakly developed vascular strand and are better understood as structures linked to branch or appendage initiation than as fully dormant buds.

Comparable structures occur in several Early Devonian taxa. Lang and Cookson (1930) described small “axillary bodies” at branching points in *Hostinella* interpreted as possible buds. Edwards (1970) showed that in *Gosslingia breconensis* each branching node bore a subaxillary tubercle penetrated by vascular strands representing the base of a lateral branch or fertile shoot. Similar cortical outgrowths in *Crenaticaulis* were interpreted by Banks and Davis (1969) as aborted branches or fertile appendage bases and comparable bud-like organs occur in zosterophylls such as *Tarella* regarded as dormant branch primordia (Edwards & Kenrick, 1986). The Svalbard material fits this pattern closely: its tubercles occupy the same position and show the same developmental potential though they remain undeveloped in most specimens.

Functionally the tubercles may have acted as reserve meristems enabling regrowth if apices were damaged, increasing vegetative plasticity in an otherwise simple plant. They may also represent incipient reproductive sites analogous to the fertile buds of *Gosslingia* (Edwards, 1970) or the sporangiate axillary organs described in *Thursophyton* (Zalessky, 1937; Edwards & Fanning, 1985) although no direct evidence of sporangia was observed.

From an evolutionary perspective, the presence of axillary tubercles in *P. svalbardensis* suggests that localised tissue differentiation at branching points had already evolved by the Early Devonian. Their consistent position in relation to the smaller lateral axes indicates that they were developmentally linked to branch formation, rather than representing random surface irregularities. They are therefore

best interpreted as a recurrent morphological feature associated with the initiation of lateral branching.

In summary, the axillary tubercles of *P. svalbardensis* are best interpreted as recurrent branch-associated structures, probably linked to lateral branch initiation. Their consistent occurrence at branching nodes suggests a genuine developmental role rather than a surface irregularity, but without anatomical continuity or fertile material their precise function remains uncertain.

Apparent trifurcate branching

Apparent trifurcate branching is rare in the Svalbard *P. svalbardensis* but provides important insight into variation in branch organisation. At least one specimen (Plate 9C, D; Text-Figure 26) shows an arrangement in which two lateral axes diverge in very close proximity from the primary axis, producing the appearance of trifurcation. However, this is better interpreted not as a true three-way division, but as the result of two closely spaced lateral axes arising within a confined apical region. The comparable size and close spacing of the two laterals suggest that they were initiated over a short developmental interval rather than by a simultaneous three-way split. Similar trifurcate appearances have been described in other Early Devonian taxa, including *Psilophyton* and *Sawdonia*, where closely successive branch initiation may produce a comparable arrangement (Edwards *et al.* 1985; Gensel & Andrews, 1984).

A second specimen (Plate 12A; Text-Figure 27) shows a similar configuration. A short lateral emerges just below the main bifurcation, while another diverges from the opposite side of the primary axis, again giving the appearance of trifurcation. The geometry of the specimen suggests that both branches developed in rapid succession within a confined apical zone rather than by simultaneous division.

These observations suggest that the apical region in *Psilophytites svalbardensis* was capable of initiating more than one lateral axis within a short developmental interval. The significance of these specimens therefore lies not in simultaneous three-way division, but in the capacity for closely spaced branch initiation within an otherwise anisotomous branching system.

Absence of Fertile Material

Despite the abundance of material, no sporangia have been identified in the Svalbard specimens of *Psilophytites svalbardensis*. This absence should be interpreted cautiously, as fertile organs are often rare or absent in Early Devonian assemblages and many taxa are represented mainly by sterile vegetative fragments (Edwards & Fanning, 1985; Hotton et al., 2001; Capel et al., 2024). In the present material, the lack of fertile structures is therefore likely to reflect preservational and sampling bias rather than genuine sterility of the plant in life.

The enclosing fine-grained sediments indicate rapid burial within low-energy floodplain deposits, conditions that may have favoured the preservation of more robust vegetative axes while less resistant or more easily detached reproductive portions were lost before burial. If sporangia were borne terminally, laterally, or on specialised short axes, they may have become detached, transported separately, or preserved in parts of the plant not represented in the available collections (Davies et al., 2021; Wellman et al., 2022). It is also possible that fertile organs were produced seasonally or were restricted to specific growth stages, further reducing the likelihood of their preservation.

The absence of fertile material does limit taxonomic resolution, as reproductive structures provide some of the most diagnostic characters for comparison among early tracheophytes (Hueber & Banks, 1967; Edwards, 1970). For this reason, the precise position and morphology of the sporangia in *P. svalbardensis* remain unknown. However, the sterile morphology is itself distinctive. The Svalbard material consistently combines spinose axes, recurrent axillary tubercles, rare apparent trifurcate arrangements produced by closely spaced lateral axes, and limited anatomical evidence for a mechanically strengthened cortex.

These characters form a coherent and repeatable morphological pattern that distinguishes the material from other Early Devonian spiny axes. Although the absence of fertile organs prevents a full whole-plant reconstruction, the available evidence justifies recognition of the Svalbard material as *Psilophytites svalbardensis*. It also highlights the morphological diversity present among early tracheophytes in the low-latitude basins of Laurussia.

Systematic palaeobotany

Genus *Psilophytites* Høeg, 1952

Type species: Psilophytites rectissimus (Høeg) Annaniev 1945

Psilophytites svalbardensis sp. nov.

Diagnosis

Axes slender (1.0–3.6 mm in diameter, mean c. 2 mm), isotomously and anisotomously branched, bearing fine spiny emergences and small axillary tubercles. Spines straight to slightly recurved, arising at approximately right angles to the axis; bases circular to slightly oval, non-swollen. Rare apparent trifurcate arrangements occur, but these are interpreted as the result of two closely spaced lateral axes rather than true three-way division. Axillary tubercles are present at the base of lateral branches, small (≤ 1 mm), hemispherical, and not developed into elongate subsidiary shoots. Cortex thickened, forming a distinct sterome of elongate, thick-walled cells; xylem unknown.

Differential diagnosis

Psilophytites svalbardensis differs from *P. rectissimus* in having narrower axes, more frequent anisotomous branching, recurrent branch-associated tubercles and rare apparent trifurcate arrangements. It differs from *P. gileppensis* in having small, non-elongate tubercles positioned close to the branch axil, rather than elongate spine-like axillary organs and in showing a more regular alternating pseudomonopodial branching pattern. It also differs from comparable spinose zosterophylls and *Psilophyton*-like taxa in the absence of attached fertile organs and in the distinctive combination of dense spine bases, mechanically strengthened outer cortex, recurrent branch-associated tubercles and rare apparent trifurcate branching. In the absence of fertile organs or diagnostic anatomy, these features support recognition of the Svalbard material as a distinct species within the morphotaxon *Psilophytites*.

Holotype: PMF12. (Plate 10B; Text-Figure 24), from the Kapp Petermann locality, Austfjorden Member, Wood Bay Formation, Spitsbergen. Housed in the collections of the Natural History Museum, University of Oslo (TBC).

Horizon and locality: Austfjorden Member, Wood Bay Formation, Pragian, Lower Devonian. Kapp Petermann, north-west Spitsbergen.

Etymology

From Svalbard, Arctic Norway, the region where the specimens were collected.

2.4 Palaeogeography and Diversity of Lower Devonian Plant Assemblages in Svalbard

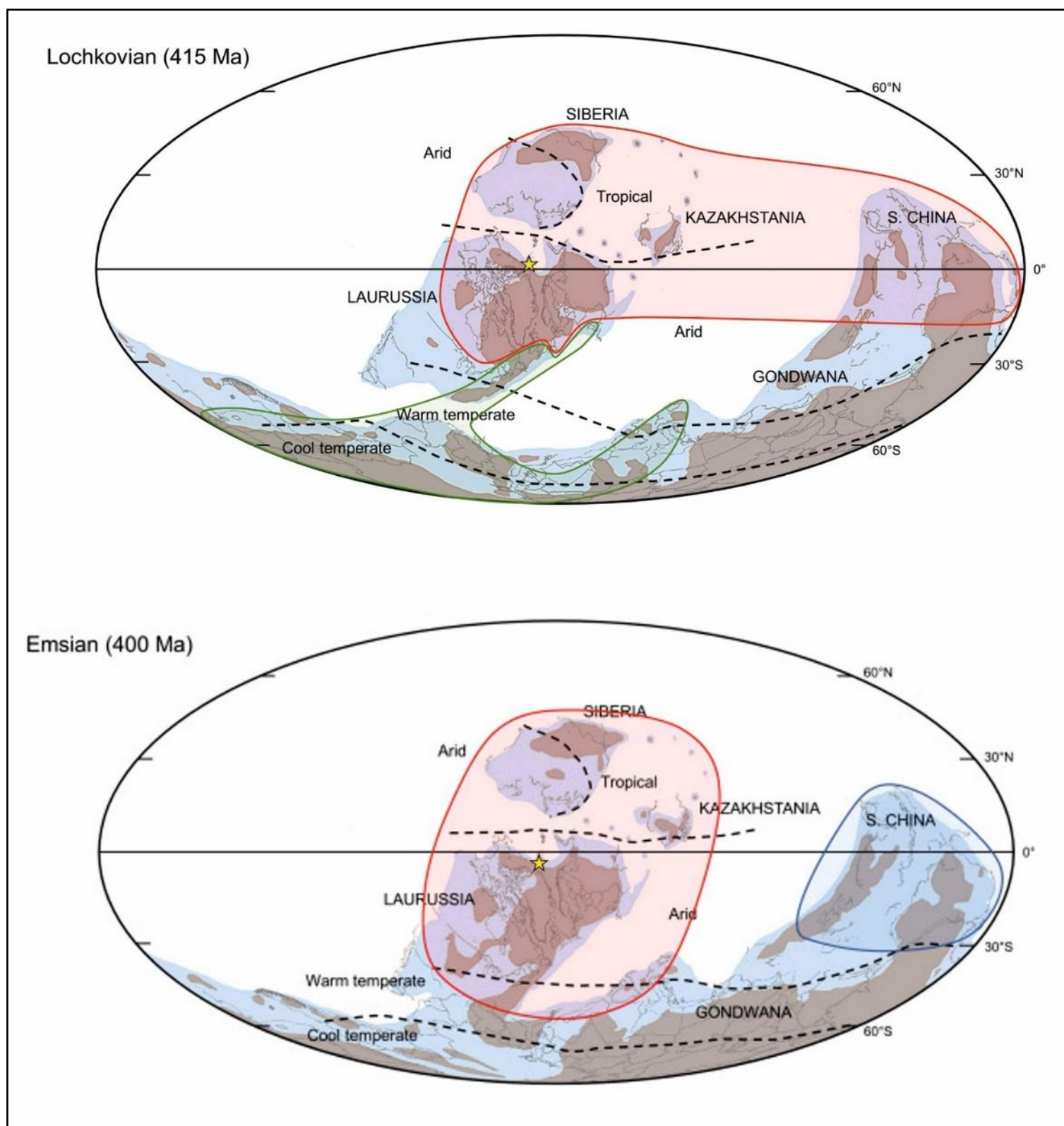
During the Silurian–Lower Devonian, northern Spitsbergen lay close to the equator on the northern margin of Laurussia (Friend & Moody-Stuart, 1970; Davies et al., 2021; Text Figure 31). However, low palaeolatitude does not necessarily indicate a humid tropical setting. Sedimentological evidence suggests that Svalbard occupied a seasonally dry to arid climatic belt, with vegetation established on intermittently wet floodplains, shallow channels and lake-margin settings (Boucot et al., 2013; Davies et al., 2021). The Svalbard assemblages therefore provide a record of low-latitude Early Devonian vegetation under semi-arid equatorial conditions, rather than a humid tropical flora.

Distribution and diversity in the Lower Devonian basin

As well as the individual taxa discussed in the main text, the collections of the 1939 E.N.S. and Høeg expeditions from the Wood Bay Formation have been analysed (Appendix A, B; summarised in Table 8). Mostly morphotaxa similar to those described above were found, including *Hostinella*, *Psilophytites* and *Aphylopteris*. Additional figured specimens and interpretative drawings are provided in Appendix A. Potential *Zosterophyllum* fossils are recognised at several sites, and there are rare occurrences of cf. *Serrulacaulis* and cf. *Drepanophycus*. The assignments to these taxa are tentative and are retained only at generic-comparison level. The cf. *Serrulacaulis* material is based on broad axes bearing marginal, tent-like emergences resembling the saw-like projections described in *Serrulacaulis furcatus* (Hueber & Banks, 1967), although reproductive structures and other diagnostic features are absent. The cf. *Drepanophycus* material is more uncertain: although lycopsid-like and spinose, it lacks clearly preserved leaves or diagnostic appendage organisation comparable with better-known representatives of the genus (Li & Edwards, 1995; Li et al., 2000). Both identifications should therefore be regarded as provisional. True diversity cannot be established because many of the morphotypes may relate to different parts of the same plants. The results suggest that the vegetation was broadly similar across the NW Spitsbergen basin.

Occurrences are plotted on the basin map (Text Figure 32). Table 8 summarises the distribution of morphotaxa and morphotypes recognised in the Wood Bay Formation

material. These assignments are used descriptively rather than as strict biological taxonomic identifications, because much of the material consists of fragmentary sterile axes and may include preservational variants, organ taxa or different parts of the same biological plants. Even with this limitation, the table shows that several recurring axial morphologies are present across the basin. *Aphylopteris*-type and *Hostinella*-type axes occur at multiple localities, while *Psilophytites*-type material is the most consistently recognisable morphotaxon, especially where the distinctive features assigned here to *P. svalbardensis* are preserved. Rarer morphotaxa or comparative assignments, including cf. *Zosterophyllum*, cf. *Serrulacaulis* and cf. *Drepanophycus*, appear to be more localised. The assemblage is therefore best interpreted as a low-diversity flora dominated by simple axial morphologies, rather than as a high-diversity flora of confidently separated biological taxa.



Text Figure 31. Lochkovian and Emsian/Pragian phytogeography. The position of Svalbard is marked with a star. In the Lochkovian, two phytochoria are recognised, Equatorial to mid-latitudes (red) and South Laurussia-Western Gondwana (blue). In the Pragian-Emsian, the latter is replaced by NE Gondwana. Climatic Belts from Boucot et al. 2013. Palaeogeography from Scotese *et al.* (2021). From Capel et al., 2023.

Phytogeography

Recent work by Capel et al. (2023) has substantially refined previous attempts to analyse Devonian plant phytogeography. Their database and analysis provide the framework for the discussion below.

Lochkovian Phytogeography.

Capel et al. (2023) recognised two well distinguished phytochoria, the Equatorial to mid-latitudes phytochorion and the South Laurussia-Western Gondwana phytochorion (Text-Figure 31). The record of *Zosterophyllum* from Buchananhalvøya was included in their analysis. Capel et al. (2023) evaluate that *Zosterophyllum* is found in 92% of their sampling areas within the Equatorial and mid-latitude phytochorion at this time.

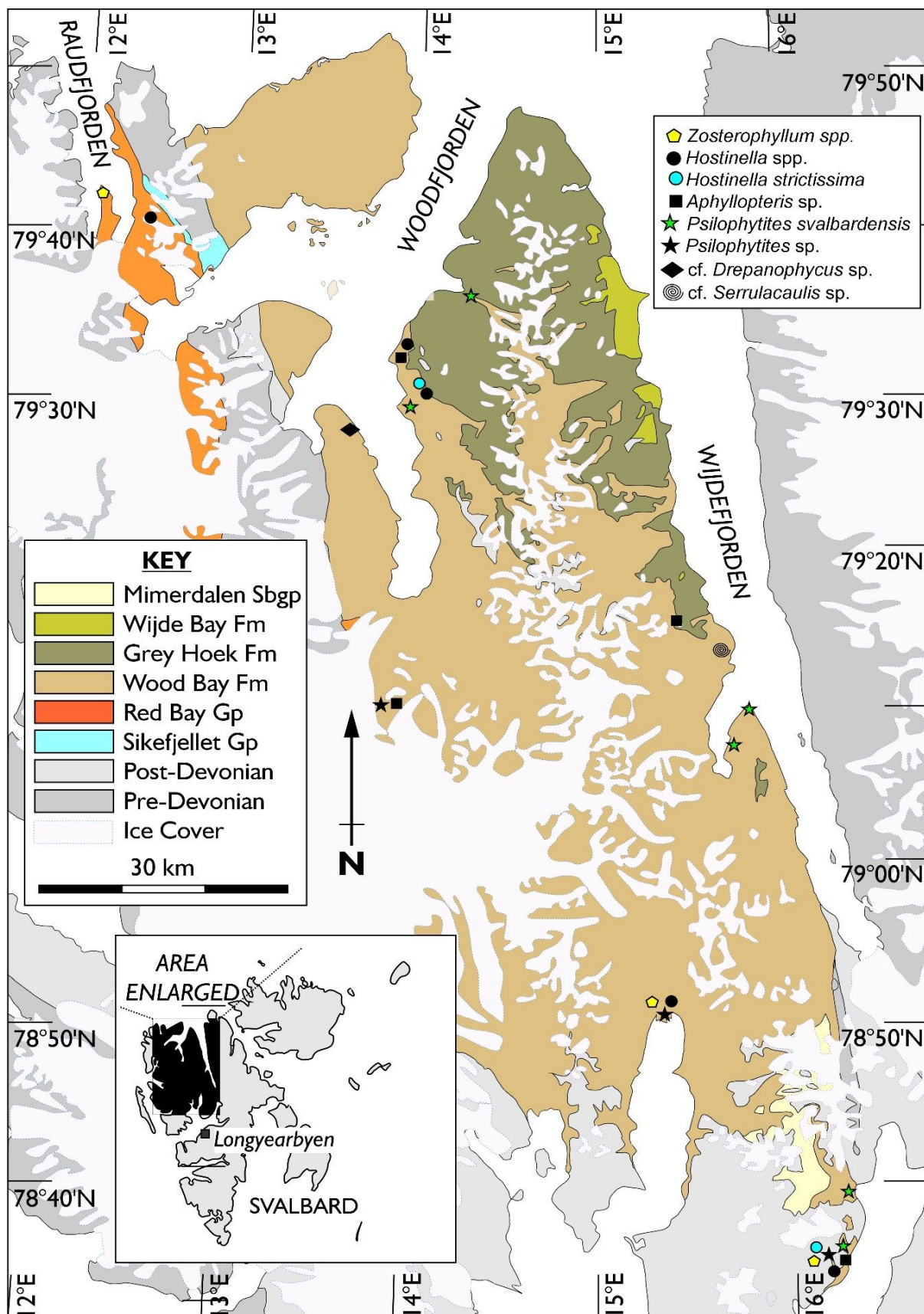
Pragian and Emsian Phytogeography

Across the Wood Bay Formation, assemblages are consistently low in richness dominated by branching axes which may have been euphyllophyte, with also strong representation from zosterophylls. Global diversity of zosterophylls was at an all time high at this time (Cascales-Miñana & Meyer-Berthaud, 2014).

Capel et al. (2023) recognised that, by the Pragian–Emsian, the Equatorial to mid-latitude phytochorion had expanded southwards into parts of Gondwana, while South China was resolved as compositionally distinct and placed within the NE Gondwana phytochorion. The second phytogeographic unit is now the NE Gondwana phytochorion (Text Figure 31), centred on the South China block. Phytochoria are weakly differentiated compared with the Lochkovian, and the Equatorial to mid-latitude phytochorion is dominated by *Zosterophyllum*, *Psilophyton* and *Drepanophycus*.

Capel et al. (2023) show provincialism peaks in cooler windows and relaxes in warmer phases. In the Silurian–Lochkovian, two well-separated units are resolved ($R \approx 0.67$; rhyniophytoid-rich South Laurussia–West Gondwana vs zosterophyll-rich equatorial belts). By the Pragian–Emsian the separation weakens ($R \approx 0.44$) as taxa disperse across low latitudes; the Middle Devonian tightens again (four phytochoria, $R \approx 0.77$) before Late Devonian homogenisation ($R \approx 0.46$). The Wood Bay assemblages are consistent with this broader pattern of reduced provincialism and

widespread low-latitude taxa during the Pragian–Emsian, although their low diversity may also reflect local environmental and preservational controls, contrasting with more humid belts in South China where diversity is higher and preservation of fertile parts is more common. The Silurian–Lower Devonian record in Svalbard captures the first basin-wide spread of land plants under semi-arid equatorial conditions. In line with Capel *et al.* (2023), diversity is low and endemism weak; the principal advance here is spatial and stratigraphic rather than taxonomic, showing where within the basin architecture plants lived and were preserved and placing Svalbard in the Equatorial–mid-latitude phytochorion of the Pragian–Emsian during a phase of reduced provincialism.



Text Figure 32. Distribution of Early Devonian taxa across the basin, plotted on a basemap from Neil Davies. Locality names are given in Text Figure 1A.

Locality Name	Sub locality	<i>Aphylopteris</i>	<i>Hostinella</i>	<i>Hostinella strictissima</i>	<i>Psilophytites</i>	cf. <i>Serrulacaulis</i>	cf. <i>Drepanophycus</i>	cf. <i>Zosterophyllum</i>
2 nd Valley N Skansbukta								<i>Z. longum</i>
Kapp Petermann					<i>Psilophytites svalbardensis</i>			
Sjettedalen		SJ1, SJ2, SJ3						
Sørliefjellet					<i>Psilophytites svalbardensis</i>			
Jørgensendalen					<i>Psilophytites svalbardensis</i>			
Mt Skansen		M1	M3		M2			
Sigurd fjellet		M1			M2			
Jakobsenbukta					<i>Psilophytites svalbardensis</i>			
Prismefjella		P1	P2					
Verdalen			V3	V2				
Krosspyntdalen						KD1		
Kronprinshøgda							KD1	
Dickson's Bay			M3		M2			D1
Klaas Billen Bay	III	M1		Yes	L1			L2
Nordenskiöld Cairn	∞			Yes	M2			
Nordenskiöld Cairn	≈				<i>Psilophytites svalbardensis</i>			
Beach section	Ø	M1						
Nordenskiöld Cairn	~			Yes	N1			
Nordenskiöld cairn	⊗	N1, M1		Yes	L1, N1			
Red bolts site	V	M1, S3			B1			

Table 8. Summary of morphotypes found in the wider Wood Bay Formation of NW Spitsbergen, based on collections from the 1939 E.N.S. and Høeg Expeditions. See Appendix A, B.

Overview and synthesis of findings

In this chapter, I have:

- 1) Identified and described the oldest vascular plant in Svalbard, *Zosterophyllum fertile* Leclercq, from the Lochkovian Andréebreen Formation, Red Bay Group.
- 2) Described a new easily recognisable morphotype, *Psilophytites svalbardensis*, from the Pragian/Emsian Wood Bay Formation.
- 3) Using historical collections, mapped the diversity and distribution of morphotypes in the North West Spitsbergen Devonian Basin.
- 4) Confirmed a relatively low level of taxonomic diversity compared with other areas of similar age.

These findings directly address the aims of this chapter, defining the composition, diversity and environmental context of the earliest vascular plant assemblages in Svalbard.

Comparison with Previous Work

The low diversity recorded here accords with Høeg's (1942) original account and the later syntheses of Capel et al. (2023), both of which noted the scarcity of species and the dominance of zosterophylls in the Lower Devonian of Svalbard. Re-examination of several hundred specimens from the English Norwegian Swedish and Høeg collections, together with new material, confirms this pattern and refines the spatial and stratigraphical context of the fossils. The recurrence of a small set of simple morphotypes: *Zosterophyllum*, *Psilophytites*, *Aphylopteris* and *Hostinella*, with rare *cf. Drepanophycus* and *cf. Serrulacaulis*, across multiple localities indicates a uniform flora across the Lower Devonian basin rather than local endemism.

Other Laurussian floras, including those of the Welsh Borderland, the Belgian Ardennes and the Gaspé region, contain a greater range of taxa and more frequent fertile or anatomically preserved material, potentially reflecting more stable substrates and broader taphonomic conditions that enabled the preservation of such features (Edwards & Wellman, 2001; Hotton et al., 2001). Bathurst Island provides another useful low-latitude comparison, as its flora ranges from the Late Silurian into the Early Devonian, including Pragian material, and was also deposited at near-equatorial palaeolatitudes (Kotyk, 1998; Kotyk & Basinger, 2000; Kotyk et al., 2002). However, the Bathurst Island assemblage differs from Svalbard in being preserved in marine sediments, with plant material transported offshore, and is therefore not directly equivalent to the fluvial and floodplain assemblages of the Red Bay and Wood Bay formations. The limited diversity in Svalbard is therefore unlikely to reflect collection bias alone, and probably reflects a combination of environmental, preservational and sampling controls. Capel et al. (2023) provide a useful global framework for interpreting these patterns, although diversity comparisons remain limited by taxonomic uncertainty, uneven sampling and preservational differences between assemblages. Their analysis suggests that Silurian–Lochkovian equatorial floras were taxonomically restricted and dominated by zosterophylls, with more cosmopolitan elements persisting into the Pragian–Emsian. The uniform composition of the Svalbard assemblages is consistent with this broader low-latitude pattern.

Recent palynological analysis of the Red Bay Group (Wellman et al., 2022) provides independent support for the low diversity recorded in Svalbard. Lochkovian spore assemblages comprise only a small number of species and are dominated by simple trilete forms, including *Retusotriletes* and *Ambitisporites*. This composition parallels the Lochkovian macrofloral record described here from Svalbard, in which a few recurring form taxa account for almost all specimens. Both datasets therefore reflect the same depauperate vegetation recorded in Svalbard during the Early Devonian.

Global compilations indicate a gradual rise in plant diversity through the Lochkovian–Pragian (Gensel & Andrews, 1984; Capel et al., 2023), yet the diversity of the Svalbard assemblages remained compositionally conservative. By contrast, floras from tropical South China and peri-Gondwanan regions, such as the Posongchong assemblage, have yielded a wider range of taxa, including early lycopsids. This contrast should, however, be treated cautiously, because these assemblages differ

from those of Svalbard in preservational style and in the abundance of fertile and anatomically informative material. Part of the apparent difference in diversity may therefore reflect preservational bias as well as genuine ecological variation.

Nevertheless, the South China assemblages are associated with evidence for more persistent humidity, including in-situ rooting and better-developed soils (Hao & Xue, 2013), suggesting that environmental differences also contributed to greater taxonomic and ecological differentiation. By contrast, the semi-arid, seasonally flooded floodplains of the Wood Bay basin (Friend & Moody-Stuart, 1970; Davies et al., 2021; Capel et al., 2023) were likely colonised intermittently by opportunistic plants adapted to disturbance and periodic desiccation.

Diversity and palaeoecological implications

Despite their low taxonomic diversity, the assemblages provide valuable insight into early land-plant ecology under equatorial conditions and represent the first basin-level analysis of Lower Devonian floras in Svalbard. They document low-diversity vegetation dominated by small axial plants occupying disturbed floodplain environments. This ecological simplicity reflects the character of the Svalbard assemblages, in which diversification is expressed mainly in external morphology and branching architecture, while anatomical information remains limited because of preservational bias.

The addition of *Psilophytites svalbardensis* expands the morphological range of the flora and shows that even within a low-diversity community, limited experimentation in form was underway. Its distribution across several localities within the Wood Bay Formation suggests it was a widespread element of the early floodplain vegetation. At basin scale, the consistent composition of assemblages from Woodfjorden, Wijdefjorden and Austfjorden indicates minimal ecological differentiation.

These findings align with the interpretation of Capel et al. (2023) that Early Devonian equatorial Laurussian floras showed broad compositional similarity, weak provincialism and low endemism, rather than strict taxonomic uniformity. The low diversity of the Svalbard assemblages is also broadly comparable with other Lochkovian–Pragian Laurussian floras, including those of the Welsh Borderland, where assemblages are dominated by small axial plants and zosterophylls but

remain limited relative to later Devonian floras (Edwards, 1970; Edwards & Wellman, 2001; Capel et al., 2023).

By contrast, South China preserves more diverse and structurally varied Early Devonian floras, including assemblages with better evidence for rooting, fertile organs and ecological differentiation (Hao & Xue, 2013). This contrast may partly reflect environmental differences, particularly water availability and substrate stability, but it is also influenced by differences in preservation and sampling. As both Svalbard and South China have been placed within low-latitude climatic belts during parts of the Early Devonian, detailed sedimentological and taphonomic comparison is needed before diversity differences can be interpreted as purely ecological.

Sedimentological and palaeosol evidence indicates that the Red Bay and Wood Bay formations developed on low-gradient floodplains under semi-arid, seasonally wet conditions (Friend & Moody-Stuart, 1970; Davies et al., 2021; Capel et al., 2023). Intermittent flooding and oxidation governed both plant distribution and preservation, favouring short-lived colonisation by opportunistic taxa. By contrast, South China supported more diverse and structurally complex vegetation, where persistent water availability may have promoted greater taxonomic and ecological differentiation (Hao & Xue, 2013). Detailed sedimentological comparison is needed to clarify whether water availability was a major factor in this contrast, as both Svalbard and South China are suggested to have occupied the same arid belt during the Pragian and Emsian (Capel et al., 2023; Text Figure 31).

Limitations

The main limitations of this study arise from the fragmentary nature of the material and uneven sampling across localities, a common challenge in Lower Devonian plant assemblages. Most specimens are preserved as sterile compressions with no internal anatomy, which limits interpretation of structure and evolutionary relationships (Edwards, 1996). The lack of anatomically preserved material makes it difficult to compare directly with better-preserved assemblages, such as those from the Rhynie Chert, where plant form and physiology can be reconstructed in detail. Temporal resolution between the Siktefjellet, Red Bay and Wood Bay formations is also coarse, preventing finer-scale assessment of evolutionary or ecological change through the Silurian–Pragian time interval. Many of the samples collected by the

1939 expeditions lack accurate locality information and sedimentary context, making understanding of the habitat of plants impossible.

Future Directions

Future work should focus on locating in-situ plant assemblages and permineralised horizons capable of preserving internal anatomy. This would allow more detailed comparison with anatomically preserved floras elsewhere in Laurussia, such as the Rhynie Chert (Edwards, 1996), and help clarify growth form and tissue organisation in taxa that are currently known only from compressions. Targeted field mapping and new measured sections through the Red Bay and Wood Bay formations would improve stratigraphic control and make it possible to place plant occurrences more precisely within the basin succession.

Further progress will also depend on expanding palynological and microfossil studies to capture cryptic diversity not visible in the macrofossil record (Wellman et al., 2022), from the Lochkovian into the Pragian/Emsian. Combining spore and megafossil data across localities could provide a more complete view of community composition and reproductive strategy.

As Laurussia and South China are both interpreted to have occupied low palaeolatitudes within an arid climatic belt during the Lochkovian–Emsian, based on sedimentological evidence (Boucot et al., 2013; Text Figure 31B), comparison with contemporaneous floras from Kazakhstan and eastern Siberia may help clarify whether the Svalbard and South China assemblages reflect regional ecological variation within Early Devonian low-latitude vegetation.

Comparative sedimentological and taphonomic studies across Laurussian, Gondwanan, Siberian and Kazakhstani basins would help separate environmental from preservational controls on apparent diversity (Hao & Xue, 2013). Integrating these lines of evidence within updated stratigraphic and palaeoecological models will improve understanding of how early vascular plants colonised equatorial landscapes and adapted to climatic variability through the Devonian. These studies would help clarify the climatic and ecological limits that shaped Early Devonian plant communities, providing a framework for interpreting later increases in vegetation complexity and the development of Middle–Late Devonian forest ecosystems.

Chapter III: Perspectives on Devonian Tree Floras: Archaeopteridales and Lycopsids

Geological Setting: Middle–Late Devonian Stratigraphy of Mimerdalen, Dicksonland

Contextual Introduction

Within the Old Red Sandstone (ORS) of Svalbard, the Mimerdalen Subgroup forms the upper part of the Andrée Land Group. It overlies the Pragian–Emsian Wood Bay Formation (Text Figure 33) and passes upward into Frasnian strata (Friend, 1961; Harland, 1997; Piepjohn & Dallmann, 2014; Davies *et al.*, 2021). A pronounced unconformity separates the Wood Bay Formation from the overlying Mimerdalen Subgroup, widely attributed to tectonism associated with the Ellesmerian Orogeny. Drainage reorganisation during strike-slip faulting further constrained the distribution of the preserved groups (McCann, 2000; Davies *et al.*, 2021).

The best-exposed sections are found in Dickson Land, including Mimerdalen and Munindalen, though thrusting (notably the Munindalen Thrust), subsequent deformation and erosion complicate correlation between sections and estimates of true stratigraphic thickness (Dallmann, 1999; Piepjohn & Dallmann, 2014). Rather than spanning most of the Givetian – Famennian (Schweitzer, 1999; Piepjohn and Dallmann, 1999), the deposits are now recognised to have been formed in a few million years spanning the Givetian / Frasnian boundary (Berry & Marshall, 2015; Text Figure 33), i.e. late Mid Devonian and early Late Devonian.

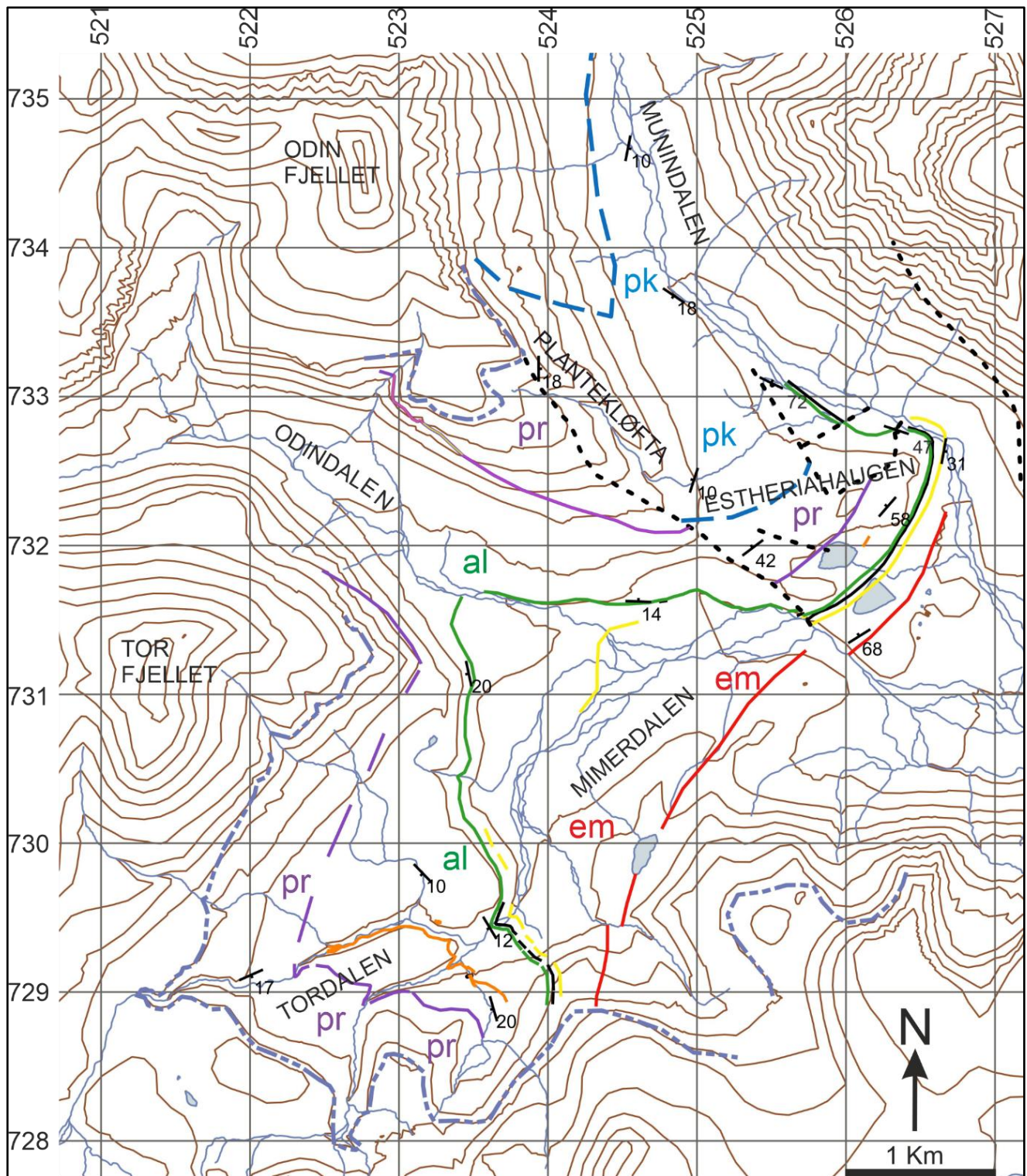
Mimerdalen Subgroup

The youngest successions of the Old Red Sandstone (ORS) in Svalbard are exposed in the south-eastern part of the Devonian Andrée Land Basin, particularly in Dickson Land, including Mimerdalen and Munindalen (Text Figures 33, 34). This interval, traditionally referred to as the “Mimerdalen Series” or “Mimer Valley Series” (Vogt, 1938, 1941; Friend, 1961), is now formally recognised as the Mimerdalen Subgroup.

There has been extensive investigation into the stratigraphy of the Mimerdalen Subgroup (Fig. 4 in Piepjohn & Dallmann, 2014). Early stratigraphic work subdivided the succession into the Estheriahaugen and Fiskekløfta “Formations,” overlain by the Planteryggen Sandstone and the Plantekløfta Conglomerate (Vogt,

Chronostratigraphy	Lithostratigraphy	Informal stratigraphy	Stratigraphic logs	Description of strata
Late Devonian (Frasnian)	Plantekløfta Formation	upper Svalbardia sandstone		Alternation of dark-grey mudstone, siltstone and thick beds of brown-weathering coarse conglomerate with some interbedded layers of red and green sandstone.
	Planteryggen Formation	Muninella Member		Sandstone and conglomerate with two light-green marker horizons of sandstone and conglomerate.
		Odineiva Member		Predominantly red and green, fine- to coarse-grained sandstone, partly violet and cherry-red coloured. Violet, white and green polymict sandstones. Basal conglomerate with pebbles derived from Fiskekløfta member below.
Mid Devonian (Givetian)	late Givetian	Fiskekløfta Member	lower Svalbardia sandstone	Yellow orange white sugary sandstones, in places large numbers of large plant stems.
			Asterolepis sandstone	Mainly siltstone with Fe-nodules and trace fossils. Dark-grey mudstone with Fe nodules.
			Fish Ravine Shale	Green, light-grey to dark brown, fine- to medium-grained sandstone, partly intercalated with mudstone. Predominantly dark mudstones and grey sandstone, extremely rich in fish fossils.
	mid Givetian	Tordalen Formation		Yellow sandstones with <i>Cruziana</i> , ?cannel coal
			Black Shale II	Fine - medium, cross-bedded sandstone, intercalated layers of dark siltstone and mudstone with fish fossils in nodules.
			Black Shale I	Increase of sandstone towards the top. Fe nodules. Alternation of dark mudstone, green and red layers of siltstone with Fe nodules. Grey sandstone.
E Dev	Wood Bay Fm.	Porolepis Sandstone		Green and red sandstones

Text Figure 33. Stratigraphic summary of the Mimerdalen Subgroup by Berry & Marshall (unpublished), showing chronostratigraphy, lithostratigraphy, informal stratigraphy and sedimentological characteristics with descriptions of each layer. Geology modified from Piepjohn & Dallmann (2014). Updated chronostratigraphy from Berry & Marshall (2015). Coloured lines indicate the base of prominent stratigraphic units, with boundaries marked on the geological map in Text Figure 34. The lithostratigraphy column illustrates the division of geological units. Sedimentological log is unmodified from Piepjohn & Dallmann (2014). Thicknesses are not shown to scale, but the log allow direct comparison of units across the subgroup.



Text Figure 34. Geological map of Munindalen and Mimerdalen showing the distribution of the Mimerdalen Subgroup. Map created by Berry and Marshall (unpublished) based on field observations from 2010–2023, with stratigraphic units modified from Piepjohn & Dallmann (2014). Colours correspond to the base of stratigraphic units shown in Text Figure 33. Key features (e.g. Munindalen, Tordalen, Plantekløfta, Estheriahaugen) are indicated. Localities refer to those described in Text Figure 33: pr = Planteryggen, pk = Plantekløfta, em = Estheriahaugen Member, alp = Asterolepis Sandstone. The map illustrates the spatial extent of formations within the subgroup and their relationship to one another. Grid = UTM zone 33N.

1938, 1941; Friend, 1961). Subsequent revisions redefined the Estheriahaugen and Fiskekløfta units as Members of the Tordalen Formation, while the Planteryggen and Plantekløfta were retained at formation rank (Murašov & Mokin, 1979; Piepjohn & Dallmann, 2014). This framework is adopted here and this account below relies heavily on the work of Piepjohn & Dallmann (2014).

The Mimerdalen subgroup spans the mid–late Givetian into the early Frasnian and is of particular significance for palaeobotany, encompassing all of the stratigraphically relevant localities for Middle–Late Devonian plant assemblages in Svalbard. These include the *Protolepidodendropsis pulchra* forests of the Plantekløfta Formation (Berry & Marshall, 2015) and occurrences of *Archaeopteris*, formerly *Svalbardia polymorpha*, which together underpin the plant descriptions that follow in this chapter.

Tordalen Formation

The Tordalen Formation forms the basal unit of the Mimerdalen Subgroup, resting unconformably on the Dicksonfjorden Member of the Wood Bay Formation (Piepjohn & Dallmann, 2014). It is formally divided into two members: the Estheriahaugen Member and the Fiskekløfta Member. These subdivisions are described in detail below.

Estheriahaugen Member

The Estheriahaugen Member (Text Figure 34) reaches several hundred metres in thickness (Piepjohn & Dallmann, 2014). It rests sharply and disconformably upon the Dicksonfjorden Member of the Wood Bay Formation, with the lower boundary defined by the transition from red sandstones and siltstones into overlying grey and green beds (Pčelina *et al.*, 1986). This colour shift is a prominent field marker across the area (Text Figures 33, 34 - red line)

Lithologically, the unit is characterised by thinly bedded grey and greenish siltstones with interbedded fine- to medium-grained, well-sorted sandstones that are typically light grey to pale green, occasionally reddish. Thick mudstone intervals in the lower and upper parts of the succession correspond to Vogt's (1941) "Black Shale I" and "Black Shale II," respectively (Text Figure 33). The latter horizon was re-examined by Newman *et al.* (2019A, Text Figure 3 labelled A), although note their stratigraphic

placement has since been revised. The upper part of the Estheriahaugen Member is marked by a resistant package of hard, yellow quartzitic sandstones that forms a distinctive marker bed on regional logs and outcrop sections (Text Figures 33, 34 -; yellow line at base)

Palynological assemblages confirm a mid Givetian age (Berry & Marshall, 2015). These assemblages, dominated by *Geminospora* and related taxa, provide the primary biostratigraphic control for the unit. Diverse fossil fishes from the Black Shale II are currently being described from Eastern Estheriahaugen (Newman *et al.* 2019A & B). Fossil plants discovered in 2022 and 2023 field seasons from the same locality form the first significant reports from the oldest Member of the Mimerdalen Subgroup and include branches and trunks of *Archaeopteris* and the crown of *Protolepidodendropsis pulchra* described below.

Fiskekløfta Member

The Fiskekløfta Member directly overlies the Estheriahaugen and represents a late Givetian interval according to palynological studies (Berry & Marshall, 2015). It has a total thickness of ~200–260 m and includes three distinct units: the Fish Ravine Shale, the *Asterolepis* Sandstone and the Lower *Svalbardia* Sandstone. Although early accounts restricted the Fiskekløfta to only the first two units, more recent stratigraphic revisions have shown that the Lower *Svalbardia* Sandstone, formerly assigned to the Planteryggen Formation, is part of the Fiskekløfta (Piepjohn & Dallmann, 2014).

The Fish Ravine Shale (Text Figures 33, 34 - black line) is 100-150 m thick and consists of thinly laminated, intensely cleaved black mudstones (<1 mm laminae) with some coalified plant remains, siltstones and fine sandstones (Piepjohn & Dallmann, 2014). Black mudstones include iron / clay nodules containing fish and rare permineralized plants. The lower boundary of the Fiskekløfta is defined by the abrupt onset of these dark mudstones above the grey and green siltstones and yellow sandstones at the top of the Estheriahaugen Member.

The *Asterolepis* Sandstone (Text Figures 33, 34 - green line) is 50–79 m thick and consists of fine-grained grey green to dark brown sandstones. The unit also preserves calcareous Fe nodules, conchoidal cleavage in the lower beds and muscovite-rich sandy siltstones in the upper parts. Trace fossils such as *Chondrites*

and the presence of Fe-rich clay galls signal biogenic activity (Pčelina *et al.*, 1986; Michaelsen, 1998). Plant fossils are rare but include *Protolepidodendropsis pulchra* and *Archaeopteris*.

The Lower *Svalbardia* Sandstone (Text Figures 33, 34 - orange line) is 55–85 m thick and forms a striking marker horizon of white to light grey, “sugar-like” massive and thick-bedded quartzose sandstones (Pčelina *et al.*, 1986; Michaelsen, 1998). The upper part of the unit passes into colourful silty fine sandstones interbedded with grey siltstones and mudstones, including palaeosols (Davies *et al.* 2021, Figure 7C, 8D). These beds yield abundant trace fossils, and critically, large parautochthonous plant material including branches and trunks up to 3 m long (Davies *et al.* 2021, Figure 7C, 8D). In Tordalen the grey mudstones have spores of latest Givetian age (Berry & Marshall, 2015).

Planteryggen Formation

The Planteryggen Formation overlies the Fiskekløfta Member, forming the middle part of the Mimerdalen Subgroup (Text Figures 33, 34; purple line). It has a thickness of ~335 m.

Lithologically, the unit consists of a succession of multicoloured medium- to coarse-grained sandstones, ranging from red and violet to grey, white and green, interbedded with shaly siltstones. Massive conglomeratic beds are also present, but exposures are generally poor and laterally indistinct (Pčelina *et al.*, 1986; Brinkmann, 1997; Piepjohn & Dallmann, 2014).

Plant material is scarce and restricted to large, indeterminate fragments and the unit has yielded little palaeontological information. An early Frasnian age is suggested based on palynology of the underlying and overlying units. Its significance lies chiefly in providing a lithological transition into the overlying Plantekløfta Formation, where well-preserved early Frasnian plant assemblages occur.

Plantekløfta Formation

The Plantekløfta Formation (Text Figures 33, 34 - blue line) is the youngest unit of the Mimerdalen Subgroup, overlying the Planteryggen Formation, and is now dated palynologically to the early Frasnian (Berry & Marshall, 2015). Its thickness has been variously estimated at >100 m (Vogt, 1941; Murašov & Mokin, 1979), 100–125 m

(Pčelina *et al.*, 1986) and a minimum of 300 m (Brinkmann, 1997; Michaelsen, 1998). It is named after the dramatic stream-ravine which falls from Odinfjellet to the northwest of Estheriahaugen (Text Figure 34).

Geographically, the unit is restricted to Munindalen and adjacent ridges, extending from Estheriahaugen and Plantekløfta in the south to the ridge between Caiusbreen and Stensiöbreen in the north. Its eastern boundary is cut by the lower Munindalen Thrust, which emplaced the Lower Devonian Austfjorden Member westwards over the Plantekløfta succession (Brinkmann, 1997; Michaelsen, 1998). Undoubtedly it is this tectonic activity which generated the large clasts of the conglomerate.

The lithology is dominated by green to dark grey siltstones and mudstones interbedded with thin (≤ 10 cm) red and green layers and occasional sandstone lenses. Characteristic deposits are chaotic conglomerates, up to 15 m thick, comprising dark grey to dark brown coarse material with rounded clasts up to 40 cm in diameter, often coated with reddish-brown to black Fe–Mn crusts (Brinkmann, 1997; Michaelsen, 1998; Piepjohn & Dallmann, 2014).

The Plantekløfta Formation is of exceptional palaeontological significance. Multiple horizons preserve *in situ* fossil forests, including dense monospecific stands of *Protolepidodendropsis pulchra* with estimated densities of ~140,000 stems per hectare and scattered archaeopterid trunks (Berry & Marshall, 2015). On Odinfjellet, a 1 m thick band of grey–green sandstone yields the rich “Upper Svalbardia Sandstone” flora of Høeg (1942), including *Svalbardia polymorpha* (= *Archaeopteris*), *Enigmophyton*, *Protolepidodendropsis pulchra* and *Ibyka vogtii* (Berry 2005), previously misassigned to the Planteryggen Formation (Berry & Marshall, 2015).

This is the most diverse plant assemblage in the area. Sedimentologically, the succession records small fluvial channels, vegetated floodplains and debris-flow conglomerates sourced from uplifted highlands during the onset of the *Svalbardian* tectonic event (Piepjohn & Dallmann, 2014).

The preservation of vegetation-induced sedimentary structures (VISS), including scour and mound forms and upturned laminae provide some of the earliest global evidence of arborescent vegetation actively shaping sedimentary processes (Davies *et al.*, 2021).

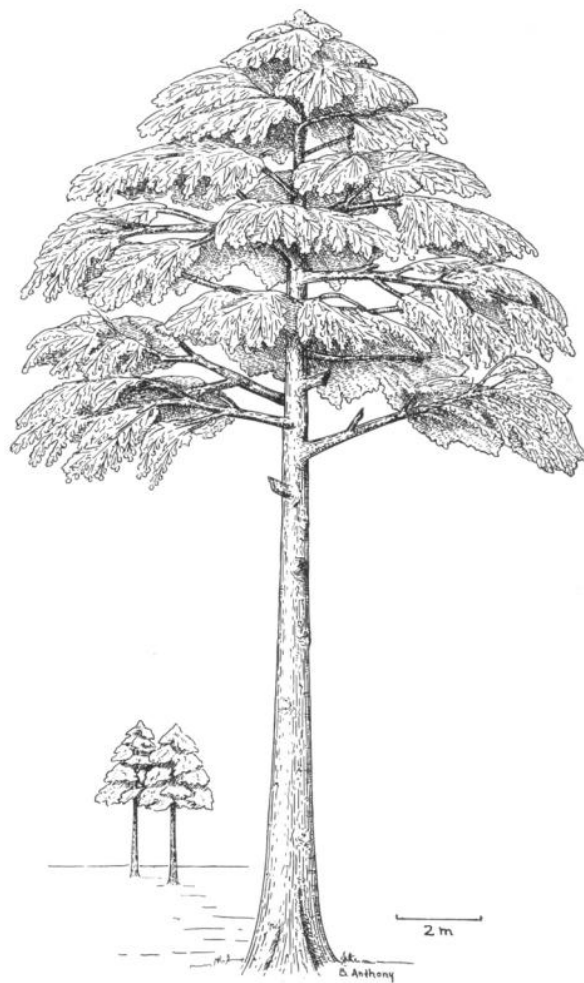
Summary

In summary, the Mimerdalen Subgroup represents the uppermost Old Red Sandstone succession in central Spitsbergen, spanning from the mid–late Givetian into the early Frasnian. It charts a progression from the lacustrine siltstones and sandstones of the Estheriahaugen Member, through the fossil-rich mudstones and sandstones of the Fiskekløfta Member and its distinctive Lower *Svalbardia* Sandstone, into the multicoloured sandstones of the Planteryggen Formation. The sequence culminates in the Plantekløfta Formation, where fluvial sandstones and coarse conglomerates preserve some of the earliest *in situ* forests. Taken together, the subgroup provides the stratigraphic and sedimentological framework for understanding Middle–Late Devonian landscapes in Svalbard and it sets the geological stage for the earliest tropical forest ecosystems. The following chapter focuses on this palaeobotanical record, examining in detail the remains of *P. pulchra* and *Archaeopteris*.

Part III:

Archaeopteridalean Trees from the Mimerdalen Subgroup

Chapter 3.1A. *Svalbardia polymorpha* and
Actinopodium nathorstii



Text Figure 35. Reconstruction of the growth habit and morphology of *Archaeopteris*, Beck (1962).

1. Introduction to *Archaeopteris* and *Callixylon*

Archaeopteris is a key genus emblematic of the Devonian transition to a forested planet, representing the first link between the 'primitive' spore-bearing plants of the Early Devonian and the seed-plant lineage that would later diversify in the Late Carboniferous (Kenrick & Crane, 1997). As an early progymnosperm, it reproduced by spores yet possessed gymnosperm-like wood, and could reach heights of up to 30 m, becoming a dominant component of palaeo-equatorial and warm-temperate ecosystems by the Late Devonian (Marshall *et al.*, 1996; Cornet *et al.*, 2012; Stein *et al.*, 2020).

Its earliest known occurrence is in the Middle Devonian, including rooting systems preserved in the well-known fossil forest at Cairo, New York (Stein *et al.*, 2020). By the Famennian, *Archaeopteris* had become widespread and ecologically dominant, with large individuals up to 20 m tall documented even at high palaeolatitudes (~70° S) in the Late Devonian of South Africa (Gess & Berry, 2024), indicating both a broad global distribution and a wide ecological tolerance (Fairon-Demaret & Leponce, 2001; Cressler, 2006; Guo & Wang, 2009). Over the ~20 million years from the Mid to Late Devonian, this evolutionary success likely coincided with increasing specialisation in growth and branching architecture, as *Archaeopteris* evolved greater structural complexity and ecological versatility.

The taxonomic history of *Archaeopteris* is long and complex (Wang *et al.*, 2011). It began with the discovery of fern-like fronds, initially described as *Cyclopteris hibernicus* by Edward Forbes (1853). These fossils were reclassified several times, with Dawson introducing the name *Archaeopteris*, though initially only as a subgenus of *Cyclopteris*. Stur's 1875 revision formally recognised *Archaeopteris* as a distinct genus.

A major turning point came in the twentieth century with the work of Beck (1960a, 1960b), who first established the connection between leafy fronds of *Archaeopteris* and anatomically preserved wood assigned to *Callixylon*. The direct association of these fern-like fronds with *Callixylon* provided the first evidence that *Archaeopteris* was a large, woody tree with substantial lateral branches. This discovery enabled a detailed reconstruction of its growth habit (Beck, 1962) (Text Figure 35). Beck (1960b) also introduced the concept of *Archaeopteris* as a progymnosperm.

2. Significant historical work on the leafy branching systems

2.1 Carluccio *et al.* (1966): Reinterpreting the 'Frond' as a Lateral Branching System

Carluccio *et al.* (1966) re-examined the long-standing concept of the '*Archaeopteris* frond', clarifying terminology and supporting Beck's conclusion that *Archaeopteris* is distinct from true ferns and belongs within the progymnosperms. Their study focused on *Archaeopteris macilenta*, using permineralized material from three early Frasnian quarries in New York State.

They demonstrated that the fern-like 'fronds' were actually flattened lateral branching systems composed of:

- **Penultimate branches (formerly 'rachis')** – supporting both ultimate branches and some leaves.
- **Ultimate branches (formerly 'pinnae')** – bearing only leaves.

Fertile ultimate branches showed a radial organisation with a small central pith and lobed primary xylem, from which vascular traces diverged to fertile appendages in a helical arrangement. Sterile ultimate branches displayed the same helical organisation but with traces leading to simple leaves. Penultimate branches showed similar anatomical complexity of traces, plus secondary xylem with *Callixylon*-type grouped bordered pits.

Two distinct vascular trace types were identified in penultimate branches:

- **A larger trace:** consistently emerging from two opposite xylem lobes, supplying the ultimate branches.
- **Smaller traces:** supplying leaves.

Carluccio *et al.* (1966) noted that branches were often flattened during fossilisation, leading earlier researchers to misinterpret them as compound fronds. Their reinterpretation concluded that *Archaeopteris* did not possess a single large compound leaf, as in true ferns, but a branched lateral shoot system more comparable to the leafy branches of gymnosperms.

2.2 Beck (1971): Phyllotaxy, Dorsiventrality and Anisophylly

Beck (1971) undertook a landmark study on the morphology and anatomy of the lateral branching systems in *Archaeopteris macilenta*, providing the first evidence of dorsiventrality and anisophylly. Using a large Frasnian-aged assemblage from Cannonsville, New York State, he found that the stele of penultimate branches possessed nine ribs, with branch traces emerging only from two opposite ribs. These branches arose sub-oppositely and displayed a distichous arrangement.

Beck also introduced a new method for determining phyllotaxy in compression specimens. Leaf bases could be recognised as horseshoe-shaped carbon slivers descending into the matrix, which could be carefully dégaged to expose leaf impressions on both part and counterpart surfaces, allowing reconstruction of phyllotactic patterns across the branch. This revealed that penultimate branches could display either:

- An equal number of leaf orthostichies on both sides or
- Dorsiventrality, with differing numbers of orthostichies on the adaxial and abaxial surfaces (e.g., three on one side, four on the other).

Some specimens also showed a higher density of smaller leaves on the adaxial surface and fewer, larger leaves on the abaxial surface, providing the first evidence of anisophylly in *Archaeopteris*. This was attributed to the presence of additional discontinuous parastichies on the adaxial surface (Text Figure 47 of Beck, 1971). Although the pattern was variable between specimens, this study was the first to document it from a large, well-preserved assemblage of material.

From this work, Beck (1971) established several key points on the organotaxy of penultimate branches in *Archaeopteris*:

1. Leaves and ultimate branches share the same ontogenetic spiral and contact parastichies.
2. Ultimate branches occur distichously in two opposite orthostichies.
3. Leaf orthostichies on either side of the branch may be equal or differ in number by one or two.
4. Leaf density is often unequal due to early abortion of leaf primordia on one side.

5. Each side of the axis bears between two and five leaf orthostichies.
6. Branch arrangement (opposite, sub-opposite, alternate) depends on orthostichy number and spacing.
7. Leaves and branches maintain consistent longitudinal spacing within orthostichies.
8. Axes typically have 7–11 total orthostichies.

2.3 Scheckler (1976): Ontogeny and Vascular Organisation

Scheckler (1976) advanced understanding of the ontogenetic framework behind the development of large woody axes, penultimate branches, and ultimate branches, based on anatomically preserved Frasnian-aged specimens from Canada. He highlighted significant variation in branching systems and linked this to their complex vascular organisation. His work showed that ultimate branches are not axillary in origin but are produced through pseudomonopodial branching, with continuous vascular connections indicating development from an apical meristem rather than an axillary bud.

Through detailed anatomical study and building on Beck's (1971) work, Scheckler demonstrated that vascular organisation varied with branch type: larger branches supported more complex branching patterns due to a greater number of sympodia (primary xylem ribs). Smaller sympodia gave rise to leaves, while larger ones produced branch traces. By studying the full length of individual branches, he documented that stele size, and thus sympodial number, varied along the branch. In penultimate branches, the stele was widest in the mid-region and narrower proximally and distally, reflecting a transition from indeterminate growth in the mid-region to determinate growth distally. He interpreted this as evidence for seasonal growth in the branching systems of *Archaeopteris*.

Scheckler also observed variation in the number of ultimate branches, with some larger penultimate branches (3–6 mm diameter) producing more than two, but only on one side, deviating from the bilateral symmetry usually seen in *Archaeopteris*. Like Beck, he noted asymmetrical leaf distribution between adaxial and abaxial surfaces, attributing this dorsiventrality to early abortion of leaf primordia on one side.

2.4 Kenrick & Fairon-Demaret (1991): Evolutionary Persistence of Dorsiventrality

Kenrick & Fairon-Demaret (1991) provided the first detailed anatomical study of Late Devonian (Famennian) *Archaeopteris roemeriana* from Belgium and the first comprehensive investigation of *Archaeopteris* material outside North America. Their work focused on vegetative and fertile ultimate branches, revealing key differences in branching ontogeny (Kenrick & Fairon-Demaret, 1991, Figure 3).

Vegetative ultimate branches showed bilateral symmetry, with five sympodia in total across both sides, typically two larger sympodia on the lower side and three smaller sympodia on the upper side, whereas fertile ultimate branches were radially symmetrical with six to seven sympodia of roughly equal size. These were interpreted as having a strobilus-like organisation, adapted for reproduction, resulting in denser packing of reproductive units increasing spore output and reproductive success. In contrast, bilateral symmetry in vegetative branches likely reflects planated architecture optimised for photosynthesis:

- Smaller adaxial leaves reducing shading
- Larger abaxial leaves increasing light capture.

Although poor preservation prevented direct confirmation, this interpretation was supported by variation in leaf-trace size between the two surfaces. Transitional zones with leaves of intermediate morphology occurred between fertile and vegetative regions, further highlighting the morphological diversity of *Archaeopteris*. The recognition of dorsiventrality and possible anisophyly in ultimate branches of Late Famennian *Archaeopteris* indicates these traits persisted for ~20 million years. The fact that these traits showed such long-term conservation suggests they were functionally significant, contributing to the ecological success and widespread dominance of *Archaeopteris* in Middle–Late Devonian forests.

2.5 Fairon-Demaret & Leponce 2001: Confirmation of Anisophyly in Late Devonian *Archaeopteris*

While anisophyly was initially inferred by Kenrick and Fairon-Demaret (1991) based on the variable sizes of sympodia, Fairon-Demaret and Leponce (2001) clearly demonstrated anisophyly in *Archaeopteris roemeriana* from the Famennian of Belgium. Based on compression fossils they found that the smaller leaves were

approximately one-third the size of the larger ones, exhibited a different morphology (reduced lamina and bifurcated twice) and occurred in higher densities, arranged in three ranks on one side of the branch. In contrast, the larger leaves were arranged in fewer (two) ranks on the opposite side of the branch. Due to the nature of the compressions the authors could not confirm which side was adaxial and which was abaxial, although they suggested in agreement with Kenrick and Fairon-Demaret (1991) that the smaller leaves likely belonged to the adaxial (upper) surface. They also confirmed that trace size is linked to differences in leaf dimensions, a relationship previously suggested but not unequivocally confirmed

Through detailed morphological and anatomical studies summarised above, researchers have significantly advanced the understanding of lateral branching systems in Late Devonian *Archaeopteris*. The presence of different symmetries across fertile and vegetative branches, along with features such as dorsiventrality and anisophylly, highlight the wide variation and therefore, developmental plasticity seen across the basic branching architecture in *Archaeopteris*.

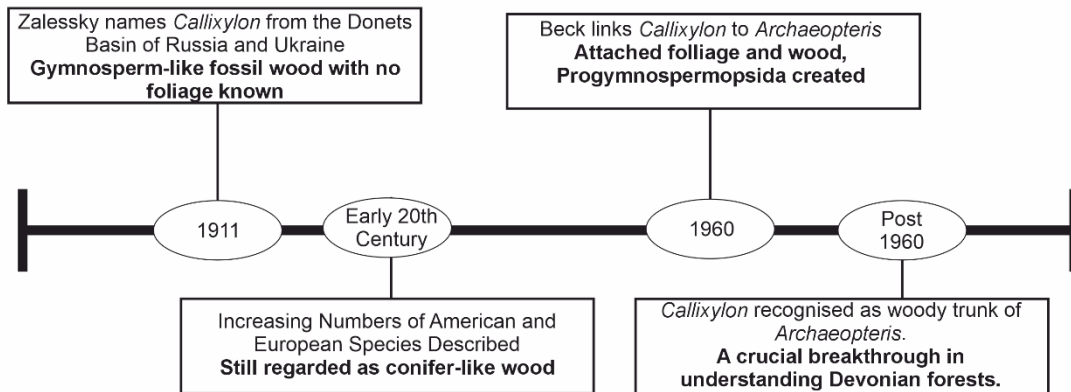
3. Branching patterns found in the trunks (*Callixylon*)

Despite the long history of research into the morphology and anatomy of *Archaeopteris* lateral branch systems, the ontogeny of branching in trunks (*Callixylon*) remains less well studied. *Callixylon* was first described from Donetz Basin collections in Russia and Ukraine as gymnosperm-like fossil wood lacking associated foliage (Zalessky, 1911; Text Figure 36). Beck (1960a, 1960b) was the first to connect leafy lateral branch systems to *Callixylon* wood, identifying it as part of large trees that produced long-lived branches. This interpretation was based on the eustelic organisation and the presence of a well-developed pith, mesarch primary xylem strands and extensive secondary xylem with ray tracheids (and characteristic grouped pits), features indicative of durable and long-lived woody branches.

Since Beck (1960a, 1960b) introduced the modern concept of *Archaeopteris*, several landmark studies have advanced the understanding of trunk and lateral branching systems into a cohesive whole-plant model. In later work, Beck (1979) examined *Callixylon* trunks from the Upper Devonian of Kentucky and New York, showing that ~40 mesarch primary xylem bundles produced traces in a regular helical pattern, all matching the anatomy of penultimate branches. No leaf traces were identified, leading him to conclude that the helices represented branch traces only, a key finding that refines our understanding of *Archaeopteris* organotaxy.

Two additional studies (Trivett, 1993; Meyer-Berthaud et al., 2000) highlighted the trunk's production of both long-lived structural branches and shorter-lived, possibly seasonal, ephemeral branches. The following section places these findings within a broader developmental framework to provide a clearer picture of the plant's overall morphology.

Historical Recognition and Reinterpretation of *Callixylon*



Text Figure 36. Historical recognition and reinterpretation of *Callixylon*. Timeline illustrating the first formal description of the genus by Zalessky in 1911 through to the modern whole-plant concept, in which *Callixylon* is explicitly recognised as the woody trunk of *Archaeopteris*.

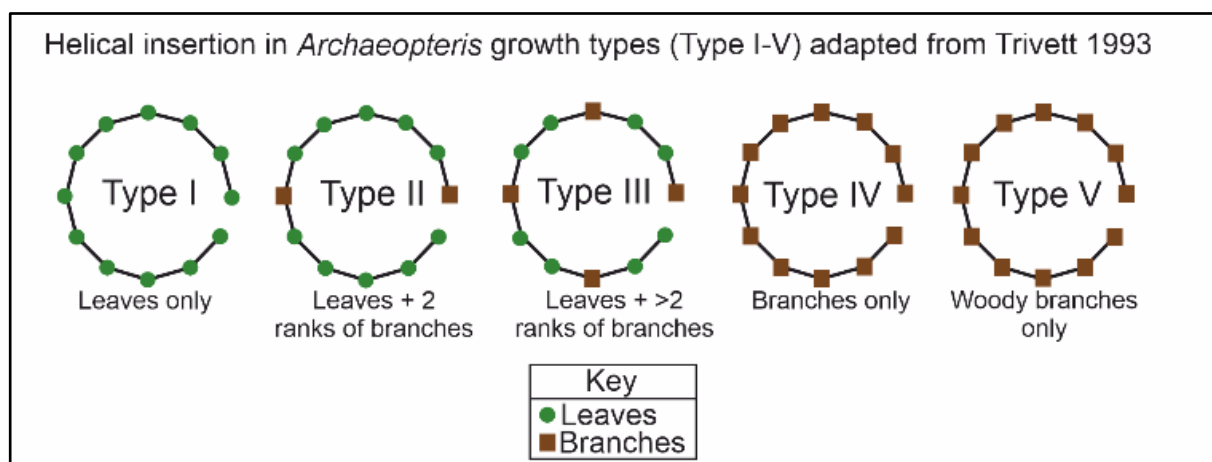
3.1 Trivett (1993):

Trivett (1993) conducted a landmark study on the branching patterns within the trunk of *Archaeopteris* (*Callixylon*), offering a comprehensive account of its organography and organotaxy, outlining a growth model she termed 'Beck's model'. This was based on a ~4 m long, ~0.6 m diameter silicified log of *Callixylon whiteanum* from late Famennian chert of the Woodford Formation (Ada, Oklahoma, U.S.A.). The specimen preserved a 2.2–3.2 cm diameter pith, 18–21 mesarch primary xylem bundles and traces 0.6–1.7 mm in diameter, all interpreted as branch traces rather than leaf traces. The log is clearly near the base of a tall tree. However, the innermost portions of the secondary xylem were produced during the early stages of growth and therefore preserve early ontogenetic development within the trunk.

Earlier interpretations had suggested a monopodial, conifer-like branching system (Beck, 1962; Hallé & Oldeman, 1970) or pseudomonopodial growth (Scheckler, 1976; Beck, 1979). Trivett's study was the first to integrate the pseudomonopodial model into a detailed developmental framework, providing a robust description of the hierarchical organisation of lateral organs and the processes underpinning both

organography and organotaxy. She concluded that branch development was influenced by the size and complexity of the apical meristem, with growth falling into five types based on apex diameter and branching complexity (Text Figure 37):

- **Type I–II** – Short-lived branches, lacking secondary growth, interpreted as ephemeral.
- **Type III** – Intermediate-lived branches, moderate in size and complexity.
- **Type IV–V** – Long-lived branches, large in diameter with complex branching patterns, forming part of the permanent architecture.



Text Figure 37. Illustrations of helical branch patterns in *Archaeopteris* based on Trivett's (1993) architectural growth model. Adapted from Trivett (1993).

This dynamic classification marked a significant advancement over the earlier, simpler division into trunk, penultimate and ultimate branches (Table A).

Trivett demonstrated that all five growth types kept the same basic helical arrangement but what was inserted in the helix changed as the axes increased in size (Text Figure 37). Type I axes carried only leaves, the simplest stage. Type II combined leaves with two ranks of ultimate branches, while Type III added further ranks, leaves and branches together. Type IV bore helically arranged Type II and Type III branches but no leaves and by Type V the trunk had become so large that every position in the helix was occupied by substantial woody branches. In other words, Type V was not a reduction in insertions but a replacement of all leaf sites by branches. This shows that helical insertion was consistent throughout the plant but the balance between leaves and branches changed as the plant developed (Trivett, 1993).

She identified numerous embedded branch bases distributed across the basal portion of the trunk. The branches appear to have diverged steeply from the trunk before extending more horizontally as they developed and increased in weight. Over time, the branch stubs became overgrown by secondary xylem (wood), leading Trivett to hypothesise that the branches were not actively shed by abscission, but were instead passively lost as the expanding trunk enveloped the remaining stubs through continued secondary growth. Based on the maximum distance that the branch trace extends into the wood, the pith diameter and the estimated bark thickness, Trivett (1993) inferred that the trunk was approximately 3.8 cm in diameter when the visible Type I branches were shed. The presence of these overgrown branch scars supports the interpretation that the lower trunk bore long-lived, structural branches.

In contrast, approximately 3 m higher on the trunk, Trivett identified smaller, closely spaced branch bases lacking secondary growth, which she interpreted as short-lived, ephemeral Type II or Type III branches. As with the lower branches, there was no anatomical evidence for abscission and the trunk diameter at the time of shedding was estimated at approximately 5.5 cm. Trivett (1993) proposed that these branches were passively shed, most likely through self-thinning or mechanical loss influenced by the plant's ecological setting.

A final key finding was the presence of adventitiously produced branches, despite the absence of axillary buds which indicates opportunistic growth triggered by environmental opportunity or stress. This regenerative capacity suggests developmental plasticity in *Archaeopteris*, allowing replacement of lost or damaged parts and maintaining architectural integrity. Together, these features likely enhanced resilience in *Archaeopteris* and contributed to its ecological dominance in Late Devonian forests.

Table 9. Summary of branch types described by Trivett (1993) in *Archaeopteris*. Each type (I-V) includes details of its position within the plant, xylem size, the organs produced by that trace, the type of growth pattern it exhibits, its longevity and any additional notes.

Type	Position	Size	Organs Produced	Growth	Phyllotaxy / Ranks	Longevity	Notes
I	Terminal tips	Very small (<0.5 mm xylem)	Leaves only	Determinate	Helical phyllotaxy of leaves; typically 3–5 leaf orthostichies	Ephemeral, no secondary xylem, strictly leafy twigs, seasonal	Ultimate axes; no branching; purely photosynthetic
II	Peripheral small branches	Small (<3 mm xylem)	Leaves + Type I branches	Determinate	2 ranks of lateral branches; helical leaf traces	Ephemeral, may persist briefly but often shed; limited wood	Intermediate axes supporting leafy shoots
III	Penultimate branches	Medium (~3–6 mm xylem)	Type I–II branches	Determinate	>2 orthostichies; often shows dorsiventrality and anisophylly	Intermediate, more persistent, especially in large trees; still potentially shed	Supports both vegetative and fertile units
IV	Upper trunk / major branch	Large (6–32 mm xylem)	Types II–III only (no leaves)	Indeterminate	6–8 orthostichies; spirally arranged branch traces	Long lived, major woody limbs; embedded stubs found in trunks	Woody, long-lived branches; may embed older stubs
V	Main trunk	Very large (>32 mm xylem)	Types III–IV only	Indeterminate	8–11 orthostichies of branch traces; spiral organisation	Long lived, Main trunk axis; perennial and foundational	Central structural axis; continuous growth and modular branching

3.2 Meyer-Berthaud *et al.* 2000

Meyer-Berthaud *et al.* (2000) expanded on Trivett's work with a 5 m-long, calcite-petrified trunk of *Archaeopteris/Callixylon erianum* from early Famennian marine deposits in Morocco, measuring 6.3 × 9 cm at the base and 3.2 × 5.4 cm distally.

Analysis of the distal 40 cm identified three vascular trace types:

- **Type A** – Short-lived apical, likely ultimate branches with a 450–750 µm primary xylem core and 300–400 µm secondary xylem, arranged helically.
- **Type B** – Long-lived adventitious branches with a 0.5–1.1 mm pith and 0.8–1.8 mm secondary xylem, forming part of the permanent architecture, which do not appear to be part of the apically produced helical organotaxy.
- **Type H** – Short-lived latent primordia, 550–900 µm wide, capable of developing into roots or shoots.

The developmental distinctiveness of Type B traces revealed a higher level of architectural complexity than previously recognised, highlighting both predetermined and opportunistic growth strategies in *Archaeopteris* trunks.

4. Introduction to *Svalbardia* and aims of this chapter

Svalbardia polymorpha Høeg is an enigmatic leafy Middle–Late Devonian plant, originally described from fossil material collected in Svalbard. It has often been regarded as taxonomically distinct from *Archaeopteris*, primarily due to perceived differences in branching morphology, particularly its presumed non-planated branching system. However, its placement has remained uncertain, in part due to the vague original description by Høeg (1942) and later reconstructions by Schweitzer (1999), which incorporated fronds originally interpreted by Høeg as part of a whole plant into a larger tree-like form. This has been compounded by problems in relocating the type locality.

Several authors have noted strong similarities between *Svalbardia* and *Archaeopteris*. Høeg himself stated that “both its vegetative characters and the form of its fructifications show that its place is in the neighbourhood of *Archaeopteris*, as a primitive relative of that genus.” Carluccio et al. (1966) likewise considered *Svalbardia* a possible precursor to *Archaeopteris* and first proposed a link between compression fossils of *S. polymorpha* and the anatomically preserved fossil *Actinopodium nathorstii* Høeg, also from Svalbard. This connection has been supported by several subsequent authors (Matten, 1968; Beck, 1971; Matten, 1981), although confirmation has been hindered by the poor preservation and limited availability of the type material, as well as the differing stratigraphic contexts in which *S. polymorpha* and *A. nathorstii* occurred.

Specimens of *S. polymorpha* from Svalbard show considerable morphological variation, directly comparable to the intra- and interspecific diversity observed among *Archaeopteris* species. Høeg also noted that the lateral branches were “probably” spirally arranged but could not confirm this definitively. Together these have influenced the diagnosis of other *Svalbardia* species and fuelled ongoing taxonomic confusion. This is reinforced by Schweitzer’s influential reconstruction of the branching system as three dimensional (Schweitzer, 1999, Abb.46).

Aims of this chapter:

1. To redescribe the lateral branching system of *Svalbardia polymorpha* using newly collected material from the rediscovered type locality, clarifying its architecture.
2. To compare the morphology of *S. polymorpha* with the anatomically preserved *Actinopodium nathorstii* and evaluate whether they represent different preservation states of the same plant.
3. To assess the taxonomic status of *Svalbardia* and *Actinopodium* and their placement within the Archaeopteridales.
4. To describe large trunk material, including specimens previously referred to as the form genus *Caulopteris*, as well as woody roots and critically assess their association with *S. polymorpha*.
5. To document new stratigraphic ranges for the above taxa within the Mimerdalen Subgroup.

Svalbardia polymorpha

Terminology

There has been ongoing confusion regarding the terminology used to describe *Archaeopteris* morphology. The term ‘frond’ has historically been applied to describe the fern-like appearance of the leafy branches. However, since Carluccio *et al.* (1966) reinterpreted these structures as narrated above, I will use the following terminology:

- Trunk: Refers to the main trunk of the tree.
- Penultimate branches: Refers to the lateral branches that emerge from the main trunk and, potentially, long lived branches.
- Ultimate branches: Refers to the narrow, leafy branches that emerge from the penultimate branches.
- Leaves: Refers to leaves borne on penultimate and ultimate branches.

Method of preparation

To determine the arrangement of leaf bases on the part and counterpart, a refined dégagement technique was used to expose leaf bases buried within the matrix beneath the preserved specimen. Following Beck’s (1971) procedure for *Archaeopteris*, horseshoe-shaped carbon impressions which face down into the matrix marking the leaf bases were carefully investigated using fine-tipped tungsten needles under a dissecting microscope, revealing their further morphology. Only the proximal portion of the leaves were generally exposed to confirm their presence, without fully dégaging the entire structure. Some leaves were <30 mm in length and further excavation risked damaging an important specimen. Some of the initial preparation of this specimen was performed by Richard Jones as a research volunteer.

Material Used in Description

The material used was collected from stratigraphic layers spanning approximately 4 million years (Text Figure 38). Three new specimens from the Planteryggen type locality, now recognised to be in the Plantekløfta Formation, where *S. polymorpha* was first described, include significant finds which provide new insights into branching morphology, leaf insertion and the base of the penultimate axis. New

collections from the Estheriahaugen Member (2022, 2023) extends its stratigraphic range significantly downwards in Svalbard (Text Figure 39).

Specimen 1: Penultimate Branch with Ultimate Branches and Leaves (2016-8/41). Locality: PR - Planteryggen type locality (PK Formation)

A compression fossil with part and counterpart, comprising a penultimate branch, lateral ultimate branches and leaves present on both the penultimate and ultimate branches. This specimen is particularly valuable as it is the only suitable part / counterpart collected from the rediscovered type locality in 2016. Following dégagement, the specimen allows a clear interpretation of the lateral branching system with paired ultimate branches. Details of leaf bases allow for analysis of phyllotaxy on the penultimate axes.

Specimen 2: Penultimate Branch with Ultimate Branches (2016-36). Locality: PR - Planteryggen type locality (PK Formation)

This specimen clearly shows the arrangement of ultimate branches emerging from the penultimate branch. It supports the interpretation of Specimen 1. Finer details of leaf bases or leaves on the penultimate axis are not preserved.

Specimen 3: Penultimate Axis Base (2016-2/1)

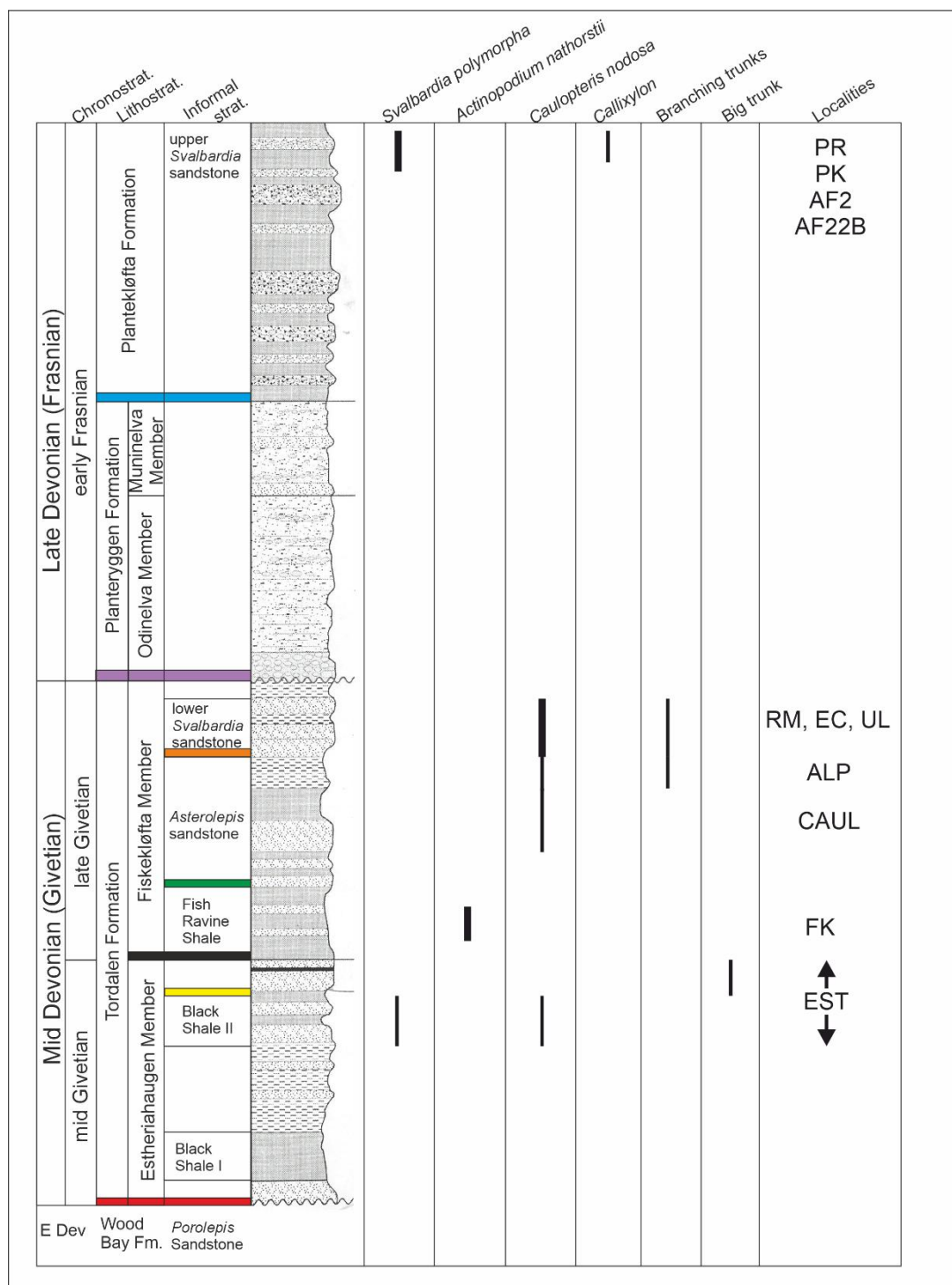
Locality: PR - Planteryggen type locality (PK Formation)

Specimen 3 demonstrates the base of a penultimate axis for the first time, with part and counterpart, showing the node where the branch attached to the main trunk.

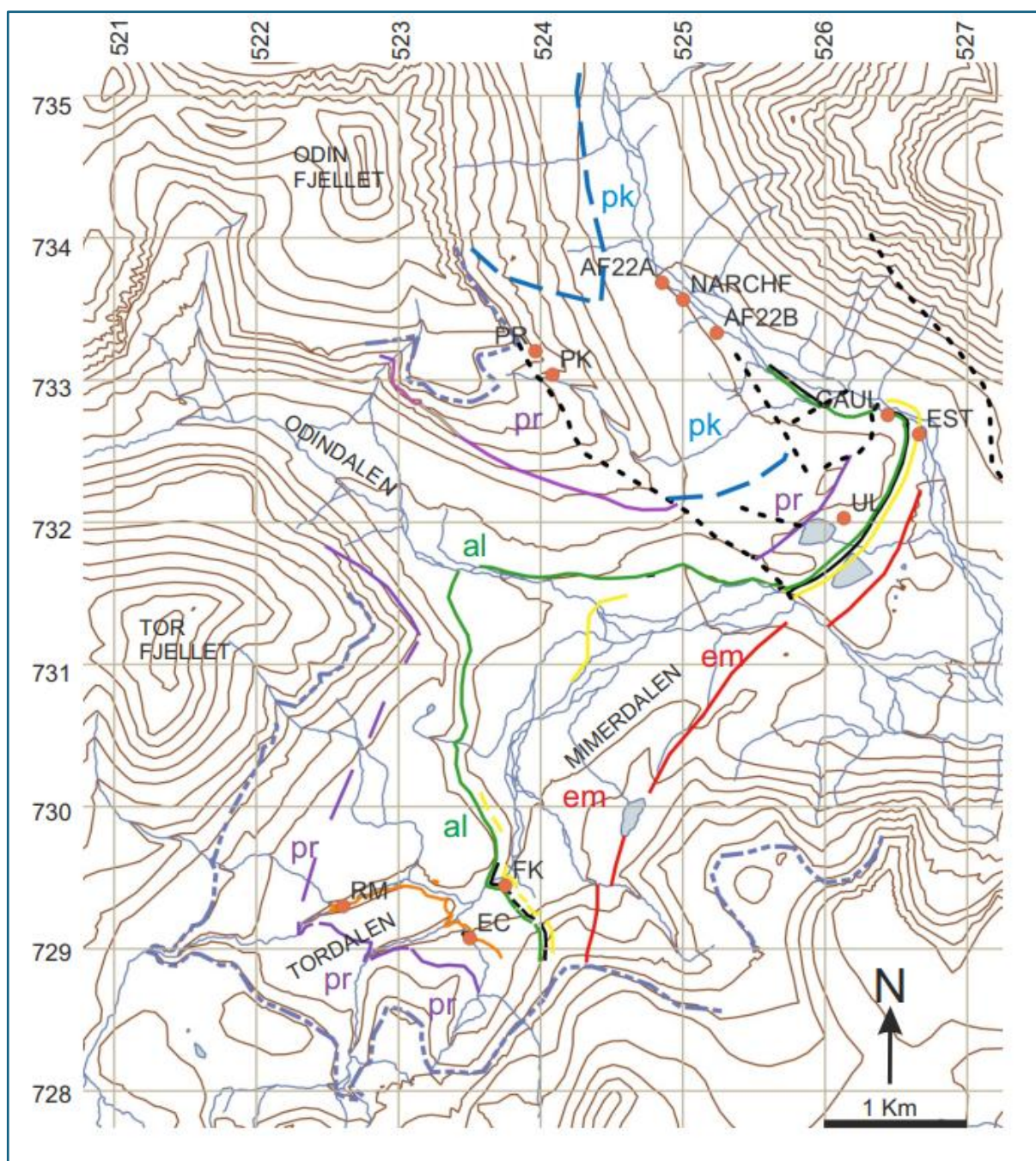
Specimen 4: Typical *Archaeopteris* 'Frond' Morphology (EST-1 A/B)

Locality: EST - Estheriahaugen (Black Shale II, Estheriahaugen Member)

Specimens collected from the mudstone are not significant in terms of morphology but are important stratigraphically. Their occurrence extends the known range of *S. polymorpha* in Svalbard to the whole of the Mimerdalen Subgroup (Text Figure 38). Abundant specimens found in intermediate levels are generally fragmentary.



Text Figure 38. Stratigraphic column showing the occurrences of plant fossils associated with *Archaeopteris* in Svalbard. These include *Svalbardia polymorpha*, *Actinopodium nathorstii*, *Caulopteris nodosa*, *Callixylon*, branching trunks and a large trunk specimen. In the localities column: PR = Planteryggen, PK = Plantekløfta, AF2 = Arc Forest 2 (from Berry & Marshall, 2015), AF22B = Arc Forest B (2022 field season), RM = River's Meet; EC = Eastern Canyon; UL = Upper Lake; ALP-2 = Asterolepis Sandstone; CAUL = *Caulopteris* horizon; FK = Fish Ravine Shale, EST = Estheriahaugen (Includes Shale II and yellow sandstone) – see Text-Figure 39. Thick lines correspond to typical localities for taxa, while thinner lines represent additional occurrences.



Text Figure 39. Geological map of Munindalen and Mimerdalen showing the distribution of the Mimerdalen Subgroup. Localities yielding fossils attributed to *Archaeopteris* are labelled. Map created by Berry and Marshall (unpublished) based on field observations from 2010–2023, with stratigraphic units modified from Piepjohn & Dallmann (2014). Colours correspond to the base of stratigraphic units shown in Text Figure 38. Grid = UTM zone 33N.

Descriptions of Morphology

Specimen 1: Penultimate Axes, Plates 14-16

General morphology

Although the exposed portion lies more or less flat on the slab (Plate 14A), the distal end arches broadly downwards. The total length of the preserved penultimate branch is 261 mm, 123 mm is exposed proximally, with the middle buried in matrix (Plate 14C). Proximally, it is 6 mm wide, tapering to 4 mm distally, with a slight widening immediately before the emergence of the ultimate branches.

The counterpart measures 106 mm in length and is 6 mm wide proximally, tapering to 4 mm distally (Plate 14B). The angle of insertion and degree of recurvation of the ultimate branches varies on each side, decreasing distally along the axis. This variation is likely the result of turbulent taphonomic conditions that displaced the branch during preservation, consistent with the observed rotation of branches and leaves.

On both part and counterpart, surface preservation of the penultimate branch is relatively good. On ultimate branches fine, poorly preserved, highly dissected leaves are present, described in detail by Høeg (1942) (Plate 14A-B - *white arrows*).

Insertion of Ultimate Branches

Pairs of ultimate branches emerge sub-oppositely from the penultimate branch on both part and counterpart. On the part, branching occurs at four nodes which are roughly equally spaced along the branch length (Plates 14A, 15D-F). The distal three nodes are also preserved on the counterpart (Plates 14B, 15A-C). Ultimate branches are incomplete, measuring 51–59 mm in length before their distal tips are lost at the edge of the slab or into the matrix. Width varies between 1-3 mm.

On the part, the left-hand ultimate branches join the penultimate branch slightly above the main plane of compression and are inserted at a narrow angle, before curving broadly outward to angles of up to 95° (Plate 14A). On the right-hand side, only the proximal (*dégagé*) and distal ultimate branches are connected to the penultimate (Plate 14A). The proximal branch (Node 1) is inserted approximately in the plane of compression of the penultimate branch and bends outward and

downward into the matrix. The next two ultimate branches (Nodes 2 and 3) are not directly connected on the part, lying slightly above the compression plane. Their attachment is visible on the counterpart, where they are inserted at 20–30° from the penultimate branch, slightly below its compression plane, before bending upright and running sub-parallel to the penultimate branch (Plate 14B). The fourth ultimate branch on the right (Plate 14A) is preserved just above the penultimate branch's compression plane and is slightly kinked at its base on both part and counterpart.

Relative insertion of the sub-opposite pairs is best seen on the counterpart (Text Figure 40). On this side, the ultimate branches are positioned slightly closer together radially than on the part. One ultimate branch emerges slightly before its opposite pair, with an offset of 5–9 mm. Successive sub-opposite node pairs are spaced 30–32 mm along the penultimate branch.

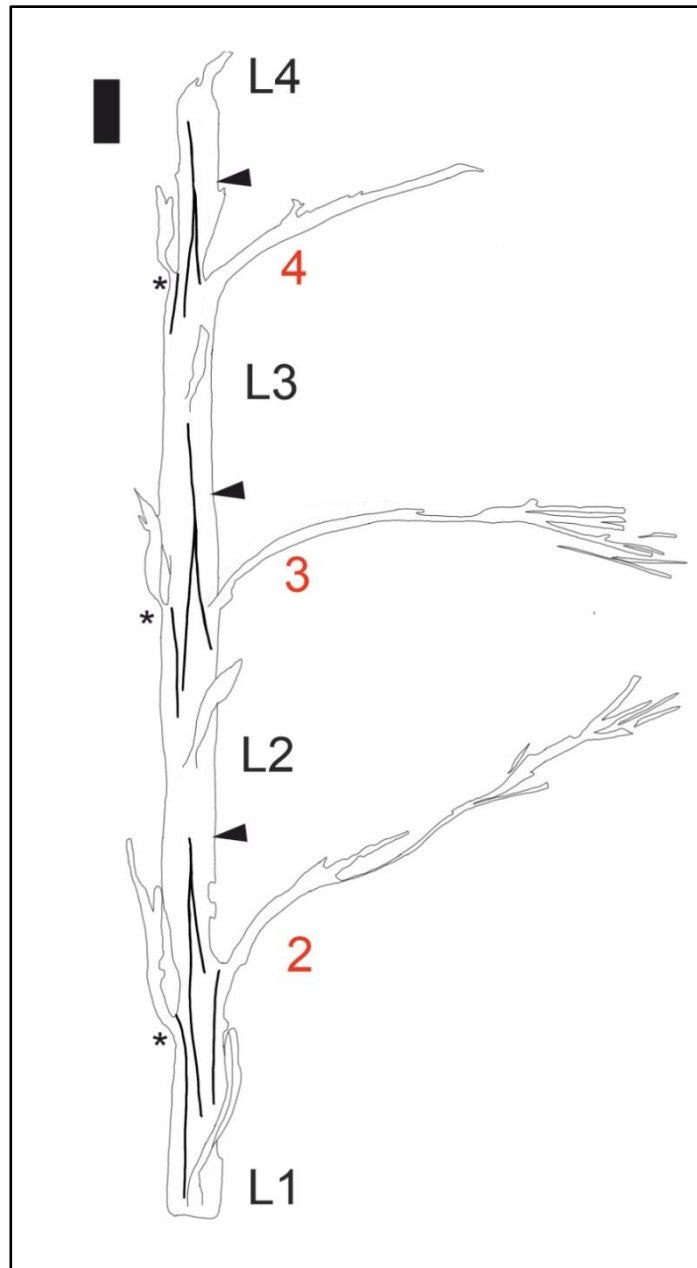
Surface Preservation of Folds in Penultimate Branch

On the surface of both the part and counterpart, longitudinal folds extend along the entire length of the penultimate branch. These folds may reflect the underlying organisation of vascular ribs and associated traces to lateral branches and leaves, although variation in fold spacing and preservation means that a direct one-to-one correspondence cannot be demonstrated.

On the part, these folds vary significantly in size, appearance and number, ranging from 3 to 8 across the width of the branch, with average width between folds 1.1 mm (range: 0.5–2 mm). In some areas, they are well-defined, while in others they merge which makes precise mapping difficult (Plate 14A). Despite this variability, they are associated with leaf and lateral branch traces, with at least one fold typically merging into the lateral branch as it emerges.

The organization of folds (depressions) in the counterpart is more predictable and ordered, with approximately three distinct ribs, which have wider spacing than those on the part. Their average width is 1.6 mm (range: 1.1–2.6 mm). Notably, starting where pairs of ultimate branches emerge two depressions converge and the middle fold is lost, forming a funnel-shaped structure in the surrounding ridges and reducing the number of folds (Text Figure 40 - *black arrows*). After convergence, the depression continues until a leaf emerges. After the leaf has emerged, the depression splits, restoring the three-fold arrangement found on most of the branch.

Similar to the counterpart, a fold is usually associated with the emergence of a lateral branch, merging into the branch as it emerges (Text Figure 40 - *black **).

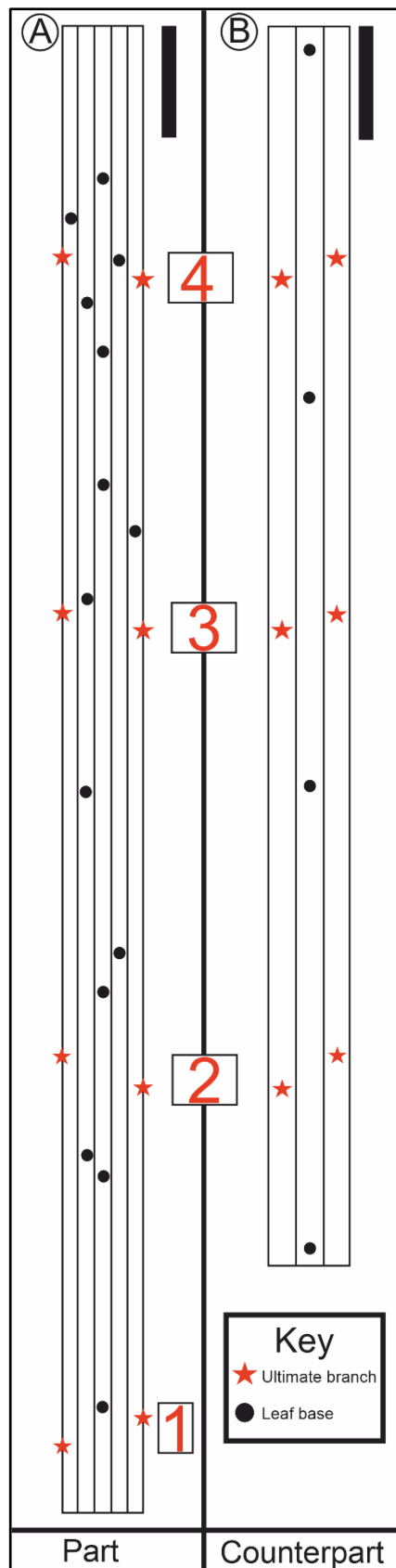


Text Figure 40. Camera lucida drawing of the counterpart of *Svalbardia polymorpha*, showing folds on the surface of the penultimate axis. Black asterisk marks the point where a fold converges into a lateral branch. Black arrow indicates where folds converge before the emergence of a leaf. Red numbers refer to the dichotomies seen on the part. L1–L4 highlight leaf bases on the counterpart. Specimen 2016-41, seen in Plate 14. Scale bar = 5 mm.

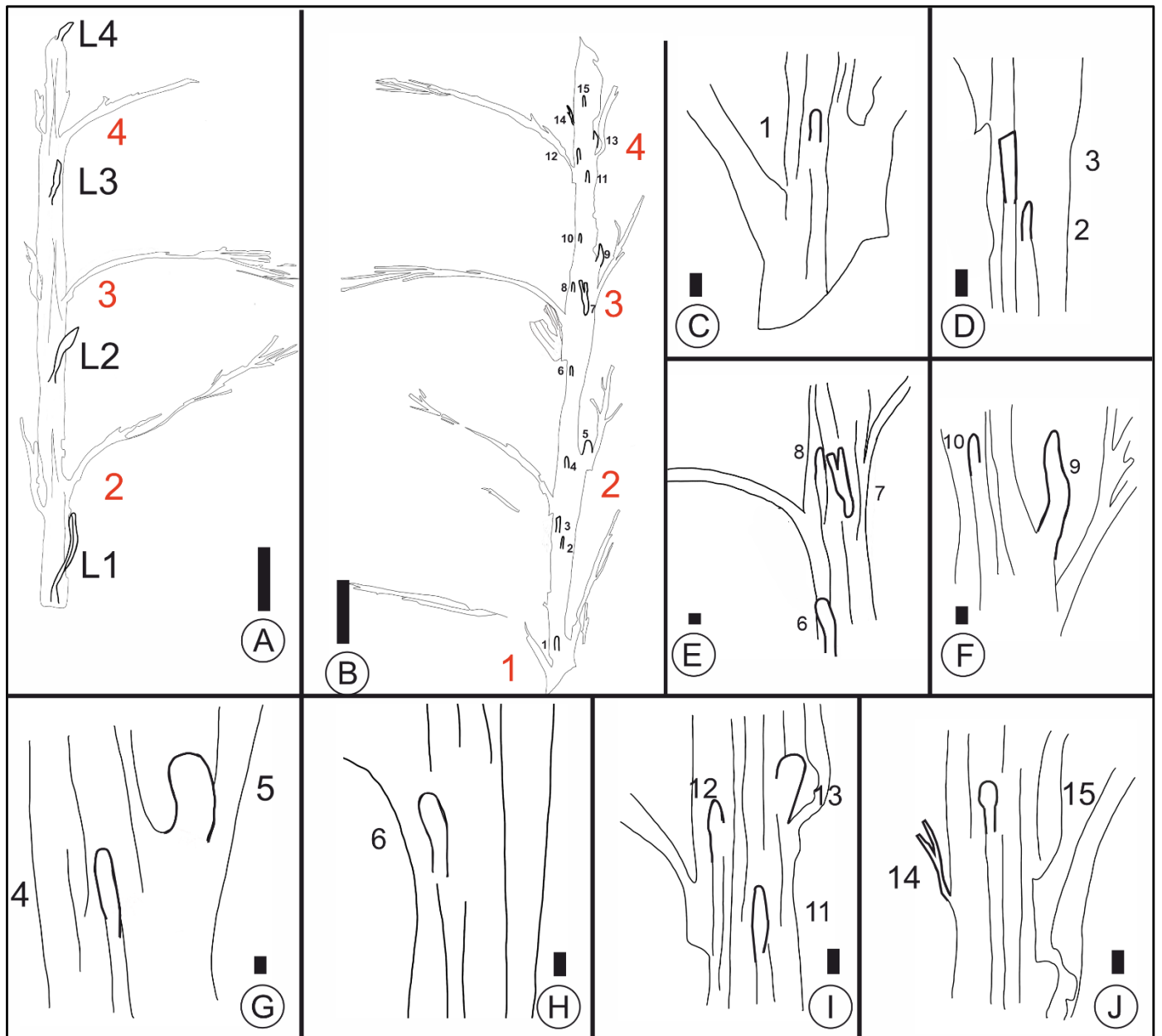
Phyllotaxy on Penultimate Branch

On the part, there are 15 visible leaf bases distributed across five apparent insertion positions on the preserved surface, along 123 mm of the penultimate branch (Text Figures 41A, 42B-J, Plate 16A, B, D; *white arrows*). The width varies from 0.65 to 1.8 mm, depending on their orientation during preservation. In cases where they are preserved more or less face-on, with the petiole descending into the matrix (Text Figure 42C), the leaf petioles appear narrower than those that have been slightly turned on their side during preservation (Text Figures 42F - 9). Leaf bases associated with ultimate lateral branches are also wider, though it is unclear whether this is due to their orientation in the sediment (Text Figures 42G - 5; 42F - 9).

On the counterpart, only four leaves (Text Figure 40 - L1-L4) are present along the entire 106 mm length of the branch, all located in a central row (Text Figure 41B), approximately equidistant between lateral branching nodes (Text Figures 40, 41B, 42A). The leaves become gradually closer together distally along the branch. The proximal two leaf bases are 37 mm apart, while the distal two are 31 mm apart. Leaf bases range from 0.6 to 0.85 mm in width, similar to those on the part that have been preserved face-down.



Text Figure 41. Phyllotactic pattern on the penultimate branch in *S. polymorpha*. (A) Illustrates the part and (B) illustrates the counterpart. See the key for details. Red numbers refer to number of sub-opposite ultimate branch pairs also labelled in Text Figure 42A-B. Scale bar = 10 mm.



Text Figure 42. Part (B) and counterpart (A) showing the pattern of leaves across the penultimate axis in *S. polymorpha*. Red numbers indicate the branching nodes for ultimate branches emerging from penultimate branches. Black letters and numbers indicate the leaves. Numbers in B represent leaf bases illustrated in C–J. (C–J) Camera lucida drawings of leaf bases numbered in (B), drawings also show finer details of rib organisation. Scale bar in A & B 5 mm, C–J 1 mm.

Morphology of Leaves on the Penultimate Branch

Part

Leaf bases are present on the part of the penultimate branch. Serial *dégagement* revealed that the petiole dichotomises approximately 5 mm above the point where the leaf base begins, with the leaf measuring 1.3 mm in width at the point of dichotomy (Plate 16C). The leaves appear relatively long, reaching at least 19 mm, but much of the lamina remains incompletely exposed, buried within the matrix or distorted during preservation. Further *dégagement* was not attempted to avoid damaging other potentially important features.

Counterpart

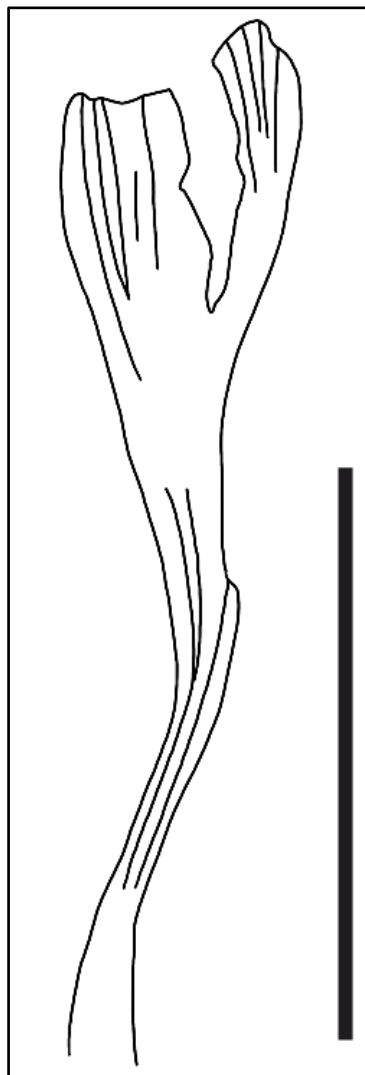
The largest exposed leaf (Text Figure 40 - L1) occurs on the proximal portion of the penultimate branch (Plate 16C - white arrow). The petiole is preserved basally on the counterpart, while the corresponding lamina is preserved proximally on the matching part (Plate 16C - white arrow), allowing a more complete composite reconstruction (Text Figure 43). At the base, the leaf measures 1.2 mm in width, narrowing to 0.7 mm before widening again distally. The preserved portion is 19 mm long, although the complete structure extends deeper into the matrix.

After approximately 14 mm, the exposed portion of the leaf bifurcates into two segments, one directed downwards into the matrix and the other angled slightly sideways and upwards. This indicates that the leaf was at least distally divided, although the full extent of division cannot be determined. Longitudinal veins extend from the petiole into the lamina, with additional parallel veins inserted before the bifurcation. The number of veins increases towards the distal portion of the leaf. Near the base, striations are approximately 200 μm wide, gradually widening along the leaf length.

The full morphology of leaves borne on the penultimate branch cannot be determined with certainty because the distal portions remain partly embedded within the matrix and further *dégagement* was avoided. The exposed leaf shows a narrow petiolate base and distal bifurcation, with veins continuing into the divided region. This suggests that the leaf was not entire throughout its length, but the degree of distal division cannot be established from the preserved material. This morphology is

consistent with the range of leaves described by Høeg (1942) for *Svalbardia polymorpha*, including wedge-shaped to fan-shaped leaves composed of dichotomising linear segments, as well as narrower, more filiform forms. The available material does not allow a clear distinction to be made between leaves borne directly on the penultimate branch and those borne on ultimate branches. Any apparent differences may reflect incomplete exposure, position on the plant or taphonomic distortion.

Text Figure 43. Interpretive drawing of a leaf (L1), reconstructed from camera lucida drawings of the petiole from the part and lamina from the corresponding portion of the counterpart. See Plate 16C, G - white arrows. Scale bar = 10 mm.



Specimen 2: Branching specimen, Plate 17C

This specimen, exceptional in its preservation of the branching system, shows a more or less intact distal 'frond' of *S. polymorpha* (Plate 17C).

The specimen measures 195 mm in length. Although surface preservation of the lateral branches and leaves is poor, the detail of the ultimate branches emerging from the penultimate branch is exceptional. The penultimate branch is 2.6 mm wide distally, widening slightly after the emergence of a pair of ultimate branches (Plate 17C - white arrow) before narrowing distally, reaching a width of 0.9 mm at its most distal portion.

Ultimate branches emerge sub-oppositely from the penultimate branch, with a slight offset of 4–7 mm between individual branching pairs. They emerge at an acute angle (20–30°) from the penultimate branch, extending up to 65 mm in length, with an average width of 0.8 mm (range: 0.6–1 mm). The length between nodes varies; proximal branching pairs are spaced 41 mm apart, reducing to 32 mm distally.

Poorly preserved dissected leaves, typical of those seen in *S. polymorpha*, are present on the ultimate branches (Plate 17C - black arrow). Some details of surface ribbing on the penultimate branch are visible, but the preservation makes it difficult to discern finer details. No leaves have been preserved on the penultimate branch.

Specimen 3: Base of penultimate branch, Plate 17A-B

This specimen comprises a part and counterpart representing the base of a penultimate branch. The branch is 64 mm long, with a maximum proximal width of 13 mm, tapering distally to 5 mm. The proximal portion is expanded, forming a convex impression on the part (Plate 17A, Text Figure 44A) and a corresponding concave impression on the counterpart (Plate 17B, Text Figure 44B). This basal structure, interpreted as the point of attachment to a larger branch or trunk, is swollen into a rounded base with angular margins that narrows and elongates distally. It measures 10 mm in width and 14 mm in length.

Three partially preserved leaves are exposed on the counterpart (Text Figure 44B, Plate 17B - black *), their distal portions disappearing beneath the matrix. Each leaf base measures 1 mm in width at its point of attachment. The first appears 39 mm

from the base of the branch, with subsequent leaves spaced at 4 mm intervals along one side (Plate 17B - black *). On the part, 50 mm from the branch base, a structure interpreted as a lateral branch is present (Plate 17A - white *). Its identification is supported by a surface fold that merges with it, matching the pattern seen in specimen 1.

Surface detail is well preserved, particularly on the part. Folds run along the branch length, narrowing from an average width of 1.5 mm (range: 1.2–1.9 mm) proximally to an average of 0.6 mm (range: 0.6–0.7 mm) distally. Near the top, six clearly defined raised ridges are visible (Plate 17B - black arrow), while at the branch base, approximately five larger but less well-defined ridges are present.

A second specimen (PK-28-2) illustrates the same basal structure, but it is slightly larger (Text Figure 44C). In this example, the branch measures 95 mm in length and up to 15 mm in width. The rounded, bulbous base is 15 mm wide and 17 mm long and is convex. No counterpart was collected.

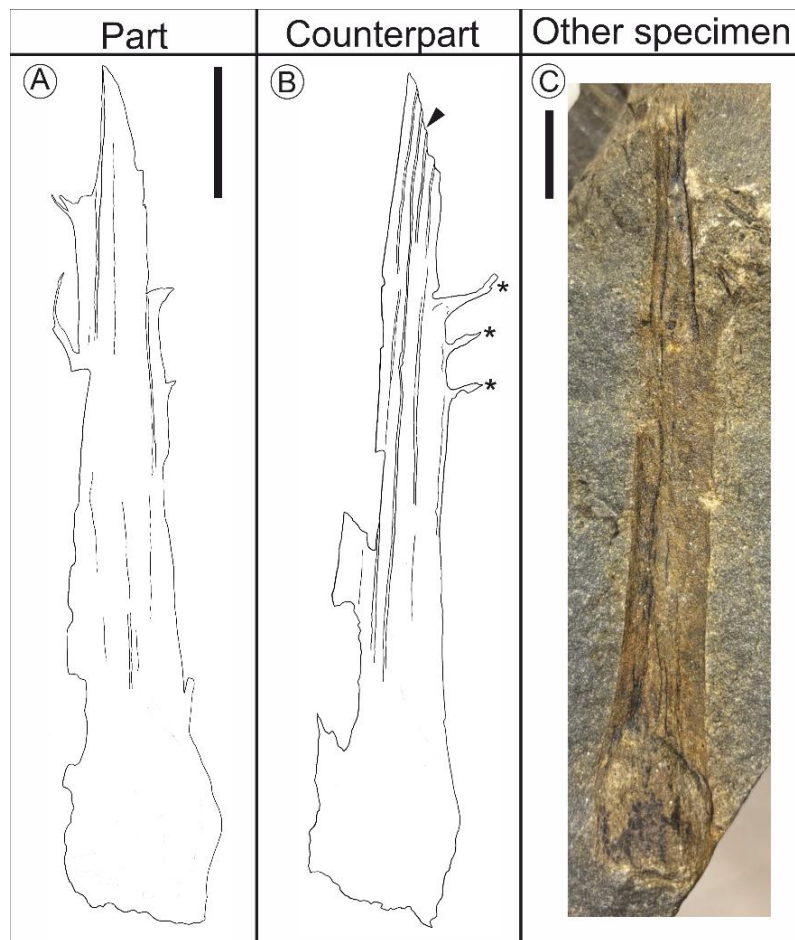
Specimen 4: New Stratigraphic Range (Estheriahaugen Member (EST), Plate 17D-E

Many fragmentary specimens were collected from the Black Shale II of the Estheriahaugen Member (Text Figure 38), mostly consisting of small, incomplete pieces of leaf or branch. One specimen is noteworthy as it provides definitive evidence for the presence of *S. polymorpha* in the oldest stratigraphic unit in the Mimerdalen Subgroup.

This specimen consists of part and counterpart of a portion of a penultimate branch, with a pair of sub-opposite ultimate branches that emerge at an acute angle (15 °) from the penultimate branch (Plate 17D - white arrow). On the part, the penultimate branch is 168 mm long, with a maximum width of 7.2 mm. Although some finer detail is not preserved, folds in the penultimate branch similar to those seen in specimen 1-3 are visible (Plate 17E - white *).

Poorly preserved dissected leaves are present on the distal portion of the ultimate branches, though their preservation differs slightly, making them less distinct than those seen in specimens from the type locality (Plate 17E - black arrow). Other

fragmentary specimens from this locality show superior preservation of dissected leaves (Plate 17F).



Text Figure 44. Interpretative line drawings of the part and counterpart of the base of the penultimate branch of *S. polymorpha*. The black asterisk in B marks leaf bases emerging from the counterpart, also shown in Plate 17B (black *). The black arrow indicates five clearly defined folds on the surface, also visible in Plate 17A. C. Shows additional specimen (PK28-2) with bulbous base, similar to that described in specimen 3 (A-B). Scale bar 10 mm.

Summary of New Observations on Morphology of *Svalbardia polymorpha*

- **Leaves on Penultimate Branches:** New specimens confirm the presence of leaves on penultimate branches.
- **Branching Architecture:** Ultimate branches occur in sub-opposite, slightly downward-oriented pairs, forming a planate, bilaterally symmetrical system.
- **Dorsiventrality:** Penultimate branches show multiple apparent leaf insertion positions on one surface and a single central row on the opposite surface, suggesting dorsiventral organisation.
- **Stratigraphic Range:** The known macrofossil range of *S. polymorpha* is extended across the full exposed Mimerdalen Group, from the Estheriahaugen Member to the Plantekløfta Formation (late Givetian–early Frasnian).

***Actinopodium nathorstii*: Description of Anatomy**

Historic Details of Material

During Nathorst's 1882 expedition, numerous ironstone nodules containing conspicuous fish remains were collected from the Fiskekløfta locality (Text Figure 38 - *FRS*) in Tordalen by Nathorst (See Nathorst 1910, Fig. 34). These nodules were subsequently sectioned by Stensiö to study the bones. However, the sectioning process also revealed rare well-preserved permineralized plant material with anatomical details.

The sections were likely randomly positioned rather than following standard botanical sectioning, where branch orientation could be carefully documented. After the plant material was identified, the sections were passed from Stensiö to Halle, who then forwarded them to Høeg for further study.

Høeg (1942) selected transverse sections from this material to serve as the holotype for *Actinopodium nathorstii*. These slides are now retained in the palaeobotanical collections of the Natural History Museum of Stockholm (Naturhistoriska riksmuseet). He noted that "the five sections (F, K, M, N, P) are evidently cut from one nodule at short distances from each other." These slides are similar in size and overall stele organization (Plate 18A, C-F), likely originating from the same branch, though their relative positions and the angle of sectioning remain unknown.

Additional sections were designated as cf. *A. nathorstii*. While Høeg recognized their anatomical similarity to the holotype, the method of preparation made it unclear whether they originated from the same axis due to variations in feature size. One of these slides (S021015, (L), Plate 18B) was selectively illustrated by Carluccio *et al.* (1966, Figure 3) and later depicted in an interpretive diagram by Schweitzer (1999, Figure 47), who described the tissue organization as "radially symmetrical."

Schweitzer (1999) later suggested a possible link between *A. nathorstii* and *Svalbardia polymorpha*, stating: "There is a possibility that *A. nathorstii* Høeg is a synonym of *S. polymorpha*, given the similarity between the anatomical structures of *A. nathorstii* and the rachides of *Archaeopteris macilenta*." He interpreted the insertion of ultimate branches as helical in both *S. polymorpha* and *A. nathorstii*.

Description

Material: Slide S021015 (L), Plate 18B, 19, Text Figure 45

cf. *A. nathorstii* (Høeg, 1942), Plate LVIII – LXII, Text Figure 33-35

A. nathorstii (Schweitzer, 1999), Plate 34, Text Figure 47

The specimen is described as being transversely cut, although the degree of obliquity is not known. This slide is significant because it preserves almost the full diameter of the axis (Plate 18B, Text Figure 45A). Although epidermal details are absent, the external outline of the axis is visible and the vascular tissues are displaced from the centre, with sediment partially filling the surrounding cavity. The axis measures 11.3 mm in width and 9.2 mm in height. The preserved vascular body measures 5.9 mm wide and 4.2 mm high and consists of an eight-ribbed xylem system arranged around a well-preserved pith (Text Figure 45B). The ribs are interpreted primarily as primary xylem strands, probably laterally connected around the pith by poorly preserved metaxylem, with sparse secondary xylem preserved around the flanks of some primary strands. The structure is therefore best described as the preserved xylem portion of the stele, rather than the complete stele itself.

From the centre of the preserved vascular body outwards, partially preserved tissues include the pith, primary xylem bundles and secondary xylem fragments. The primary xylem bundles are well preserved in places, particularly rib 7 (Plate 19B, Text Figure 45B-D), which remains largely intact. Outer cortex cells are present around the margins (Plate 19A).

The pith is poorly preserved, with degraded areas infilled by sediment. It has an estimated diameter of ~3 mm and height of 1.1 mm, though compression of the axis means these measurements likely underestimate the original size (Plate 19D). The tissue is largely disorganised, with some regions containing irregularly shaped cells resulting from wall degradation or sediment infill (Plate 19D - black *). Intact cells reach a maximum diameter of 25 µm (range: 11–25 µm).

The primary xylem bundles are comparatively well preserved. Eight distinct bundles form broadly triangular ribs that taper from base to tip (Text Figure 45D - green; Plate 19D). Rib length ranges from 0.6–1.6 mm and basal width from 0.6–0.8 mm.

Although the preserved xylem body is slightly compacted, it shows clear dorsiventrality and bilateral symmetry. The superior portion contains five closely spaced ribs (Text Figure 45B; 1-5), whereas the inferior portion has three more widely spaced ribs (Text Figure 45D, 6-8; Table 10). The ribs in the inferior portion are not only fewer in number but also larger and more widely spaced than those in the superior portion. Compared with other specimens, there is little preserved metaxylem tissue between the ribs, or this tissue has been degraded or broken, leaving the inter-rib regions apparently disconnected. The inter-rib distance on the superior side ranges from 1.1 to 2.9 mm, whereas on the inferior side the inter-rib distances are broader, ranging from 4.1 to 6.1 mm.

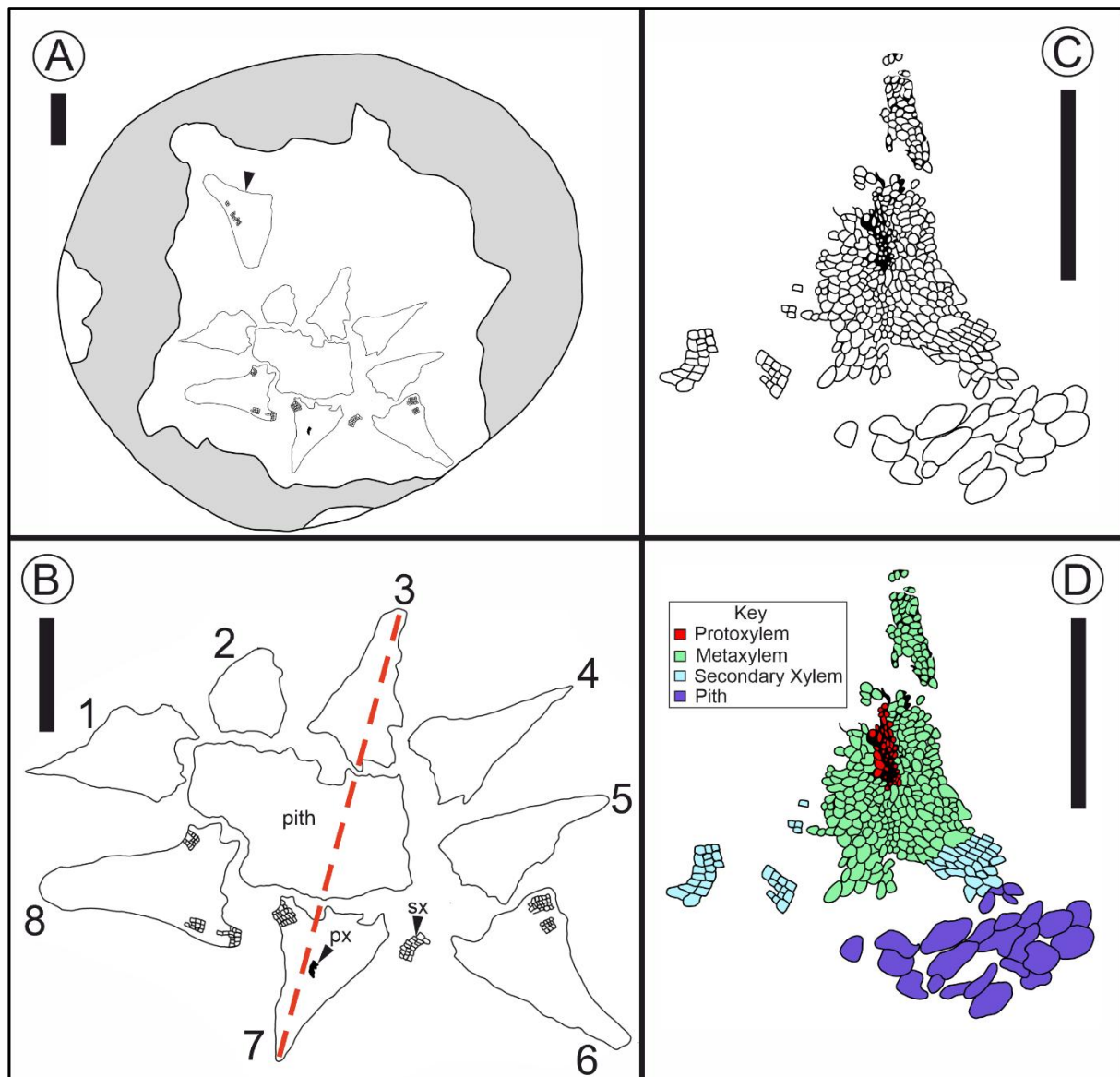
In the upper section of the axis there is a single, displaced rib (Text Figure 45A - black arrow; Plate 20D). Present in the rib are metaxylem tracheids and some evidence of secondary xylem. Small protoxylem tracheids occur in a constricted tip (Plate 20D - white arrow), giving the appearance that the rib may have been about to depart as a leaf or branch trace. This rib is not attached to the preserved xylem body, making it unclear whether it remained in situ before the vascular tissues shifted, or whether it represents a duplicate mapped rib displaced longitudinally along the axis during preservation. It has similar dimensions to the ribs in the intact vascular body (Text Figure 45A).

Metaxylem tracheids are relatively well preserved. They are small, somewhat uniform in size and shape and consistent across the ribs of the preserved xylem system. The average diameter is 10 μm (range: 6–15 μm). The tracheids are uniformly round with slightly thicker walls toward the outer edge of the bundle.

In rib 7, a strand of protoxylem tracheids is preserved at the centre of the bundle (Plate 19B - PX; Text Figure 45C-D), identified on the basis of size (2.5–8 μm in diameter). Their shape is difficult to discern in some areas due to the closely packed, darkened cell walls, which create a denser appearance. The radial extent of the protoxylem strand is approximately 500 μm . There may also be protoxylem tracheids in rib 6, inferred from the size of some tracheids at the centre of the bundle and the darkness of the cell walls, though their presence is less obvious than in rib 7.

Secondary xylem is largely absent, except for a few intermixed patches at the outer edges of primary xylem bundles where they appear as discrete wedges (Text Figure

45D). Where preserved, the secondary xylem tracheids are regular in shape, appearing as rectangular cells arranged in radial files. In some areas as many as nine cells are preserved in a single radial file. They have an average diameter of 7 μm (range: 5–10 μm) and thicker secondary cell walls, which appear darker along the outer edges of each cell.



Text Figure 45. Interpretative line drawings of *A. nathorstii*. A. Line drawing of the entire thin section S021015 (L). Black arrow depicts displaced rib. Grey shading shows where outer cortex is present (see Plate 18B). B. Interpretative drawing of actinostele in A with labels indicating rib number, pith, protoxylem (px) and secondary xylem (sx). Red line depicts line of symmetry. C. Interpretative line drawing of rib 7 including cell details. D. Same as (B), but with cells coloured according to their type. See key for explanation. Scale bar = 1 mm.

The small diameter of the axis, limited development of secondary xylem and preservation of a relatively discrete eight-ribbed primary xylem system suggest that this specimen may represent a young or relatively distal archaeopteridalean axis, rather than a mature woody branch. This interpretation is consistent with its proposed relationship to the leafy branching systems assigned to *Svalbardia polymorpha*, although no organic connection is preserved.

Most cortical tissue is not preserved, but distinct regions around the external portion of the axis contain at least two types of cells from the outer cortex, though in a poor state of preservation. These include thick-walled cells of varying sizes (Plate 18B - black arrow). Larger thick-walled cells have an average diameter of 65 μm (range: 40–101 μm), while smaller thick-walled cells average 32 μm (range: 18–39 μm).

Small vascular traces (83–89 μm in diameter) are present within the cortex (Plate 19A - black arrow; Plate 19C - white arrow). These traces are roughly circular in shape and contain tracheids 5–10 μm in diameter with darkened cell walls. The tracheids are similar in size to those in the protoxylem strands at the centre of rib 7. It is unclear whether these traces are in their original position or whether they have been displaced during deformation and movement of the vascular tissues away from the centre of the axis.

Specimen Number	Max Axis Width (mm)	Max Axis Height (mm)	Max Stele Width (mm)	Max Stele Height (mm)	Range of rib length (mm)	Range of rib width (mm)	Inter-rib distances					
							Rib number (Top)				Rib Number (Bottom)	
							1-2	2-3	3-4	4-5	6-7	7-8
S021014 (K)	18.9	8.5	14.2	6.3	1.7 – 2.2	1.3 – 1.8	2.1	4.6	4.8	4	N/A	7.6
S021019 (P)	N/A	N/A	13.8	6.3	1.4 – 2.3	1 – 1.9	2.6	3.9	5	4.1	5	6.8
S021009 (F)	N/A	N/A	13.7	6.9	1.5 – 2	1.4 – 2.8	2.9	5	4.4	4.4	3.7	6.6
S021016 (M)	N/A	N/A	14.4	7.5	1.4 – 2.1	1.1 – 1.7	2.8	4.5	4.3	4.4	4.2	6.3
S021017 (N)	N/A	N/A	15.2	7.3	1.5 – 2.5	1.3 – 1.7	2.8	5.3	4.6	4.3	4.4	6.9
S021015 (L)	11.3	9.6	5.7	4.3	0.7 – 1.5	0.6 - 0.8	1.9	1.4	1.6	1.1	4.1	2.6
Average	15.1	9.1	12.8	6.4	1.8	1.3	2.5	4.1	4.1	3.7	4.3	6.1

Table 10. Range of anatomical measurements for *A. nathorstii*. Summary of axis and stele dimensions, including rib length, width and inter-rib distance across multiple specimens. All measurements are reported in mm. Rib number is divided into superior (top) and inferior (bottom) portions of the stele. Inter-rib distance indicate the spacing between adjacent ribs. N/A values indicate measurements not available due to incomplete preservation. Note: specimens are likely orientated in oblique sections.

Holotype slides: S021014 (K), S021009 (F), S021016 (M), S021017 (N), S01019 (P)

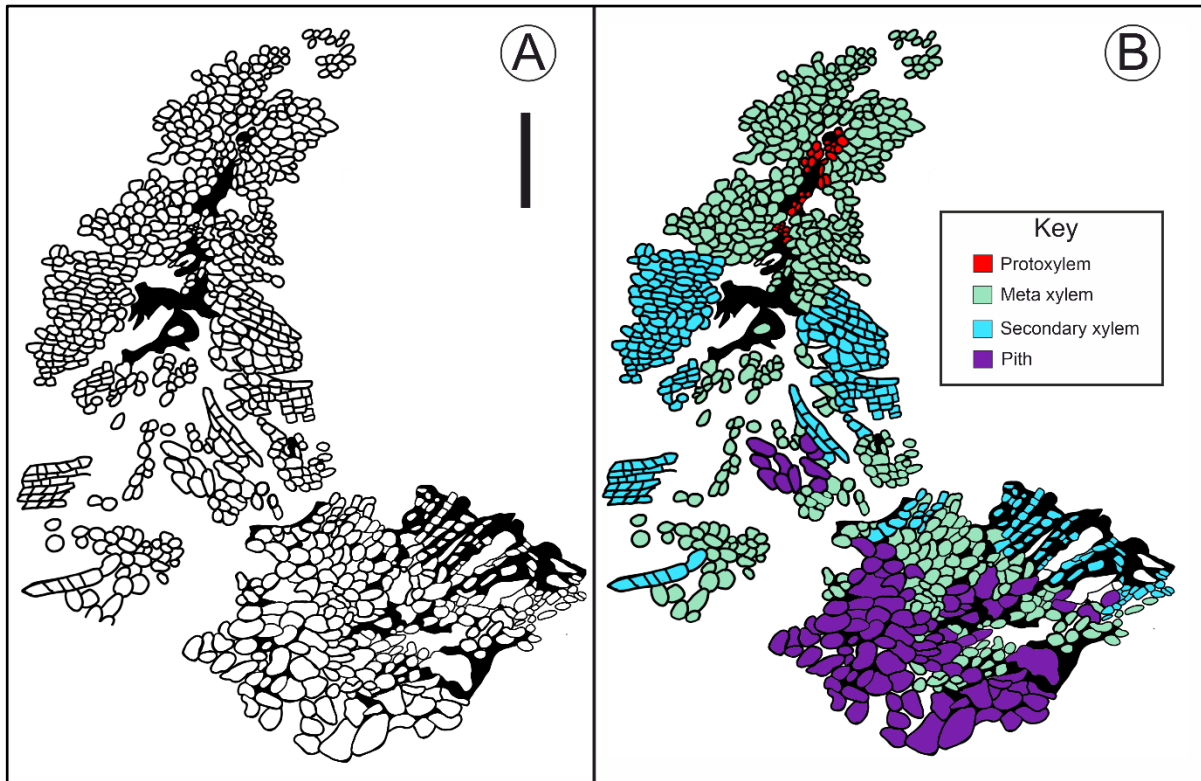
These slides form the holotypes for *A. nathorstii*. Each slide preserves different features and structural details owing to preservation, offering complementary perspectives. The spatial relationship and orientation of slides is unknown. From the centre of the stele outwards, partially preserved tissues include the pith, primary xylem bundles with metaxylem and protoxylem tracheids and secondary xylem fragments. Partial preservation of the outer cortex is present in some slides (Plate 18A, C–F). Descriptions are complementary to those of Høeg (1942) and Schweitzer (1999) with clarification and correction.

Slides show variable preservation of the stele, which appears as an eight-lobed, flattened, star-shaped eustele with five ribs on the superior portion and three on the inferior portion. In some slides, one of the lower ribs is poorly preserved and appears merged with an upper rib (Plate 18A, D). The stele measures 13.7–15.2 mm in width and 6.3–7.5 mm in height (Table 10). In slide S021014, the axis measures 18.9 mm in width and 8.5 mm in height. In other slides, tissues outside the stele are too fragmentary to determine complete axis dimensions. No definable epidermis is present in any section.

The best-preserved arrangement of stele tissue and outer cortex is in slide S021009 (Plate 18D), which retains the pith, metaxylem and protoxylem tracheids, secondary xylem tracheids and two distinct outer cortex cell types. The most detailed preservation of secondary xylem tracheid organisation occurs in slide S021019 (Plate 18C), although other tissues in this slide are moderately preserved particularly rib 3 of the superior portion (Text Figure 46).

The pith is poorly preserved across all slides but is best retained in S021014 (Plate 18A - *P*) and S021009 (Plate 18D - *P*; Text Figure 47 - *pith*). Its estimated width is 7.7 mm, and its height is 2.4 mm. The tissue is disorganized, with most parenchymatous cells having ruptured, resulting in irregular shapes and extensive infilling. There is variation in cell size and shape, with a mixture of larger, thin-walled parenchymatous cells (Plate 20A-B - black *) and smaller, thicker-walled cells (Plate

Text Figure 46. Tissue organization of a rib from the upper portion of the stele in *A. nathorstii*, slide S021019 (P), Plate 18C. (A) Interpretative line drawing of rib 3. (B) Same as (A) but with colour coding to illustrate tissue organization within the rib and inner stele, see key for explanation. Note: the orientation of the rib is reversed from that seen in Plate 18C. Scale bar = 500 μ m



20A-B - black arrow), the latter being more concentrated toward the centre of the stele.

Primary xylem bundles exhibit varying degrees of preservation, but all slides show eight distinct primary xylem bundles forming broadly triangular ribs that taper slightly from the centre of the stele to tips (Text Figure 46). Ribs are gently curved towards their tips and length ranges from 1.4 to 2.5 mm, while rib width varies from 1 to 2.8 mm (Table 10).

The stele exhibits dorsiventrality and bilateral symmetry (Text Figure 47), with five ribs on the superior portion (Plate 18A, C-F - 1-5) and three on the inferior portion (Plate 18A, C-F - 6-8). Ribs in the superior portion are smaller and more closely spaced (range 2.1 – 5.3 mm), with an average inter-rib distance of 4 mm, whereas ribs in the inferior portion of the stele are larger and further apart.

Metaxylem tracheids are preserved in discrete wedges or sections in most slides, but in S021019 they are exceptionally well preserved, particularly in rib 3 (Text Figure 46, green shading). They are small, uniform in size and shape across the ribs, with an average diameter of 10 μm (range: 5–17 μm). The tracheids are consistently round, with thicker cell walls toward the outer edge of each bundle.

Protoxylem tracheids are rarely preserved but the best examples are found in rib 3 of slide S021019 (Text Figure 46 - red shading). They are arranged in a broadly strand-like arrangement, extending from the tip of the rib toward the centre. Their shape is difficult to discern in some areas due to the closely packed, darkened cell walls which create a denser appearance. Protoxylem tracheids are significantly smaller than metaxylem tracheids, with an average diameter of 4 μm (range: 2–7 μm). The approximate length of the protoxylem strand in rib 3 is 850 μm .

Entire sections where secondary xylem is preserved as a continuous tissue layer are rare, with most occurrences limited to patches at the outer edges of primary xylem bundles, where they appear as discrete wedges (Text Figure 47 - sx). Where present, the secondary xylem layer is 0.3–0.6 mm thick and consists of thick-walled tracheids arranged in radial files. Each file contains 6–9 tracheids, extending from the outer edge of the rib to its core, where metaxylem tracheids are present. These tracheids are more uniform in size than those in the protoxylem and metaxylem, measuring 6–10 μm in diameter, forming the woody outer xylem layers surrounding the primary xylem bundles. In some cases, gaps between files of secondary tracheids suggests rays are present (Plate 20H-I - black arrows).

Preservation of cortical cells varies across the slides. At least two distinct outer cortex cell types are present: smaller, round cells with thick walls (Plate 20G - black *) and larger, irregularly shaped cells with thin cell walls (Plate 20G - white *). The smaller, thick-walled cells have an average diameter of 7 μm (range: 4–10 μm) and are arranged toward the outer axis near the presumed epidermal boundary. The larger, thin-walled cells have an average diameter of 14 μm (range: 7–25 μm) and are more concentrated around the external portion of the stele.

In some slides, traces destined to form leaves or lateral branches occur at the tips of certain ribs, appearing as small bundles that enlarge before presumed departure. In

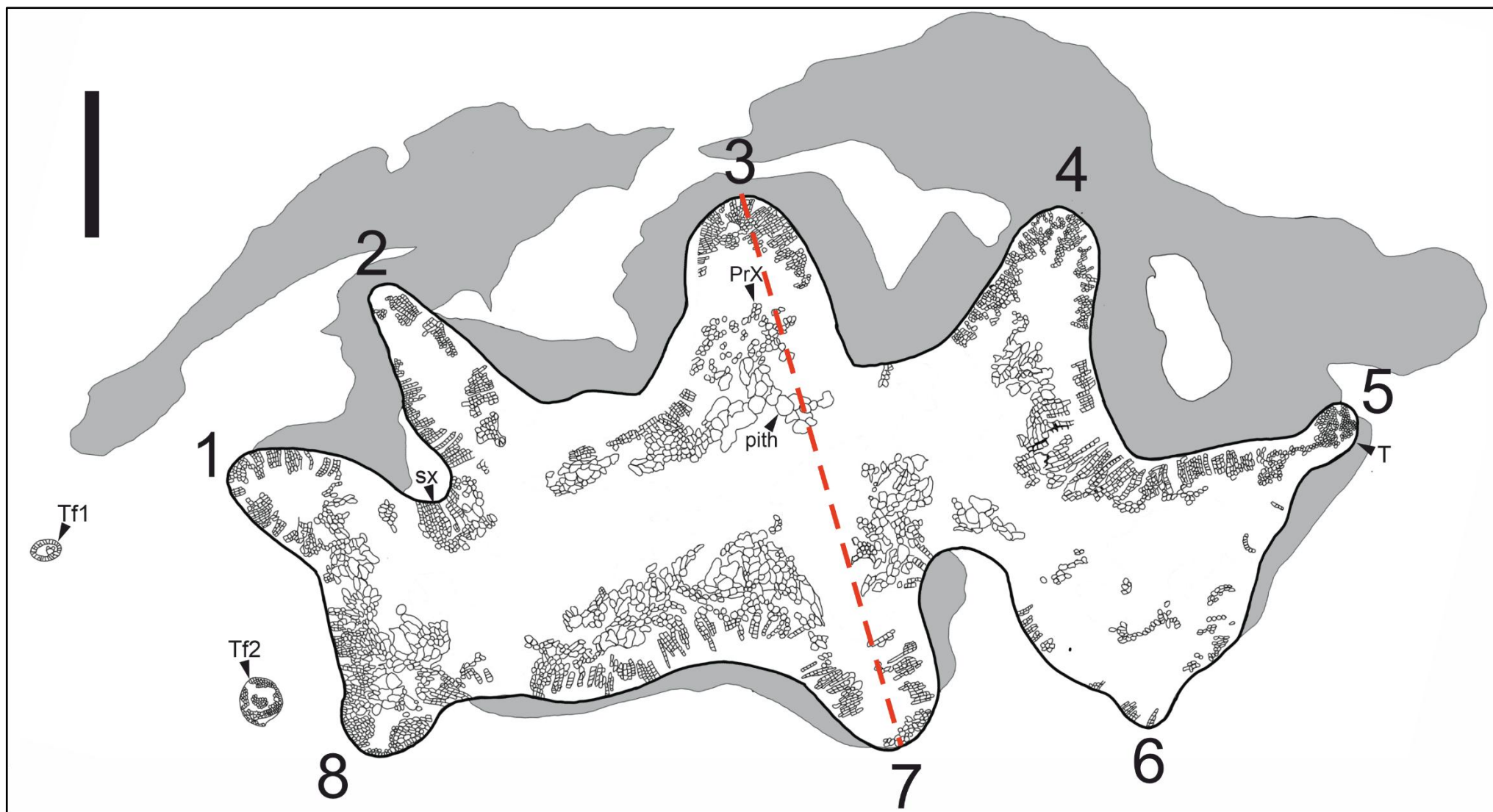
four slides (Plate 18C–F, rib 5), a trace extends from the distal portion of rib 5, swelling and budding before presumably separating from the rib.

In some slides, small circular traces are visible in the region where the cortex would have been if it was preserved (Plate 18E - *T*; Plate 20E-F). One of these traces is considerably smaller (0.5 mm diameter, Text Figure 47 - *Tf1*) than the other (1.1 mm diameter, Text Figure 47 - *Tf2*) with the former possibly representing a leaf trace and the latter possibly representing a branch trace. Both traces contain small tracheids (3–12 µm in diameter). The smallest and most densely packed tracheids occur at the centre, where their size and arrangement suggest they represent protoxylem.

New Conclusions on the Anatomy of *Actinopodium nathorstii*

- **Symmetry:** Xylem of *Actinopodium* is bilaterally symmetrical.
- **Dorsiventrality:** The upper surface bears five smaller ribs and the lower surface three larger ribs.
- *Actinopodium nathorstii* and cf. *A. nathorstii* of Høeg (1942) have the same overall organisation and characteristics and are therefore considered to both represent the same species.

Text Figure 47. Interpretative diagram of the preserved xylem portion of the stele and surrounding cortical tissue (grey shading) in *A. nathorstii*. Pith = parenchymatous pith cells. PrX = primary xylem tracheids. Sx = secondary xylem tracheids. T = possible budding leaf trace from rib. Tf = free traces not attached to ribs, Tf1 = smaller trace and Tf2 = larger trace. Red dotted line shows line of symmetry. Slide S021009 (F), Plate 18D. Scale bar = 2 mm.



Discussion (Part I – *Svalbardia polymorpha* and *Actinopodium nathorstii*)

Part I. Architecture and morphology of *Svalbardia polymorpha*

Historical Context

When *Svalbardia polymorpha* was first described by Høeg (1942), he recognised considerable variability in morphology and taphonomy. The features he stated caused particular concern for unity of the material, specifically because not one specimen showed all of these characters combined, included:

1. The branch angles (acute or wide),
2. The arrangement of branches, i.e. ultimate branches (opposite or ‘spirally’ arranged)
3. Small lateral appendages, i.e. leaves or branchlets (standing out at the base, then curved upwards and appressed or absent)
4. Branch systems (either long and divided dichotomously into filiform segments or short but with frond like morphology)
5. Fertile shoots (either present or absent).

Some of these concerns can be immediately addressed with the knowledge that Høeg assumed the material represented more or less the entire plant, estimating its size to be between one and two metres. Schweitzer (1999) later clarified that the ‘frond-like’ morphology probably represented a detached branch from a much larger trunk.

This issue of variability is not unique to *Svalbardia*. Extensive research over the past six decades has demonstrated that *Archaeopteris* also displays significant inter- and intraspecific morphological variation, particularly in branching and leaf form which makes diagnoses based solely on compression fossils problematic (Meyer-Berthaud et al., 2000; Fairon-Demaret & Leponce, 2001; Moreno-Sánchez, 2004). More reliable identifications are achieved when external features are linked with the distinctive secondary xylem (*Callixylon*), but such fossils are rare. This broader

context helps explain why Høeg and later authors struggled to consistently diagnose *S. polymorpha* from fragmentary compressions.

We now know that the fossils Høeg described were one unit of a much larger plant. Rather than representing a diminutive whole plant, *Svalbardia polymorpha* is better understood as part of a larger plant composed of stems bearing leafy penultimate branches, which in turn bear leafy ultimate branches. This revised interpretation provides a clearer understanding of the plant's true structure and helps resolve some of the issues that concerned Høeg.

Finally, the variation in the presence of fertile shoots also makes sense when considering that these specimens represent branches from a larger tree rather than individual plants. In a determinate-growth model, one would expect an entire plant to exhibit some form of reproductive structure at its apical portion. However, since *Svalbardia polymorpha* is now understood as a component of a larger, modular system, it follows that not every branch would necessarily bear reproductive structures. This hierarchical organisation explains the morphological variability seen in the fossil record and resolves some of the inconsistencies Høeg encountered in his diagnosis.

Reproductive Evidence

Whilst the taxonomic uncertainty surrounding the branching systems and leaves of *S. polymorpha* is understandable given the poor preservation of the type material, the reproductive structures provide far less ambiguity. Both Høeg (1942) and Schweitzer (1999) recognised that the fertile organs of *S. polymorpha* are virtually indistinguishable from those of *Archaeopteris*. Schweitzer noted strong similarities in the organisation of fertile zones at the distal ends of branches, directly comparable to those in *A. fissilis*.

In his original description, Høeg recorded isolated sporangial units alongside *S. polymorpha* and suggested they might belong to *Archaeopteris*, placing them under 'Svalbardia sp. Fructification' to reflect his uncertainty. The size range of the sporangia (1.5–2.0 mm) is very close to that of *A. fissilis* (1.6–2.0 mm; Andrews et al., 1965). When size, arrangement and general appearance are considered, there is no meaningful distinction between the fertile portions of the two species.

Schweitzer (1999) further elaborated on variability in sporangial size and shape, attributing it to a combination of taphonomic distortion and genuine morphological variation, possibly reflecting heterospory. This suggestion is consistent with earlier observations by Arnold (1930) and is now well documented across multiple *Archaeopteris* species (Kräusel & Weyland, 1941, 1960; Beck, 1960; Phillips et al., 1972; Bateman & DiMichele, 1994; Fairon-Demaret et al., 2001).

Branching architecture

The assumption that *Svalbardia polymorpha* was fundamentally different from *Archaeopteris* due to the presence of helically arranged, non-planate branching system has been one of the major barriers to understanding how this species fits within the current framework of Devonian plant evolution. Høeg also did not recognise leaves as being present on the penultimate branch. When he observed scars, he interpreted them as being branch scars which he therefore assumed to be helically arranged. Høeg did not, however explicitly include spirally inserted ultimate branches as a definitive diagnostic trait in his original description. Rather, he noted that the branches were ‘(probably) spiral’. Schweitzer (1999) reaffirmed this point, stating that ‘planation of fronds is either not developed or in the early stages of development’. His reconstruction showed helical insertion explicitly (Schweitzer, 1999; Text Figure 46).

Later researchers have subsequently treated spiral insertion as a key morphological trait of the genus *Svalbardia*, resulting in its widespread use in the diagnosis of new species (Petrosjan & Radczenko, 1960; Krausel & Weyland, 1960; Chaloner, 1972; Matten, 1981; Krassilov *et al.*, 1987; Jurina & Raskatova, 2014). This assumption has had significant taxonomic consequences, leading to the description of multiple *Svalbardia* species and reinforcing the perception of *Svalbardia* as distinct from *Archaeopteris*. This is despite Høeg stating in his original description that ‘both its vegetative characters and the form of its fructifications show that its place is in the neighbourhood of *Archaeopteris*, as a primitive relative of that genus.’

Leaves

Another issue concerning the original description of *Svalbardia polymorpha* is the nature and variability of its leaves. Both Høeg (1942) and Schweitzer (1999) noted a high degree of morphological variation among the collected specimens, even

between leaves found on the same individual specimen, including the holotype (Høeg, 1942). The species name '*polymorpha*' was even chosen in reference to the highly variable nature of leaf and branch morphology. While both authors agreed on the extent of this variability, they generally described the leaves as highly dissected, bifurcating multiple times (up to four), with parallel venation. These dissected segments often taper into filamentous structures that appear to be spirally inserted around the ultimate branch.

Høeg went so far as to compare some specimens of *S. polymorpha* with *Archaeopteris fissilis*, describing them as “virtually indistinguishable”, a view that was strongly supported by Beck (1971) who argues that *S. polymorpha* is a synonym of *Archaeopteris fissilis*. This comparison alone raises important questions about why *S. polymorpha* has historically been treated as a taxonomically separate entity from *Archaeopteris*, particularly in light of ongoing debates surrounding the interspecific and intraspecific variability of leaf morphology within *Archaeopteris*. It is now generally accepted that leaf shape alone is not a reliable character for distinguishing species in this genus, due to the significant intraspecific variation observed across specimens (Moreno-Sánchez, 2004). Instead, more dependable diagnostic criteria, such as branching patterns, internal anatomy and reproductive structures, are required for accurate species identification.

Whilst Høeg does not explicitly describe planation of the lateral branching system, he notes that “there is evidently not formed a composite leaf regularly expanded in one plane, but the branches of higher and lower order, as well as the filiform ramifications at the ends of the branches, may be arranged in all directions.” This implies that the leaves on the terminal portions of the plant may have a tendency toward insertion in multiple directions. Schweitzer highlights the ambiguous nature of the leaf organisation and emphasises the poor preservation of the material which contributes to the uncertainty around this species. He suggests that the leaves were three-dimensionally branched but also states that “it is uncertain whether leaves were arranged in a single plane or this is an artefact of preservation.” Additionally, he mentions that planation may have been possible and hints that this could have been an eco-physiological response to sunlight, a trait which has been well documented and justified in species of *Archaeopteris* (Krausel & Weyland, 1960; Carluccio *et al.* 1966).

New Understanding of Branching Patterns

The results of this study demonstrate that the insertion of ultimate branches on the penultimate branches in *Svalbardia polymorpha* is lateral and planate. On the penultimate branch, sub opposite pairs of ultimate branches emerge at acute angles. This branching pattern has been confirmed in multiple specimens and is particularly evident in the specimen shown in Plate 17C. With this new understanding, it becomes easier to re-examine the type material, despite its poor preservation and to appreciate why both Høeg and Schweitzer may have interpreted the branching system differently or were ambiguous over its description, particularly Høeg. Their interpretations can be attributed to the taphonomic limitations of the original material, which lacked the clarity necessary to reveal the true branching architecture and also a lack of dégagement of specimens. The branching pattern is directly comparable with that observed in *Archaeopteris* species (e.g. Carluccio *et al.* 1966; Beck, 1971; Scheckler 1978).

New Observations of Phyllotaxy

This study also shows that (A) penultimate branches of *Svalbardia polymorpha* bear leaves (Plate 17) and (B) these leaves display dorsiventral organisation (Text Figure 41). On the lower surface of the penultimate axis, a single row of leaves occurs between the sub-opposite branch pairs, while on the upper surface multiple insertions are present in several rows. The exact arrangement is difficult to determine, but the three-dimensional organisation of the foliage suggests a helical pattern, with some leaves perhaps not fully expanded at the time of preservation.

Helical phyllotaxis on penultimate axes, combined with dorsiventral organisation, is a trait that has been documented in several species of *Archaeopteris* (Beck, 1971; Scheckler, 1978; Kenrick & Fairon-Demaret, 1991; Fairon-Demaret & Leponce, 2001). The combination of dorsiventral planation with helically arranged leaves is typical of Archaeopteridalean penultimate branches and provides a clear morphological link between *S. polymorpha* and *Archaeopteris*.

Recognising this feature helps to resolve earlier uncertainties in interpretation and supports the view that *Svalbardia* represents compression morphologies of archaeopteridalean branch systems, rather than a distinct genus. Limited evidence also suggests that the upper leaves were smaller than the lower leaves, similar

anisophylly found in *A. macilenta* (Beck, 1971) and *A. roemeriana* (Kenrick & Fairon-Demaret, 1991).

Taphonomic Challenges and Preservation Bias

Some of the confusion surrounding the interpretation and precise taxonomic identity of *Svalbardia polymorpha* can be attributed to the poor preservation quality of the original material. Based on my own preparations, specimens collected from the type locality at Planteryggen are generally not well preserved. They are often preserved obliquely within the bedding plane, orientated in three dimensions within the matrix rather than lying flat and with distorted leaves and ultimate branches, which makes interpretation of branching patterns particularly challenging.

Davies et al. (2021, p. 6) suggested a river channel depositional setting for the Planteryggen locality, which would explain the observed disarticulation and distortion of collected specimens. This setting is further complicated by the very fine, filamentous leaves of *S. polymorpha*, which tended to splay out during deposition. After extensive dégagement, it was evident that these planate leaves were frequently twisted in all directions, sometimes rotating 180° within only a few millimetres, and in places continuing beneath or around the penultimate branch. Complete dégagement of these delicate leaves would have risked destroying the specimen.

Recognition of these taphonomic and preservational biases provides an important explanation for the discrepancies in earlier diagnoses. Many of the features that Høeg (1942) and Schweitzer (1999) found ambiguous can be better understood as artefacts of preservation rather than genuine taxonomic differences, highlighting the importance of careful re-preparation and contextual interpretation. Specifically the dégagement technique was not employed by either Høeg or Schweitzer, who appeared to have relied on surface features only.

Reassessment of *Svalbardia polymorpha* within the *Archaeopteris* Lineage

In my view, the presence of deeply dissected leaves with parallel lateral venation and observable intraspecific variability provides strong justification for comparing *Svalbardia* with species of *Archaeopteris*, a position also supported by both Høeg and Beck (1971). Høeg noted in his original description that some leaves of *S.*

polymorpha appeared smaller, less dense and less ‘fern-like’ than those of *Archaeopteris fissilis*, acknowledging the large variability seen in specimens to which *S. polymorpha* has frequently been compared. However, the specimens he used for this comparison were poorly preserved. Through serial dégagement and direct observation, I have demonstrated that the leaves can exceed 30 mm in length and in some cases appear significantly longer, often disappearing into the matrix after widening without any indication of terminating. It is therefore likely that some of the larger leaves in *S. polymorpha* are directly comparable to *A. fissilis* collected from Canada (Andrews et al., 1965). No modern study of *A. fissilis* from the Donbas type locality is available (Schmalhausen, 1894).

Høeg’s statement that the leaves of *Svalbardia polymorpha* are less ‘fern-like’ than those of *Archaeopteris fissilis* is not problematic when making a direct comparison between the two species. As Carluccio *et al.* (1966) clarified, describing *Archaeopteris* as ‘fern-like’ is inaccurate. Since then, our understanding of the branching architecture that diagnostically defines *Archaeopteris* has significantly improved. In fact, the intraspecific variation observed in the branching patterns of *S. polymorpha* falls well within the known range of variation in various *Archaeopteris* species (Beck, 1971; Kenrick & Fairon-Demaret, 1991; Fairon-Demaret & Leponce, 2001).

This variation is consistent with the architectural framework outlined by Trivett (1993), who showed that archaeopteridalean growth is better understood as a developmental continuum rather than as fixed categories of branch orders. Within this model, changes in leaf form and branching pattern occur as axes increase in size and develop through different growth stages. In this context, the dissected leaves and variable branching seen in *S. polymorpha* are expected features of *Archaeopteris* growth, rather than evidence of a distinct taxon. This helps to explain why earlier authors, who focused heavily on individual characters such as leaf shape or apparent phyllotaxy, placed too much emphasis on differences that are now better explained as part of normal developmental variation.

I would argue that relying on singular morphometric traits, such as leaf morphology, to diagnose *Archaeopteris* species is problematic due to the substantial intraspecific and interspecific variability observed within the genus. For example, Moreno-

Sánchez (2004) demonstrated that leaf morphology alone could not reliably distinguish *Archaeopteris halliana* from *A. hibernica*, *A. gaspiensis*, *A. jacksoni*, *A. latifolia*, or *A. roemeriana*. Accurate diagnosis therefore requires the integration of multiple morphometric characters and, where possible, anatomical comparisons, along with consideration of stratigraphic context and associated floral elements to make the best-informed estimate of species identity.

This study presents new evidence that *Svalbardia polymorpha* and *Archaeopteris* are explicitly linked by re-evaluating key morphological characters that were once thought to diagnostically separate the two genera. It is now clear that earlier interpretations of the branching architecture and highly variable leaf morphology were affected by preservation bias and lack of preparation. With a more refined understanding of the intraspecific variability observed in *Archaeopteris* species, the features seen in *S. polymorpha* can be confidently placed within the expected morphological range for the genus. To support this interpretation that *S. polymorpha* falls within *Archaeopteris*, a comparative table of the key morphological features shared between the two taxa has been compiled (Table 11). The results of this study show a great overlap between morphological features for both taxa, reinforcing the hypothesis that *Svalbardia polymorpha* represents a member of the Archaeopteridales.

Table 11. Summary table of key morphological traits used to diagnose *Svalbardia polymorpha* and their relevance to diagnosis of species and genus level discernment in *Archaeopteris*.

Morphological Feature	Description and Diagnostic Traits	Taxonomic Importance	Present in <i>Svalbardia polymorpha</i>
Branching Pattern	Ultimate branches arranged alternately along the penultimate branch (rachis), forming a regular pinnate pattern.	Species/genus-level	Yes – seen clearly in specimens collected in 2016.
Stem (Trunk)	Woody axis with distinct secondary growth (secondary xylem), showing typical <i>Callixylon</i> -type anatomy.	Genus-level	Present in anatomical form (<i>Actinopodium nathorstii</i>), however group pitting not definitively confirmed.
Lateral Branches	Penultimate branches alternate regularly; differentiation into sterile (vegetative) and fertile (sporangium-bearing) zones is common. Fertile zones are typically distal.	Species/genus-level	Yes – ultimate branches alternate. Fertile portions form distinct distal zones above sterile appendages.
Leaf Morphology	Simple to deeply dissected, fan-shaped leaves. Venation is dichotomous or sub-parallel. Leaf dimorphism may be present in some taxa.	Species-level	Yes – deeply dissected leaves (similar to <i>A. fissilis</i>). No clear dimorphism, though some variation in shape and size is noted (Høeg and current study).
Leaf Arrangement on Penultimate Branch	Dorsiventral arrangement – more leaves on one side (higher orthostichy number); the opposite side bears fewer leaves, with a mid-point leaf often appearing between ultimate branches.	Species-level	Yes – pattern matches dorsiventral leaf distribution; single leaves appear midway between alternate ultimate branches on the side with fewer orthostichies.
Leaf Arrangement on Ultimate Branch	Spiral leaf insertion. Differences in leaf shape and organisation occur between vegetative and fertile branches, with transitional forms also present.	Differentiation of fertile vs vegetative zones	Yes – spiral insertion observed. Morphological variation supports vegetative vs fertile differentiation.
Vascular System (Stele)	Actinostelic structure with a star-shaped cross-section. Bilateral symmetry in vegetative axes; radial symmetry in reproductive axes. Sympodia vary in size and continuity.	Genus-level	Yes – clear bilateral symmetry observed in vegetative branches. Fertile axis unknown.
Reproductive Structures	Fertile branches bear clusters of sporangia and differ morphologically from sterile branches. Some taxa exhibit heterospory.	Species/genus-level	Yes – fertile zones present distally, bearing sporangial clusters. Fertile leaves/branches occur proximally.
Secondary Xylem	Well-developed woody tissue, with defined secondary xylem and tracheids with grouped pitting on radial cell walls.	Genus-level	Yes – secondary xylem present in anatomical form (<i>Actinopodium</i>). Preservation is poor, but tracheids are identifiable. Rays are not well preserved. No observed group pitting, but orientation of longitudinal sections unknown.

Part II. Structure of *Actinopodium nathorstii*

While compression fossils such as *Svalbardia* provide valuable information on external branching and phyllotaxy, they do not preserve anatomical detail. To assess the internal structure of archaeopteridalean axes, anatomically preserved material is required. *Actinopodium nathorstii* therefore represents a critical counterpart to *Svalbardia* and its structure must be reassessed in light of historical interpretations. Høeg (1942) stated that the axes were sectioned in the transverse plane. However, since he was not involved in the original preparation of the material and given its relatively poor preservation, this interpretation cannot be confirmed with confidence. The lack of contextual information, combined with the degraded state of the specimens and clearly oblique orientation of some cell walls has contributed to the misinterpretation.

When Høeg (1942) first described *Actinopodium nathorstii*, he characterised the stele as stellate, comprising seven ribs. This description was based on five thin sections that he formally designated as the holotype. In addition, he designated another slide as cf. *A. nathorstii*, noting that its anatomy was bilaterally symmetrical. It was this latter specimen that Schweitzer (1999) subsequently described in detail.

The slide used by Schweitzer had been explicitly labelled by Høeg as cf. *Actinopodium nathorstii*, rather than being definitively assigned to the species. Høeg also noted that this specimen differed from the holotype in size, shape, and the number of ribs (eight instead of seven), although he acknowledged that both shared a broadly stellate organisation of the stele. Despite these differences, Schweitzer rejected Høeg's interpretation of bilateral symmetry and instead argued that the stele was radially symmetrical.

In the present study, the specimen designated by Høeg as cf. *A. nathorstii* is reassigned to *A. nathorstii*, as its anatomical organisation and overall morphology are consistent with the holotype series when re-examined in detail. This reassignment clarifies the original uncertainty surrounding Høeg's material and supports a unified interpretation of *A. nathorstii* as bilaterally symmetrical in stele architecture.

The slide used by Schweitzer does indeed preserve several xylem bundles clearly and shows the overall outline of the stele in excellent detail, as well as the outer

margins of the axis which is the only slide which gives a good indication of the axis dimensions, if their anatomical details have not been preserved. It even includes well-preserved protoxylem tracheids in at least one rib (Text Figure 45D).

I do not agree with Høeg's initial observation that the holotype slides show seven ribs, though I understand how he arrived at this conclusion. He himself noted there were "about seven rays," which already suggests uncertainty. In several slides, particularly the inferior right portion of the stele, one rib is either missing or poorly preserved (e.g. Plate 18D - rib 6), and this loss of detail likely led to his underestimated rib count. By contrast, Schweitzer's interpretation relied on a non-holotype slide, which preserved the stele outline clearly but differed in rib number and dimensions. This introduced a different error, exaggerating the variation and leading him to reject Høeg's view of bilateral symmetry. When preservation quality is taken into account, however, slides S021019 (Plate 18C), S021009 (Plate 18D) and S021016 (Plate 18E) consistently reveal eight xylem ribs and their spatial arrangement, which can be mapped with a high degree of confidence (Slide S021009, Text Figure 47). These observations strongly support an eight-ribbed, bilaterally symmetrical stele.

To better understand the sources of error and uncertainty in the interpretation of *Actinopodium nathorstii*, I have compiled a comparative table outlining the key morphological features as described by Høeg (1942), Schweitzer (1999) and this study (Table 12). The aim is to highlight both the similarities and discrepancies among these interpretations, and to assess how these differences may have contributed to the ongoing confusion and problematic taxonomy surrounding *A. nathorstii*. By directly comparing these features, it becomes possible to trace the development of previous hypotheses and clarify where reinterpretation is warranted. Some issues remain because of the lack of orientated longitudinal (radial and transverse) sections.

Table 12. Comparative interpretation of key anatomical features of *Actinopodium nathorstii* and cf. *A. nathorstii* based on descriptions by Høeg (1942), Schweitzer (1999) and this study (2025). The table highlights major areas of agreement and disagreement between the studies.

Feature	Høeg (1942)	Schweitzer (1999)	This study (2025)
Stele Structure	Elongated, star-shaped stele with 8 gently curved rays and sinuses.	Star-shaped, eight-armed stele, evenly distributed.	Star-shaped with 8 distinctive xylem ribs, broadly triangular, with gentle tapering and slight curvature toward the tips.
Stele Symmetry	Bilateral symmetry (cf. <i>A. nathorstii</i>); stele is elongated with one axis longer than the other.	Radial symmetry; arms arranged evenly around a central pith.	Bilaterally symmetrical; clear dorsiventrality with 5 smaller ribs on the superior side and 3 larger ribs on the inferior side.
Number of Ribs	7 ribs.	8 ribs.	8 ribs, with distinct dorsiventral distribution.
Pith	Mixed pith due to metaxylem intrusion.	Originally parenchymatic, later mineralized.	Poorly preserved, disorganised tissue infilled with sediment. Composed of irregularly shaped cells (11–25 µm), estimated diameter ~3 mm, but likely compressed.
Protoxylem Position	Protoxylem in ray centres and scattered along inner xylem.	Protoxylem in two distinct groups in star arms, separated by metaxylem.	Protoxylem preserved at the centre of primary xylem ribs, especially rib 7; visible as small, dense tracheids (2.5–8 µm diameter). Occasionally inferred in other ribs (e.g., rib 6).
Metaxylem Structure	Multiseriate pits, variable tracheid size.	Polygonal metaxylem cells, increasing in size outward.	Well-preserved metaxylem tracheids, small and uniform (6–15 µm), round with thicker walls towards periphery; consistent across ribs
Secondary Growth	Potential cambial activity but not confirmed.	Cambium present, secondary growth starts in sinuses and spreads.	Secondary xylem preserved as discrete wedges at the outer edges of primary xylem. Tracheids in radial files (6–9 cells per file), 5–10 µm in diameter with thick walls. Rays occasionally present.
Phloem	Indistinct boundary with cortex, some cells filled with fossilized contents.	Irregular, isodiametric cells, boundary with cortex indistinct.	Not clearly observed; some small vascular traces (83–89 µm) in the outer cortex may indicate phloem elements but position unclear due to displacement.
Cortex	Thin-walled cells with intercellular spaces, thick-walled towards the surface.	Similar to phloem but generally larger, no distinct zones.	Two cortex cell types: thick-walled large cells (40–101 µm) and smaller thick-walled cells (18–39 µm). Preservation poor; outer cortex fragments present, no epidermis defined.
Leaf Trace Bundles	Leaf trace bundles originate from circum-medullary region, no leaf gaps.	Occasionally present but too poorly preserved to confirm arrangement.	Traces observed in some ribs, particularly rib 7; protoxylem tracheids suggests branch/leaf origin. Small circular vascular traces also present in cortex region, though position likely altered by stele displacement
Dorsiventrality	Not explicitly recognised. Bilateral symmetry implied from the description of an elongated stele, but not interpreted as functional dorsiventrality	Denied dorsiventrality by favouring a radially symmetrical interpretation of the stele	Clear dorsiventral organisation demonstrated: 5 smaller ribs on the superior side and 3 larger ribs on the inferior side, consistent across multiple slides (e.g. S021019, S021009, S021016).

Part III. Comparison of *Actinopodium nathorstii* with *Svalbardia polymorpha* morphology

The revised anatomical interpretation of *Actinopodium nathorstii* provides a useful point of comparison with the external morphology observed in *Svalbardia polymorpha*. In this reinterpretation, *A. nathorstii* shows bilateral symmetry and dorsiventral differentiation between the superior and inferior portions of the stele. The superior region contains five smaller xylem ribs, while the inferior region contains three larger ribs, with both regions occupying broadly comparable spatial areas. This difference in rib size between the dorsal and ventral surfaces has not been sufficiently discussed in previous studies, nor has its potential significance for interpreting dorsiventrality, branching architecture and vascular organisation.

The number and distribution of xylem ribs in *Actinopodium nathorstii* are broadly consistent with the vascular organisation expected to supply the leaves and lateral branches in *Svalbardia polymorpha*, following the morphological interpretation presented above. On the dorsal surface of the axis, five smaller ribs were mapped. These may correspond with the up to five apparent leaf insertion positions recognised on the dorsal surface of the penultimate axis, although these cannot be demonstrated as continuous orthostichies throughout the preserved length.

On the ventral side of the axis in *A. nathorstii*, three larger vascular ribs are visible. The two outer ribs are consistent with a possible vascular supply to the lateral branches, which emerge in sub-opposite pairs in *S. polymorpha*. The central ventral rib may correspond to the row of leaves positioned between branching nodes. This arrangement suggests a close correspondence between the external organisation of leaves and branches in *S. polymorpha* and the internal stelar organisation of *A. nathorstii*. Although an organic connection has not been demonstrated, the observed anatomical and morphological correspondence supports the interpretation that *A. nathorstii* may represent the anatomical form of a *S. polymorpha*-type penultimate branch.

Part IV. Comparisons with *Archaeopteris*

The results presented above raise the central taxonomic question:

‘Is *Svalbardia* really a distinct genus, or should it be considered within the variation of *Archaeopteris*?’

Morphologically, the bilaterally symmetrical branching system of *S. polymorpha*, with sub-opposite pairs of ultimate branches and leaves borne on the penultimate axis, is closely comparable with branching patterns described in *Archaeopteris* (Carluccio et al., 1966; Beck, 1971; Scheckler, 1978; Trivett, 1993; Kenrick & Fairon-Demaret, 1991; Fairon-Demaret & Leponce, 2001).

The main argument for treating *Svalbardia* separately has been the supposed presence of non-planate or “spirally arranged” fronds (Høeg, 1942; Schweitzer, 1999). However, these interpretations are best explained by the poor preservation of the type material and misinterpretation of features. Apparent spiral insertion results from three-dimensional preservation of otherwise planate systems and the fragmentary nature of the fossils exaggerates variation in leaf and branch arrangement. Similar problems are seen within *Archaeopteris* itself, where both interspecific and intraspecific variation in branching and leaf morphology are well documented and can be problematic where preservation is lacking (Meyer-Berthaud et al., 2000; Moreno-Sánchez, 2004).

The anatomical evidence from the study of *A. nathorstii* adds a critical dimension. The eight-ribbed, bilaterally symmetrical stele of *Actinopodium nathorstii* matches the vascular organisation described in archaeopteridalean axes (Beck, 1971; Scheckler, 1978; Trivett, 1993). More importantly, the distribution of ribs in *A. nathorstii* aligns directly with the organisation of leaves and lateral branches in *S. polymorpha*, five dorsal ribs supplying the leaf orthostichies and three ventral ribs corresponding to lateral branches plus a single leaf row. This close correspondence supports the interpretation that the two fossils record different preservational aspects of the same plant.

Taken together, the available evidence weakens the case for maintaining *Svalbardia* as a clearly distinct genus on morphological grounds alone. The characters previously used to separate it from *Archaeopteris*, including the apparent spiral

insertion of ultimate branches, highly variable leaves and supposed lack of dorsiventrality, can be reinterpreted as the result of preservation, incomplete preparation or morphological variation comparable with that documented in *Archaeopteris*. On this basis, *Svalbardia polymorpha* is best interpreted as an archaeopteridalean branch system and probably falls within the morphological range of *Archaeopteris*.

Stratigraphic considerations

One reason *Svalbardia polymorpha* and *Actinopodium nathorstii* were not explicitly linked in earlier studies is that their stratigraphic positions were poorly constrained. When Høeg (1942) described *S. polymorpha*, and even when Schweitzer (1999) produced his reconstruction, the full stratigraphic range of *S. polymorpha* was not understood. Høeg regarded the type locality at Planteryggen as within the *Asterolepis* sandstone above Fiskekløfta, which he interpreted as older beds (Høeg, 1942, Table 5, p. 170) and this separation contributed to keeping the taxa apart.

Subsequent revisions to the stratigraphy of the Mimerdalen Subgroup have clarified the relationships between the Estheriahaugen, Fiskekløfta and Planteryggen formations. Field evidence presented here confirms that *S. polymorpha* occurs within the Estheriahaugen Member of the Tordalen Formation, stratigraphically just below the Fiskekløfta Member from which *A. nathorstii* was collected (Text Figure 38). This places the two taxa within the same geological interval, extending the known stratigraphic range of *S. polymorpha* by approximately one million years. The new correlation removes a major historical barrier to comparison and strongly supports the interpretation that *Svalbardia* and *Actinopodium* represent different preservational modes of the same archaeopteridalean plant.

Conclusion

The revised anatomical interpretation of *A. nathorstii* demonstrates a bilaterally symmetrical stele with eight xylem ribs, arranged as five smaller dorsal ribs and three larger ventral ribs. This dorsiventral organisation maps directly to the position of leaves and branches newly established for *S. polymorpha*, where dorsal ribs supplied the dorsal orthostichies of leaves, the outer ventral ribs supplied the lateral branches, and the central dorsal rib a single leaf row. This precise correspondence between vascular anatomy and external branching pattern supports the conclusion

that *A. nathorstii* represents the anatomically preserved form of sterile penultimate branches of *S. polymorpha*. The overall structure of the combined *Svalbardia/Actinopodium* branch system is consistent with morphological and anatomical expectations for *Archaeopteris*-type sterile branch systems. This interpretation aligns with the broader understanding of the organisation of sterile *Archaeopteris* branch systems. *Svalbardia polymorpha* should be transferred to *Archaeopteris*.

Chapter 3.1B: Large trunks possibly related to *Svalbardia polymorpha* (*Caulopteris*, large trunks, branched trunks, roots and *Callixylon*)

1. *Caulopteris*

Historical considerations and previously described specimens

Caulopteris is a form genus originally used to describe impression fossils of Carboniferous tree fern stems with elliptical scars arranged in a helical pattern (Lindley & Hutton, 1832). These scars represent the points of branch or frond attachment, left behind after the abscission of branches during the plant's life. Although historically associated with tree ferns, *Caulopteris* is a purely morphological designation and does not imply taxonomic affinity. As such, the genus has also been applied to fossils outside of the tree fern lineage, particularly to stems or trunks of uncertain biological affinity that display similar branch-scar patterns

The first specimen attributed to the form genus *Caulopteris* from Mimerdalen was collected from the Eastern canyon above Fiskekløfta and described by Høeg (1942, Text Figure 32, page 143). The specimen comprised a poorly preserved stem 75 mm in width bearing longitudinal furrows and oval scars or 'tubercles' between 15 – 20 mm in height arranged in steep spirals. Høeg was of the opinion that they were completely unrelated to *Archaeopteris* stating:

'There is no reason to assume that they have been of the type of *Archaeopteris*: *Caulopteris* stems and *Archaeopteris* foliage have never been known to have anything to do with each other.' (Høeg, 1942; page 143).

Schweitzer (1999) first suggested a link between *Caulopteris* and *Svalbardia polymorpha* stating that the two may be 'conspecific'. Schweitzer spent a week at the original *Caulopteris* site first investigated by Høeg. Several specimens were collected, many of which were embedded in the hard, sugary sandstone of the upper part of the Fiskekløfta Member (Text Figure 39 - localities *EC*, *RM*). Schweitzer stated that *Caulopteris* was first found in association with *Svalbardia polymorpha*

material *in situ*, however there was no documentation or evidence presented in support.

Although Schweitzer was confident in this connection between the two taxa, a thorough investigation did not reveal any evidence of *S. polymorpha* attached to *Caulopteris* stems. However, the dimensions of both matched and they were frequently found adjacent to one another *in situ*. According to Schweitzer, the best specimens were sent to Høeg in Oslo but states they have since been misplaced so were not available for study. Only two of the most poorly preserved specimens remained accessible (Schweitzer, 1999; Plate 34, Figures 1 & 2). These two specimens were 125 and 75 mm in width with oval branch scars 15 – 20 mm long and 10 mm wide, arranged in steeply ascending parastichies around the stem.

New specimens: Since 2010, 15 new specimens of *Caulopteris* have been located from Tordalen, Mimerdalen and Munindalen with the oldest specimen coming from the Estheriahaugen shale unit (late Givetian) and the youngest coming from the lower *Svalbardia* Sandstone of the Fiskekløfta Member (late Givetian). These specimens were collected by Høeg (unpublished material), Newman, Garrouste, Berry and Wyatt (Table 13). All specimens share a broad resemblance to the specimens initially described by Høeg and Schweitzer. However, there are some exceptional specimens that provide new features for description.

Across the available material, three distinctive preservational morphotypes were recognised and form the basis of the following descriptions. One specimen is considerably larger than the others and is preserved only as a fragment (Plate 10G–H). Owing to its fragmentary condition, it was excluded from detailed analysis, although its occurrence is noteworthy. The morphotypes described herein are designated *Caulopteris*-1, *Caulopteris*-2, and *Caulopteris*-3. It is probable that all specimens represent the same or closely related plants, with the observed morphological variation reflecting differences in taphonomic setting and preservation rather than taxonomic distinction.

Aims:

To use this new material to explore further the basis for the union of *Caulopteris* and *Archaeopteris*, taking into account variation.

Specimen name	Morphotype	Collector	Locality	Lithology	Length (mm)	Width (mm)	Figured in
EH-Nodule-Vogt	<i>Caulopteris</i> -1	Newman	Estheriahaugen Shale Unit (EST)	Shale (Black Shale II)	95	45	Plate 8E
No-Label-SS	<i>Caulopteris</i> -1	Berry	Eastern Canyon, Tordalen (EC)	Sugary sandstone (Lower <i>Svalbardia</i> Sandstone)	85	84	Plate 8G
Stem-64-68	<i>Caulopteris</i> -1	Garouste	Eastern Canyon, Tordalen (EC)	Sugary sandstone (Lower <i>Svalbardia</i> Sandstone)	115	41	Plate 8H
Stem-76-79	<i>Caulopteris</i> -1	Berry	Eastern Canyon, Tordalen (EC)	Sugary sandstone (Lower <i>Svalbardia</i> Sandstone)	165	87	Plate 8G
Stem-80-83*	<i>Caulopteris</i> -1	Garouste	Eastern Canyon, Tordalen (EC)	Sugary sandstone (Lower <i>Svalbardia</i> Sandstone)	173	105	Plate 8F
Stem-86-88	<i>Caulopteris</i> -1	Garouste	Eastern Canyon, Tordalen (EC)	Sugary sandstone (Lower <i>Svalbardia</i> Sandstone)	117	82	Plate 10C
Stem-89-91	<i>Caulopteris</i> -1	Berry	Eastern Canyon, Tordalen (EC)	Sugary sandstone (Lower <i>Svalbardia</i> Sandstone)	61	72	Plate 8B
Caul-2010-A	<i>Caulopteris</i> -1	Berry	North East Estheriahaugen (CAUL)	Asterolepis Sandstone	128	73	Plate 8A
Caul-2010-B	<i>Caulopteris</i> -1	Berry	North East Estheriahaugen (CAUL)	Asterolepis Sandstone	58	57	Plate 8D
Stem-84-85	<i>Caulopteris</i> -2	Garouste	Eastern Canyon, Tordalen (EC)	Sugary sandstone (Lower <i>Svalbardia</i> Sandstone)	104	NA	Plate 10A
UL-1-1	<i>Caulopteris</i> -2	Wyatt	Upper Lake, Estheriahaugen (UL)	Sugary sandstone (Lower <i>Svalbardia</i> Sandstone)	129	63	Plate 10B
PMO.250.220A	<i>Caulopteris</i> -2	Høeg	Eastern Canyon, Tordalen (EC)	Sugary sandstone (Lower <i>Svalbardia</i> Sandstone)	209	72	Plate 9A-F
PMO.250.220B	<i>Caulopteris</i> -2	Høeg	Eastern Canyon, Tordalen (EC)	Sugary sandstone (Lower <i>Svalbardia</i> Sandstone)	74	56	Plate 9G-J
Big_ <i>Caulopteris</i> *	NA	Berry	River's Meet (RM)	Sugary sandstone (Lower <i>Svalbardia</i> Sandstone)			Plate 10 G-H
E-H-Nodule	<i>Caulopteris</i> -3	Wyatt	Estheriahaugen Shale Unit (EST)	Shale (Black Shale II)	89	25	Plate 10 D-F

Table 13. Details of newly available *Caulopteris* specimens from Spitsbergen. Information on the specimen number, associated morphotype, collector, locality, lithostratigraphy, length and width are included.

Taphonomic considerations

A morphotype-based approach has been adopted to describe these specimens due to their number and variability, however, many of the observed morphological differences are likely influenced by the differing taphonomic conditions under which the individual specimens were fossilised. These factors have undoubtedly shaped the preservation of surface features and structural details, making a detailed discussion of taphonomic influences that caused them highly relevant in explaining the fossil forms observed. Further clarification of these taphonomic effects will be provided in the interpretation section following the individual morphotype descriptions. The implications of these taphonomic effects will be discussed in the discussion section.

Despite the variability in preservation, several distinctive features are recognisable across all morphotypes, allowing the specimens to be grouped into the same taxon:

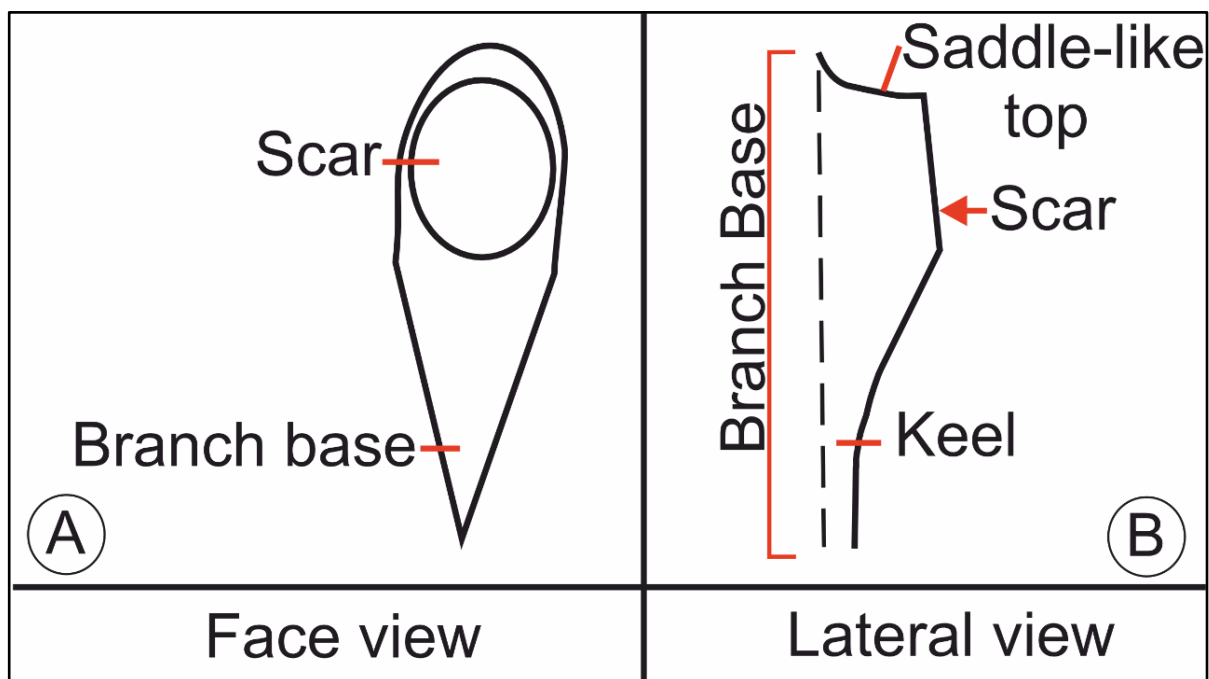
- Each specimen represents a fragmentary portion of a much larger axis, most likely a stem or young, growing trunk.
- Regardless of preservation quality, all specimens exhibit a broadly cylindrical axis bearing a series of scars arranged in a roughly helical pattern.
- These scars, likely marking the former positions of lateral branches, vary in shape, size, and degree of protrusion between morphotypes. However, their overall helical insertion supports a consistent structural organisation across specimens.

Terminology

The terminology surrounding *Caulopteris* can be imprecise, as it represents a form genus rather than a taxonomically valid genus. To maintain clarity and consistency throughout this section, I define the following terms as they are used in the description of specimens (Text Figure 48):

- Branch scar – The surface from which a branch has detached. In modern botanical terminology, this corresponds to the zone of abscission.
- Branch base – The structure protruding from the stem surface that may bear the branch scar distally

- Keel - A prominent, often elongate ridge running longitudinally along the branch base or axis, typically positioned centrally beneath the branch scar. It may represent the continuation of vascular or supportive tissue extending from the branch into the main axis.
- Saddle like top - The raised, arched upper margin of a branch scar, curving downward toward the lateral edges to produce a concave outline when viewed from above. This feature often gives the scar a characteristic saddle-shaped appearance.



Text-Figure 48. Line drawings illustrating the morphology of branch bases and branch scars in *Caulopteris* specimens, shown in (A) face view and (B) lateral view.

Morphotypes

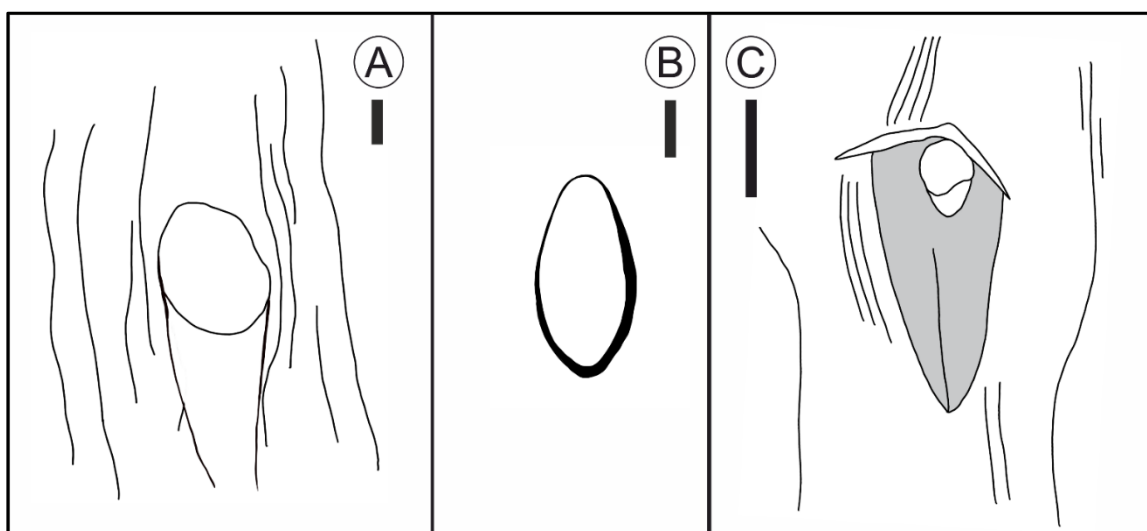
Caulopteris-1 (Plate 21)

This morphotype includes eight specimens that share distinctive morphological features. These include:

- **Branch scar morphology:** Scars are rounded to circular in shape and exhibit protrusion from the trunk surface, carried on a decurrent branch base which protrudes from the surface.
- **Surface texture of stem/trunk:** The surface between branch bases is uneven, displaying longitudinal furrows and ridges that vary in visibility depending on preservation. These ridges are frequently decurrent around the branch bases, usually extending below the scar (e.g. Plate 21E, F, H - white arrows) and in some instances above it (e.g. Plate 21E - black arrow), producing a tear-drop shaped outline around the branch scar. The specimens preserve only part of the original stem surface, rather than the complete circumference. The opposite surface or margin is either absent or compressed flat, probably as a result of post-burial deformation.
- **Preservation quality:** Surface detail varies among specimens. In well-preserved examples, surface ornamentation is clearly discernible between branch scars.
- **Collected from:** Estheriahaugen (Shale unit II, EST), Eastern Canyon (lower *Svalbardia* Sandstone, EC), *Asterolepis* sandstone (CAUL) (Text Figures 38, 39).

Description

Caulopteris-1 is represented by eight specimens with an average length of 126 mm (range 61–173 mm) and an average width of 75 mm (range 41–104 mm). These specimens are interpreted as portions of stems bearing branch scars, rather than detached lateral branches. Specimens are all partial internal casts. The preserved



Text Figure 49. Interpretative line drawings of the branch scar and branch base morphology (see text figure A) of the three different *Caulopteris* morphotypes. (A) Rounded branch scars of *Caulopteris*-1. (B) elongate branch scars of *Caulopteris*-2. (C) complex branch scar morphology of *Caulopteris*-3. Scale bar = 5 mm in all.

stem surface is either mostly flat or slightly curved, representing a portion of one side of the original stem before burial.

Branch scars (Text Figure 49) are rounded to circular in outline, arranged in a broadly helical pattern and protrude slightly from the surface of the trunk (<5 mm). The branch scars are 12 mm in average length (range 7 – 20 mm) and have an average width of 8 mm (range 4 – 12 mm) (Table 14). There are no other defining surface features of the scars, they are mostly smooth or slightly textured depending on sediment type.

One of the defining features of this morphotype is the presence of surface texture between branch scars, a feature notably absent in the other two morphotypes. This consists of longitudinal furrows and ridges, which varies in height and depth. In some specimens the ridges and furrows are quite deep, making the appearance of the trunk very textured (Plate 21A, B, D, H). In others (e.g. Plates 21C, E, F, G), the surface topography is more superficial, but remains visible in the upper few millimetres of the cast.

In well-preserved specimens (Plates 21E, F), the branch base projects slightly from the trunk surface and bears the branch scar distally (Text Figure 48). The upper margin of the base often forms a saddle-like top, curving downward toward the lateral edges and giving the scar a lobed appearance. Bordering the base are

decurrent ridges that extend below the scar, forming keel-like structures that may reach up to four times the length of the scar. These ridges typically create a slightly raised area beneath the scar (Plates 21E, F, H - white arrows) and may reflect taphonomic folding or deformation of the surrounding woody tissue (see Taphonomic Considerations). In some examples, the ridges curve inward beneath the scar, producing a teardrop-shaped structure that gradually flattens into the trunk surface (Plates 21F, H), likely representing the structure that supported the branch (Text Figure 48B). One specimen also shows ridges extending above the scar, producing a negative impression flanked by longitudinal furrows, which appear to encase the scar and further emphasise its lobed morphology (Plate 21E - black arrow).

Branch organotaxy

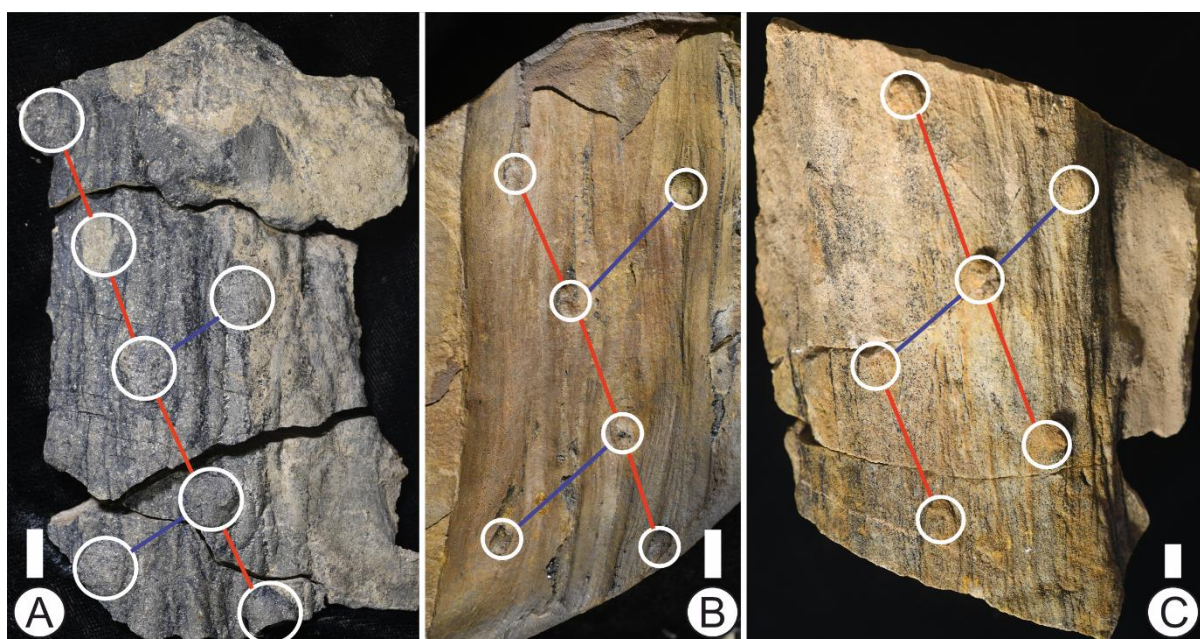
Across three of the best-preserved specimens, a partial pattern of branch scar arrangement could be determined (Text-Figure 50). The scars are organised in a broadly helical pattern around the stem axis. Angular divergence between successive scars in the same phyllotactic spiral vary between specimens. One specimen displays a tight clockwise spiral and internode distances of 13–16 mm (Text Figure 50, red lines). In contrast, the other two specimens exhibit a looser helical arrangement, with branch scars inserted in a clockwise direction at wider intervals, with internode distances ranging from 17–30 mm. Although less completely preserved, partial anticlockwise spirals could be determined in all three specimens (Text-Figure 50, blue lines). Internode length between anticlockwise branch scars ranged from 13 – 25 mm in successive branch scars in a helix.

Taphonomic considerations and interpretation:

Caulopteris-1

Asymmetry of preservation

In this morphotype, most trunks are preserved as partial casts that expose only part of the original stem surface, while the opposing surface is absent, flattened or poorly preserved. This consistent asymmetry may reflect a shared taphonomic pathway, although the repeated occurrence of this preservation style across several specimens is striking (Text Figure 51). Available specimen data indicate that most *Caulopteris-1* examples from Eastern Canyon occur in sugary sandstone of the Lower *Svalbardia* Sandstone, with additional material from the Asterolepis



Text Figure C. Phyllotactic spirals of branch scars preserved on *Caulopteris* trunks. White circles indicate the position of branch scars, blue lines show clockwise spirals and red lines show anticlockwise spirals. All are morphotype *Caulopteris* 1. (A) Caul-2010A. (B) EH-Nodule-Vogt. (C) Stem 76–79. Scale bar 10 mm in all.

Sandstone and one specimen from the Estheriahaugen shale unit. The repeated occurrence of asymmetrical casts in sandstone-dominated units may suggest burial within relatively energetic fluvial or channel-margin settings, where trunks were deposited horizontally, partly buried and exposed to decay before complete sediment infilling. It is also possible that mature stems already contained a structurally weak or partially hollow central region before final burial. The pith and adjacent inner tissues may have been more susceptible to early decay than the surrounding woody tissues, allowing sediment to enter the central region during burial. In this scenario, the sediment-buried surface could have been infilled and preserved as a cast, while the exposed surface was more vulnerable to decay, erosion or later compression. Decay of internal woody tissues outward from the pith, combined with the possible greater resistance of external tissues preserved locally as coalified patches (Plate 21E), may have contributed to the preservation of fine surface detail on only one part of the stem circumference. However, because detailed sedimentological data are not available for all specimens, this interpretation remains tentative.

Surface ornamentation of trunk

The surface ornamentation around the branch scars is an important distinguishing feature of this morphotype, but its origin remains uncertain. Several explanations are possible, including biological structure, taphonomic modification or a combination of both. Available specimen data show that most *Caulopteris*-1 examples occur in sandstone-dominated units, particularly the sugary sandstone of the Lower *Svalbardia* Sandstone, with additional examples from the *Asterolepis* Sandstone and *Estheriahaugen* shale unit. The repeated occurrence of similar surface ornamentation across several specimens is therefore striking and may suggest that comparable depositional or decay conditions affected multiple trunks.

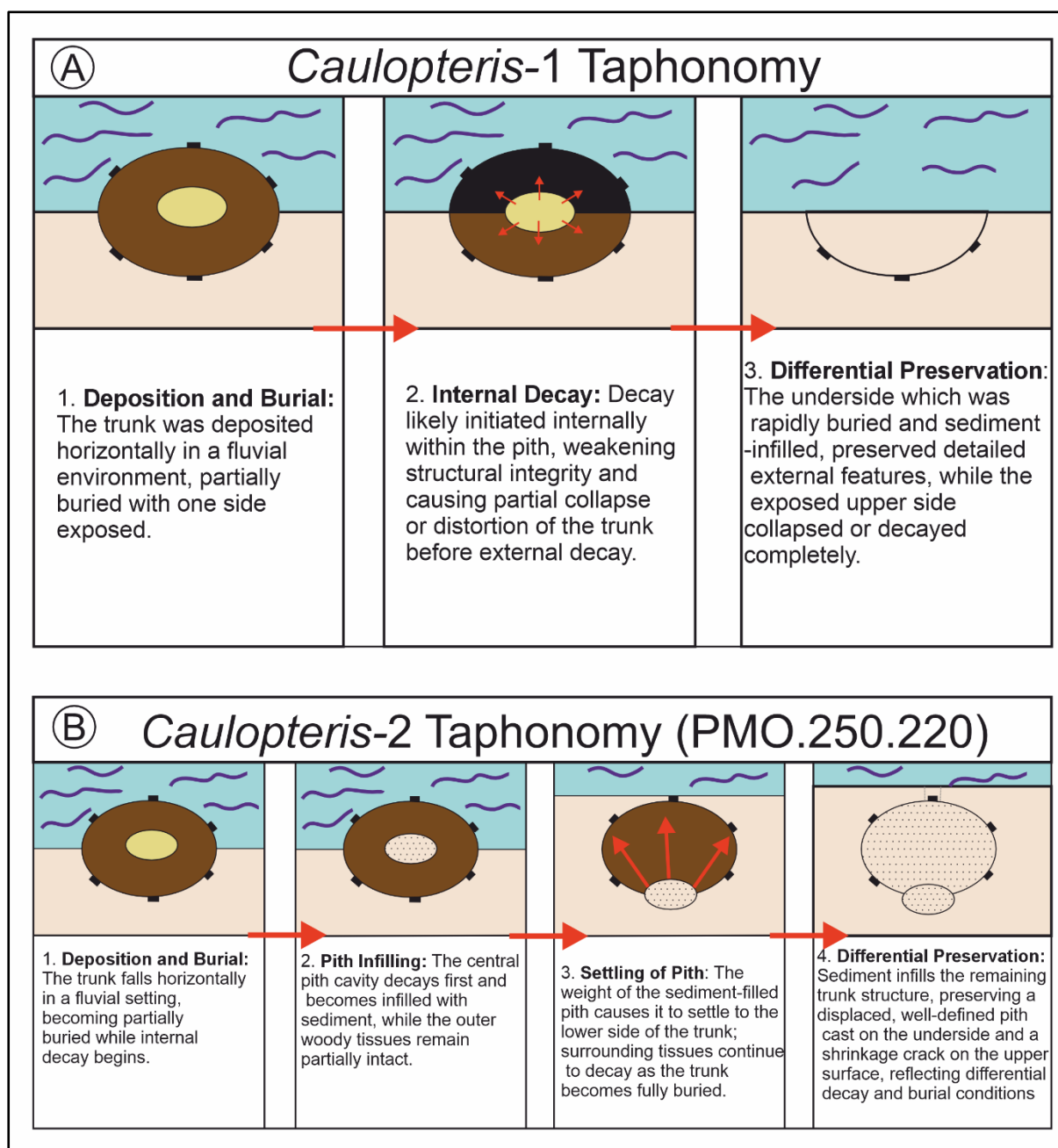
If the ornamentation is partly taphonomic, it may have developed through differential decay, compaction or warping of waterlogged woody tissues during burial. In a fluvial or channel-margin setting, one surface of a horizontally deposited stem may have been buried in sediment while the opposite surface remained more exposed to decay, erosion or compression. This could have produced differential preservation around resistant branch bases, creating raised ridges, furrows and decurrent structures around the scars. The fact that this ornamentation appears consistently across specimens of the morphotype, although with varying degrees of detail, lends some support to a repeated taphonomic pathway.

It is also worth considering whether these ridges reflect the structure of the bark, outer cortical tissues or the underlying wood. In the specimens described here, there is no clear evidence of preserved external bark features such as lenticels, rhytidome layering or a distinct peridermal surface. The ridges themselves appear sharply defined, continuous and angular, which may suggest that the ornamentation reflects the surface of the secondary xylem, tissues close to the branch base or an internal mould rather than the original outer bark. However, this interpretation should remain cautious. Resistant outer tissues, including periderm or sclerenchymatous cortex, may persist locally and could also contribute to the preserved surface patterning. Conversely, softer cortical tissues may have been lost during decay, transport or exposure before burial. The preserved texture may therefore reflect a combination of original anatomy, differential decay and the stage at which sediment infilled or moulded the trunk.

An alternative possibility is that the ridges represent the internal surface of an external tissue layer that decayed or separated from the wood during preservation. In this scenario, the bark or cortex may have persisted long enough to influence the final mould. However, without clearer anatomical preservation of the outer tissues, this cannot be demonstrated. The ornamentation is therefore interpreted cautiously as either an expression of woody tissue around the branch bases, a taphonomic surface produced during decay and compaction, the moulded surface of resistant outer tissues, or a combination of these factors.

Morphotype	Descriptive statistic	Length	Width	Branch Scar Length (mm)	Branch Scar Width (mm)
<i>Caulopteris</i> -1	Minimum	61	41	7	4
	Average	126	75	12	8
	Maximum	173	105	20	12
<i>Caulopteris</i> -2	Minimum	74	14	6	5
	Average	156	63	11	7
	Maximum	209	72	25	14
<i>Caulopteris</i> -3	Minimum	89	25	4	3
	Average			9	4
	Maximum			13	7

Table 14. Descriptive statistics for the three morphotypes of *Caulopteris*. The table includes morphotype designation, trunk length, trunk width and branch scar length and width. Descriptive statistics provided are the minimum, maximum and average values for each feature.



Text Figure 51. Taphonomic models illustrating possible preservation pathways for *Caulopteris-1* (A) and specimen PMO.250.220 of *Caulopteris-2* (B). **A.** In *Caulopteris-1*, asymmetrical preservation resulted from partial burial with only the lower surface infilled and preserved while the upper surface decayed. **B.** In specimen PMO.250.220 of *Caulopteris-2*, early sediment infill of the pith cavity and gravitational settling led to displacement of the pith, with a shrinkage crack forming on the exposed upper surface (grey dotted lines).

***Caulopteris-2* (Plate 22 & Plate 23A-C)**

This morphotype includes four specimens that share distinctive morphological features. These include:

- **Branch base morphology.** In *Caulopteris-2*, the structures are best interpreted as branch bases rather than branch scars, as their pronounced three-dimensional relief is more consistent with retained bases than with abscission scars. They are elongate, with an oval outline, contrasting with the more rounded scars typical of *Caulopteris-1*. These bases lack both a saddle and keel which makes their orientation more ambiguous. They protrude prominently from the trunk surface, with some extending up to 19 mm outward. Unlike the scars in *Caulopteris-1*, which often appear integrated with the surface ornamentation, the branch scars in *Caulopteris-2* are distinct and sharply defined, forming discrete structures that stand out clearly from the otherwise smooth trunk surface.
- **Surface texture of trunk:** The surface of the trunk is consistently smooth across specimens, lacking the surface ornamentation that characterise *Caulopteris-1*. No folds or surface relief are visible between scars in any of the specimens.
- **Trunk preservation:** The trunks retain a rounded cross-section, with most specimens preserving the full circumference, unlike the partial preservation *Caulopteris-1*. This suggests more complete burial during fossilisation, resulting in complete preservation of the trunk. A possible pith cast will be discussed below.
- **Collected from:** Lower *Svalbardia* Sandstone at Eastern Canyon above Fiskekløfta (EC), and River's Meet (RM), 300m above Fiskekløfta, Tordalen. See Text Figures 38, 39.

Overarching morphology

This morphotype includes four specimens, two of which (PMO.250.220A and PMO.250.220B) likely represent adjacent fragments of the same trunk although the section linking them is missing. The *Caulopteris-2* specimens are incomplete, ranging from 74 to 209 mm in length and 14 to 82 mm in diameter, although the

lower end of that range is from a specimen with abnormal preservation and likely represents only part of the width (Plate 23A).

Two specimens (Plate 23A, B) are fragmentary and will be used solely to estimate the size of the branch bases; they have been assigned to this morphotype based on the absence of surface ornamentation between bases and the more three-dimensional nature of branch scars which protrude further than those described in *Caulopteris-1*. However, as they represent only partial trunks, they offer limited morphological detail. In contrast, the remaining three specimens are more complete and form the basis for the description and discussion of branch arrangement.

Branch scar morphology is elongate to elliptical in outline and clearly differentiated from the smoother trunk surface. They are often surrounded by a thin layer of carbon that penetrates into the underlying trunk tissue (Plate 22A - black arrow). Base lengths range from 6 to 25 mm, with widths between 5 and 14 mm. These branch bases protrude more prominently than in the other two morphotypes appearing slightly tapered when viewed in side profile (Plate 23C - white arrow), with some extending outwards up to 19 mm from the trunk surface. The surface texture of the branch scars is smooth, with no discernible ornamentation.

Exceptional specimen – PMO.250.220A & B.

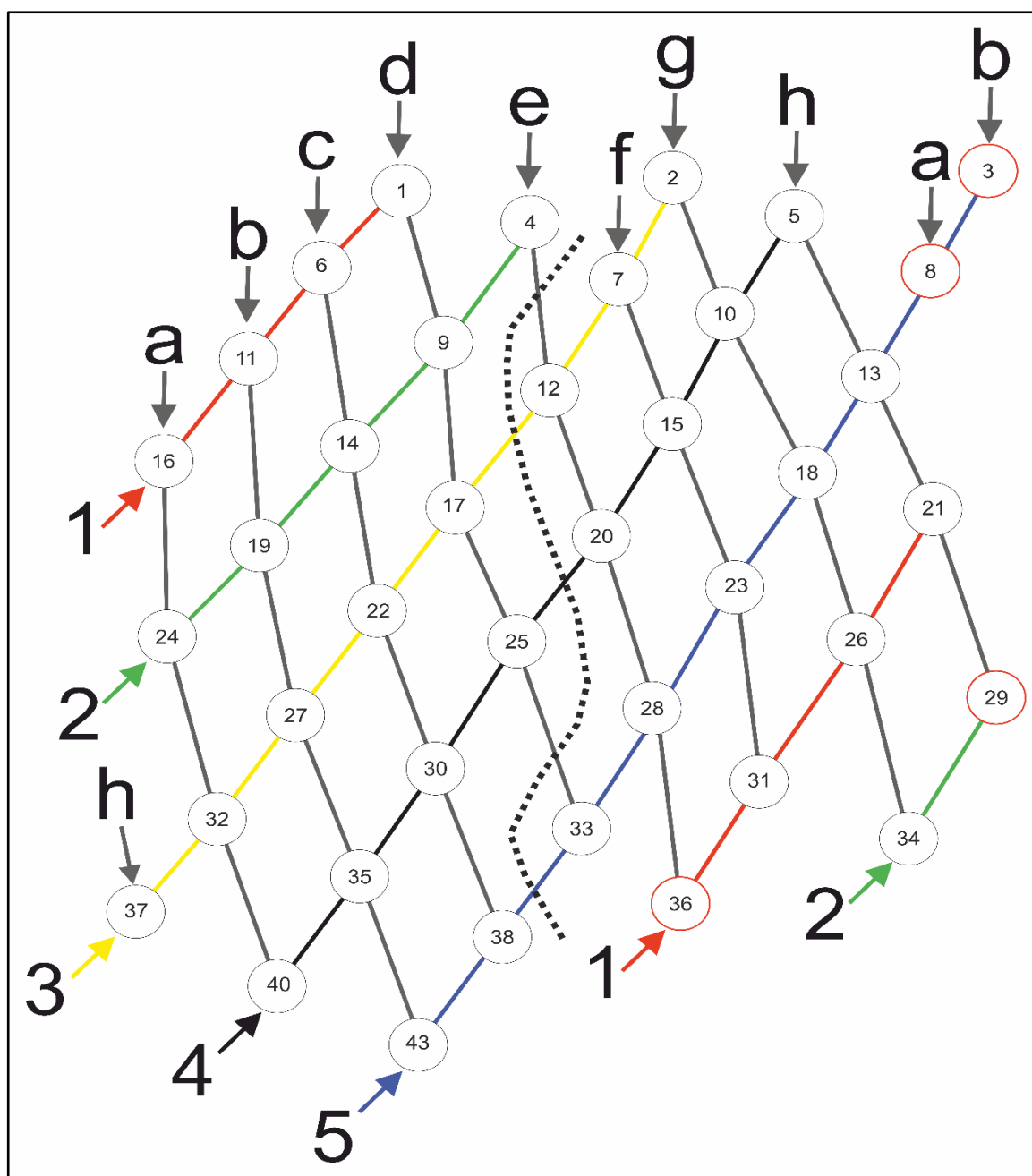
The most exceptional specimens forming the basis for the remainder of the description of this morphotype are PMO.250.220A (Plate 22A-F, J) and PMO.250.220B (Plate 22G-I), collected by Høeg in 1939 from the locality described as '300m above Fiskekløfta' (likely Eastern Canyon). During my visit to Oslo in 2023, I identified these specimens among unpublished material; although originally found in fragments, they were subsequently reassembled to reflect their original form. It is clear that they represent portions of the same axis, with PMO.250.220B likely belonging to a more distal part of the trunk, as indicated by its slightly smaller diameter. This interpretation is supported by their matching surface features, similar size and pattern of branch scars and the presence of a central pith cavity cast, a characteristic feature of this specimen pair. The presence of this cast may indicate that the central region of the mature axis was structurally weak, degraded or partially hollow prior to final burial, although later decay, sediment infilling and compaction are

also likely to have influenced its preservation. This feature is discussed further below.

Branch bases are arranged helically around the circumference of the trunk, forming two intersecting sets of parastichies oriented in opposing spiral directions, producing a 5:8 Fibonacci pattern of organotaxy (Text Figure 52). In the anti-clockwise direction five spirals are discernible, with distance between branch bases in the same spiral ranging from 11–22 mm. The clockwise direction comprises eight distinct spirals, characterised by a steeper helix and larger distances between branch scars of 27–37 mm.

The most extraordinary feature of this specimen is the presence of a prominent cylindrical cast running along the side of the trunk, visible most clearly in specimen A (Plate 22C–F - white arrows). The structure is up to 30 mm in width and protrudes from the trunk surface by as much as 26 mm. It appears consistently cylindrical and well-defined along its length. Longitudinal ridges and furrows, rarely anastomosed, run along its surface, with carbonised material occasionally present in the depths of the furrows (Plate 22D–F - white asterisks). In lateral view of specimen B (Plate 22J), the structure is clearly distinct from the trunk (Plate 22J - white arrows). This interpretation is supported by the well-defined surface texture of the structure, which contrasts with the smoother surface of the trunk, implying it is not part of the original trunk surface. However the two cylinders share sedimentary fill (Plate 22J) and the smaller cylinder is adjacent to, and enveloped by, branch bases on both sides. The origin and possible taphonomic significance of this feature will be discussed further below.

On the opposite side of the trunk, present on both portions A & B, there is another protruding structure but it is much flatter and more flanged in appearance (Plate 22A, H - white *). This likely represents a shrinkage crack or joint, a feature commonly observed in large trunks of *Callixylon/Archaeopteris*. This interpretation will be discussed further below.



Text Figure 52. Diagram showing the phyllotactic arrangement of branch scars (organotaxy) in a *Caulopteris* trunk (specimen PMO.250.220A – Plate 22). The pattern follows a 5:8 Fibonacci sequence, comprising five anticlockwise and eight clockwise helices of branch scars around the stem. Numbers and coloured lines indicate the anticlockwise helices; letters and associated spirals denote the clockwise helices. The black dotted line marks the position of the preserved pith cast within the specimen. Numbering follows the system of Beck (2010, fig. 7.14). Red-circled branch scars were not preserved on the specimen surface but are inferred from the phyllotactic sequence, as that part of the stem is missing (36) or they are located where the stem is cracked (3, 8, 29). The pattern was established by wrapping tissue around the axis and marking the bases with a pen.

Taphonomic considerations and interpretation:

***Caulopteris*-2**

The preservation of a mostly intact, albeit slightly compressed trunk suggests that burial may have occurred relatively early in the decay process, before all of the woody outer tissues had decomposed. This contrasts with specimens in *Caulopteris*-1 and -2, which preserve only one surface of the trunk.

Another defining feature of this morphotype is the absence of strong surface ornamentation between branch scars, a characteristic notably present in both of the other morphotypes. The surface relief and ornamentation seen in *Caulopteris*-1 and -3 may be the result of more advanced stages of decay, where the wood of the trunk swelled or warped prior to burial. As sediment infilled these deformed surfaces, it produced a more textured external mould. In contrast, the smoother surface of this morphotype may reflect direct infilling of the internal trunk cavity, preserving less external detail. However, it is also possible that not all specimens represent internal casts. Some may reflect internal moulds of trunks with external tissues still attached at the time of burial, while others may record examples where these tissues were lost prior to sedimentation. Differences in surface texture may therefore relate to how quickly external tissues decayed across specimens, introducing additional variability in preservation.

Exceptional specimen PMO.250.220 A & B

PMO.250.220A/B (Plate 22) preserves a rounded, cylindrical structure running longitudinally adjacent to both portions of the trunk. It is distinctly circular in cross-section, with sediment fill continuous with that of the main cast, but has been displaced to one side of the axis. Its position suggests gravitational settling to the lower side of the trunk, likely when it was lying horizontally in a fluvial environment during decay (Text Figure 51B). This structure is tentatively interpreted as a sediment-filled pith-like cast, which may have become infilled early in the decay process (Text Figure 51B, 2). The added weight of the infill may have caused it to settle downward within the decaying woody trunk. As decomposition progressed, the surrounding tissues were also infilled, preserving the overall form as an internal cast. The result is a well-defined, pith-like cylinder positioned at the base of the trunk, consistent with gravitational settling in a water-saturated burial environment.

On the opposite side of the trunk a single, flange-like fissure runs its full length. Similar longitudinal shrinkage cracks are well documented in large fossil trunks of *Callixylon* and *Archaeopteris* (Arnold 1934, 1936; Cross & Hoskins, 1951). Although most published examples describe transverse cracks, the orientation here is not unexpected if the pith cavity shifted toward the lower surface during decay. As the wood dried and contracted the crack may have opened in the same vertical plane as the displaced pith. In a fluvial setting this makes functional sense: the upper surface of a partly submerged log is exposed to air, encouraging desiccation and wood checking, while the underside remains water-logged and gradually fills with sediment (Text Figure 51B). The sediment-laden pith cavity then sinks, the upper side dries, splits and is filled in with sediment and the result is the differential preservation seen in this specimen.

Interpretation of the cylinder as a pith cavity cast is not the only explanation. It could, perhaps represent a liana. Support for it being a pith cavity includes:

- Surface texture of longitudinal ridges / grooves (Plate 22E) is comparable with the branching network of sympodia found in the *Archaeopteris* eustele (Beck, 1971)
- Size is comparable with *Archaeopteris* pith

The position of the cylinder on the outside of the stem cast is also complex to interpret. Supports for the cylinder having originated inside the stem includes:

1. Branch bases partially enclose the cylinder on both sides (Plate 22E, F)
2. The presence of a prominent longitudinal fracture on the opposite side of the stem demonstrates considerable readjustment of the stem surface tissues during taphonomic process.

***Caulopteris*-3 (Plate 23D-F)**

This morphotype is represented by a single specimen, but its significance lies in its stratigraphic context. Notably, a specimen of *Caulopteris*-1 (Plate 21E) was also recovered from the same unit. Together, these finds extend the known stratigraphic range of *Caulopteris* in Svalbard downwards and co-occur with the oldest specimens of *Svalbardia polymorpha*.

The specimen displays the following morphological features:

- **Branch scar morphology:** Branch scars are the smallest of all three morphotypes but show exceptionally fine detail. The scars are flattened due to compression, however they exhibit well-defined outlines and internal structuring which is not observed in *Caulopteris*-1 or -2.
- **Surface texture of trunk:** Surface is mostly smooth, but with fine textural features mainly concentrated around the branch scars. These include subtle ridges and furrows that are generally confined to the immediate margins surrounding the scars.
- **Branch spacing and distribution:** The spacing between branch scars decreases progressively along the length of the stem/trunk. This may reflect an ontogenetic shift in branching pattern as the stem tapered, but could also record changes in growth rate linked to environmental conditions. Reduced spacing may indicate slower axial extension during periods of stress or disturbance, although this remains uncertain.
- **Preservation context:** The specimen is preserved as a flattened impression within an ironstone nodule, which has facilitated the preservation of delicate surface details found within branch scars. However, this mode of preservation obscures the true diameter and three-dimensional form of the original trunk, only one side of the trunk was collected the counterpart was not found.
- **Collected from:** Black Shale II, Estheriahaugen Member, East Estheriahaugen (EST) (Text Figures 38, 39).

Overarching morphology:

This morphotype is represented by a single external impression fossil 89 mm long and up to 25 mm wide. The fossil is relatively flat, with a gentle concave curvature on

its surface, but has been mostly compressed. It is one of the smallest specimens found and may represent a juvenile form (i.e., potentially bearing large leaves directly on its trunk rather than on lateral branches).

Branch scars are on average 9 mm long (range: 4–13 mm) and 4 mm wide (range: 3–7 mm) and exhibit finer surface detail than the other two morphotypes (Table 14). The scars are generally circular (Text Figure 49C), with some displaying a thin, horizontal raised sliver above them representing some taphonomic artefact (Plate 23G - white arrow). Each scar forms a slightly positive impression and is then surrounded by a circular negative depression (Text Figure 49C). Fine longitudinal furrows and lines radiate across the surface surrounding the scars, forming delicate surface ornamentation (Plate 23E).

Toward the presumed basal end of the axis, identified by the wider spacing between branch scars, each scar sits atop a slight swelling, projecting 1–2 mm above the surrounding surface. As the axis narrows, branch scars become noticeably more crowded and the surrounding ornamentation becomes increasingly disordered due to overlapping ridges and furrows, obscuring ontogenetic patterns but an overall helical organotaxy can be determined (Plate 23D - white *).

Distance between successive branch scars in the clockwise direction range from 9 to 12 mm, with insertion angles between 60° and 80°. In the anticlockwise direction, internode distances range from 9 to 16 mm becoming progressively shorter toward the narrower, apical portion of the axis, where surface ornamentation also becomes more disordered. Insertion angles of branch scars anticlockwise spirals range from 45° to 70°, reflecting the decreasing width of the axis from basal portion to apex.

Taphonomic considerations and interpretation:

Caulopteris-3

This specimen is one of only two preserved as an impression within an ironstone nodule and retains finer branch scar detail than other morphotypes. However, this preservation mode also introduces artefacts, including distortion of scar morphology and apparent crowding toward the apical end, the origin of which (biological or taphonomic) remains uncertain.

Compression has affected the stem/trunk, although the degree to which this altered its original width is uncertain. If the specimen was already partly surrounded by sediment during compaction, lateral expansion may have been constrained and the preserved width may approximate the original stem width. However, compression has still affected the surface relief and may have distorted the apparent arrangement of branch scars, with only one surface preserved. Near the apex (Plate 23D - white asterisk), ornamentation becomes increasingly disordered, potentially due to growth pattern, environmental variation or post-burial deformation. Flattening may have exaggerated crowding and altered apparent insertion angles, complicating reconstruction of the original branch arrangement.

One of the key distinguishing features of this morphotype is the exceptional preservation of branch scar detail, especially where scars are more widely spaced near the presumed base. The scars exhibit a more complex morphology than the simple, raised knob-like features of the other two morphotypes, which likely represent internal casts. Fine positive and negative impressions are present, with some showing exceptional preservation. In several cases, coalified material extends into the impressions (Plate 23F - white arrow), possibly representing remnants of the vascular supply to the scars. Minor surface artefacts also occur, including thin horizontal slivers above or below some scars (Plate 23F - white arrow), likely formed during early diagenetic compression rather than reflecting original biological structures.

Historical Interpretations of *Caulopteris* in Mimerdalen

Høeg (1942) was the first to describe a single specimen of *Caulopteris* from Mimerdalen, based on the elliptical, 'fern-like' branch scar morphology arranged in steep helices around the stem of the trunk, which he interpreted as the abscission sites of lateral branches. He noted the poor preservation of both the stem and branch scars, highlighting the difficulty in attaining a correct taxonomic diagnosis due to this preservation quality. He observed that the branch scars bore a resemblance to both the Carboniferous genera *Halonnia* (Zeiller, 1886) and *Knorria*, as well as the lycopsid *Bergaria mimerensis*. However, he ultimately rejected these comparisons and concluded that the fossil had most in common with the Middle Devonian *Caulopteris antiqua* (Newberry, 1889).

While he acknowledged that the specimen most closely resembled this form species, particularly in the arrangement and morphological shape of the elliptical scars around the trunk, he also pointed out disparities in size between the Mimerdalen specimen and *C. antiqua*. Ultimately, Høeg expressed caution in making any direct comparisons between taxa, citing the lack of anatomical study and the absence of associated lateral branch material found *in situ* with the trunk. He stated that a genus-level identification of *Caulopteris* was sufficient and all that could reasonably be implied based on the available material at the time.

Interestingly, although the taxonomy of *Archaeopteris* had not yet been resolved and it was still considered a 'higher fern' at the time, Høeg firmly rejected any association between *Caulopteris* and *Archaeopteris*. This was despite early discussions surrounding *Callixylon*, which had not yet been definitively linked to *Archaeopteris*. Høeg's rejection was therefore based on the absence of any fossil material found in direct association between *Caulopteris* and *Archaeopteris* and the lack of a connection between *Archaeopteris* and *Svalbardia polymorpha*.

Reassessment: Schweitzer's *Caulopteris nodosa*

While I conclude that Høeg's comparison to *C. antiqua* was justified on morphological grounds, I agree that the incomplete nature of the fossil makes it difficult to confidently assign a species-level taxonomic label to the specimen and his cautionary approach was appropriate for this single specimen. Schweitzer (1999) later supported this view, initially agreeing that the specimen resembled *C. antiqua*. After collection of approximately ten new stem fragments from the same stratigraphic unit as the original specimen was found, Schweitzer named it *Caulopteris nodosa* based on a broader range of material. His diagnosis was based on the presence of knot-like branch bases arranged in steep parastichies and the presence of distinctive longitudinal ridges not seen in other *Caulopteris* species. Both Høeg and Schweitzer acknowledged the absence of attached lateral organs, which limited taxonomic certainty. However, Schweitzer's work demonstrates how additional specimens from the same locality helped to clarify and refine earlier interpretations. This study provides a detailed and fresh insight into *Caulopteris* from Mimerdalen, with 15 new specimens, some of which show exceptional preservation of features not previously described.

Taphonomic and Preservation Differences Between Morphotypes

I have chosen a morphotype-based approach because of the consistent differences observed between the three *Caulopteris* morphotypes represented in the Mimerdalen material. This does not necessarily imply that the specimens belong to different taxa or distinct species. Instead, the morphotypes may reflect a combination of biological, ontogenetic and taphonomic factors. Relative maturity and position along the plant may have influenced the size of the stem, branch scar spacing and development of surface features. However, differences in preservation may also relate to the entombing sediment, including lithology, matrix grain size, degree of sediment infill and the timing of decay relative to burial. The repeated occurrence of similar preservation styles within each morphotype is striking and suggests that comparable depositional or early diagenetic conditions may have affected multiple specimens. For example, trunks buried in coarser sandstone-dominated settings may have undergone different patterns of decay, infill and compaction compared with material preserved in finer-grained shale or siltstone. The morphotypes are therefore treated here as descriptive categories that allow these recurring anatomical and taphonomic patterns to be compared, without assuming that they represent separate biological taxa.

Comparison with Previously Described Material

The three morphotypes described in this study each show distinctive preservational features that probably reflect differences in plant maturity, decay stage and burial conditions. *Caulopteris*-1 is characterised by asymmetrical preservation, with longitudinal surface ornamentation and ridges between branch scars. These features may have developed through partial burial, with one side of the trunk more heavily exposed to decay processes in a fluvial environment. This preservation style is notably similar to the specimen described by Høeg (1942), who also reported asymmetrical preservation and a textured surface with helically arranged scars. Another possibility is that the exposed surface represents the collapsed outer surface of one side of a decaying branch or stem, rather than the internal surface of the lower side. In this scenario, the upper part of the rounded organ may have collapsed down onto the lower part during decay and compaction.

Unlike *Caulopteris*-1, which is typically preserved as flattened and incomplete trunk impressions, *Caulopteris*-2 is mostly preserved as complete, rounded trunk sections with smooth surfaces and prominently protruding branch scars. This improved preservation likely results from earlier and more uniform burial, where the entire trunk was quickly covered by sediment on all sides. Such symmetrical burial would have protected the specimen from prolonged exposure to decay and weathering, allowing the three-dimensional structure of the trunk to be retained as well as some internal features, like the pith cavity. Some of these features closely resemble those described by Schweitzer (1999), who named similar material *Caulopteris nodosa*, based on the presence of steeply ascending branch scars and the absence of surface ridging. However, the preservation of a likely displaced pith cylinder in one specimen represents a previously undocumented feature that may offer further insight into decay processes and internal trunk structure.

Caulopteris-3, preserved as an impression within an ironstone nodule, retains exceptionally fine detail around its branch scars but lacks the three-dimensional form seen in the other morphotypes, likely a result of compression. This flattening may partly reflect the smaller size and possibly less mature developmental stage of the specimen. It is also possible that the so-called 'branch scars' do not represent true lateral branch abscission points, but rather the bases of large leaves emerging directly from an immature stem. This specimen, with its unusually detailed scar morphology and fine surface features, has no clear analogue in the previously published material and may represent a different anatomical region or developmental stage, as well as a distinct taphonomic pathway.

2. Evidence of Medium Sized Trunks with Attached Branches

Several specimens collected from the *Asterolepis* Sandstone and Upper Lake locality represent medium-sized trunks exhibiting potentially significant lateral branch features, previously undocumented from this succession. These specimens are fragmentary, ranging from 60–256 mm in length and 61–140 mm in width.

The first specimen from the top of the Estheriahaugen Member (ALP-1), though poorly preserved, contains notable structural details, including what appear to be multiple branches emerging from a main trunk axis (Plate 24A - white *). Notably, one branch appears to extend into the matrix beneath the specimen (Plate 24A - white arrow). However, the point of attachment is not visible, so it remains unclear whether the axis is directly connected to the trunk. This may suggest partial three-dimensional preservation. Branch width is approximately 12 mm. Trunk width 70 mm at least.

A second specimen from the Upper Lake locality (lower *Svalbardia* Sandstone, UL-1) displays a similar feature, with at least one lateral branch 13 mm in width emerging from the main axis (Plate 24B - black arrow). The trunk surface exhibits broad longitudinal striations, which appear to fan out near the apex and continue along the entire length of the specimen (Plate 24B - white *). The divergence of these striations near the point of branching suggests that they may be related to the emergence of a branch, or may represent additional poorly preserved lateral branches, possibly representing an artefact of the underlying vascular organisation exposed during decay and compression. Trunk width is not complete but at least 40 mm.

A third specimen, identified in the field, is the longest of the group with what appears to be a large main trunk (70 mm) and lateral branch (~15 mm wide) emerging on the one side of the trunk (Plate 24C - black arrow), although less well preserved.

Potential branch bases are also seen on the surface of the trunk.

While all three specimens are fragmentary and poorly preserved, making detailed interpretation of the branching architecture difficult, the presence of medium-sized trunks with apparent lateral branches suggests the possible occurrence of *Archaeopteris* at these localities and further adds weight to the argument that an

Archaeopteridalean plant is present. Evidence is consistent with other material presented in this chapter for helically inserted small branches on substantial trunks.

3. Evidence of Big Trunks in the Field (Plate 25)

Field Collection and Documentation

During fieldwork, several large trunks were found within the sandstone layer above the Estheriahaugen Shale Unit, in the upper most beds of the Estheriahaugen Member (Text Figures 38, 39 - *EST*). Some trunks had eroded from the layer and were recovered in collections made from the scree below. However, one exceptional discovery consisted of an *in-situ* trunk of significant size. When first observed, the surface was seen underneath the base of a small overhang. This material was carefully excavated to facilitate detailed study. High-resolution photographs and a photogrammetric model were produced, enabling detailed analysis and surface reconstruction.

Morphology of the Large Woody Trunk

The large woody trunk is preserved as a substantial impression, reassembled from seven blocks following excavation (Plate 25A). All photographs show the specimen with the lower surface (as it was orientated *in situ*) facing upward. The trunk measures up to 102 cm in preserved length and 185 mm in maximum width (Plate 25A - white arrows).

The surface is broadly flattened, with a prominent raised sandstone ridge running longitudinally along its length (Plate 25B–C) with a maximum width of 20 mm. In transverse view, this feature appears rounded and elevated above the surrounding sandstone matrix (Plate 25E - white arrow) and is marked by longitudinal ridges and folds which run down the entirety of its length (Plate 25D - black arrow). Its continuous extent and position slightly off-centre, suggest it represents an infilled pith cavity. This interpretation is supported by the specimen's orientation: since the photographed surface corresponds to the underside *in situ*, the pith which would have been relatively hollow and sediment-infilled, may have settled under gravity to the lower portion of the trunk during decay and burial.

On either side of the pith-like structure, shallow grooves and depressions are present, potentially representing deformation or collapse of decaying internal tissues. At one end of the specimen, coalified grooves penetrate into the surrounding sandstone, indicating areas where resistant plant tissue has been preserved,

although it is unclear whether this represents xylem, sclerenchyma or another supporting tissue. A prominent transverse/oblique ridge along one portion of the trunk may represent a shrinkage crack or joint, comparable to features observed in large *Callixylon/Archaeopteris* trunks (Plate 25D - white arrow) and discussed previously in relation to *Caulopteris*-2.

Overall, the morphology suggests a large woody axis with a prominent pith-like central structure and evidence of differential decay, sediment infill and tissue collapse. These features are consistent with a partially decayed but rapidly buried stem deposited in a fluvial environment. No branch scars are evident.

4. *Callixylon* (Plate 13 & Plate 14)

Material used in description

The material described here was collected from the Plantekløfta Formation (Early Frasnian) and comprises material from a woody tree preserved *in situ* (locality: NARCHF – Text Figure 39). Davies et al. (2021) provide a detailed account of the sedimentology of this locality (see Figures 12 and 13). Field notes by Berry describe the specimen as originating from the trunk of an *in situ* tree, with a trunk measuring 62 cm in height and 8 cm in diameter (Plate 15A, B) with woody roots.

The samples were transported to Cardiff University for analysis, where scanning electron microscopy (SEM) was employed to identify diagnostic features of *Callixylon* and confirm its association with *Archaeopteris*. Several SEM stubs were prepared from the collected material; however, only two samples were sufficiently well preserved to yield anatomical detail. Samples from several other trees from the same and other sites were collected in 2023, however no details were seen after investigation using SEM.

Description of material

The coalified wood is composed of tracheids with an average diameter of 30 μm (range: 21 - 41 μm) (Table 3). The exact length of the tracheids could not be determined due to poor preservation. However, in some specimens the basal ends of tracheids are visible. Where visible, the tracheid ends are poorly preserved and their degree of tapering cannot be determined with confidence. In some cases, particularly in areas with poorer preservation, the tracheid wall has collapsed resulting in a concave shape and slight distortion of the bordered pits (Plate 26B-C). In contrast, better-preserved samples exhibit tracheid walls that retain their original shape, appearing flat and aligned with the middle lamella that separates adjacent cells (Plate 27).

Radial tracheid walls have poorly preserved, oval – circular bordered pits (Plate 26D), which are 7 μm in average height (range: 5–9 μm) and 6 μm in average width (range: 3–9 μm). Across all specimens, pits are consistently arranged in 2 rows, forming discrete groups of 10 - 22 pits (average = 14). These groups are separated by smooth, unpitted areas measuring 20 to 40 μm in height (e.g. Plate 26B - white *).

In one sample, there are details of structures that run perpendicular to the radial tracheids (Plate 26A - *black arrow*), although the cellular details and internal organisation are not well preserved (Plate 26A - *white arrow*). Based on their orientation, it is possible that these represent rays. Cross fields of rays between tracheids not visible due to poor preservation. In a few areas, potential ray cells are suggested by narrow spaces or discontinuities between adjacent tracheid walls, with diameters of up to 9 μm (Plate 26E - *white arrow*).

	Tracheid diameter (μm)	Number of pits in group	Pit Length (μm)	Pit Width (μm)	Number of rows of pits
Range	21 - 41	10 - 22	5 - 9	3 - 9	2
Average	30	14	7	6	

Table 15. Measurements from coalified *Callixylon* collected from the Planetkløfta formation.

Comparisons of *Callixylon*

Despite poor preservation, the material exhibits key anatomical features consistent with *Callixylon*, the permineralized wood of *Archaeopteris*. These features include secondary xylem composed of tracheids within the expected size range for *Callixylon*, with distinct groups of oval, biseriate bordered pits on the radial walls. These pits are arranged in two longitudinal rows and separated by smooth, unpitted regions. Possible rays are also present, although their preservation is limited.

Tracheid diameters range from 21–41 μm , matching values previously reported for *Callixylon* from Frasnian deposits (Campbell, 1963; Meyer-Berthaud et al., 2004; Orlova & Jurina, 2011). The arrangement of grouped bordered pits into paired rows separated by smooth regions with an average of 14 pits per grouping and pit group spacing of 20–40 μm is also commonly found in *Callixylon* (Chitaley & Cai, 2001; Orlova & Jurina, 2011; Lyubarova & Snigirevsky, 2020).

When considering the species assignment of the *Callixylon* material described here, it is essential to refer to the landmark study by Orlova and Jurina (2011) which provides a robust comparative framework for distinguishing *Callixylon* groups based on anatomical features. These features include tracheid diameter, bordered pit arrangement and ray structure.

Based on these criteria the wood collected from the Plantekøfta Formation may be associated with the *Trifilievi* group, which is characterised by tracheids with diameters of 10–70 µm, biseriate radial pits arranged in groups of 3–40 (with 10–14 pits per group being most common) and the absence of radial tracheids. However, tracheid diameter alone could place the specimens within any of the recognised *Callixylon* groups. Furthermore, the number of pits per group is consistent with all groups except the *Newberryi* group. Given this overlap in diagnostic features, it is not possible to categorically assign the specimens to a specific group, but it can be suggested that the most likely group for these specimens is the *Trifilievi* group.

The geological age of the material is consistent with this assignment as the *Trifilievi* group spans from the Frasnian to the Early Carboniferous.

Ray structure is an important diagnostic feature in Devonian woods, but preservation here is too limited to make a firm identification. In a few places (Plate 27E), narrow junctions up to 9 µm wide occur between adjacent tracheids and could represent the transverse expression of uniseriate rays, but this is not definitive. If these features do represent rays, they would be consistent with the *Trifilievi* group which is characterised by narrow, predominantly uniseriate to biserial rays and a lack of radial tracheids (Table 16).

The observed bordered pit morphology is also consistent with the *Trifilievi* group. The biseriate rows of oval to circular bordered pits (averaging 7 × 6 µm) closely match descriptions for *Callixylon trifilievi*. Pit dimensions (ranging from 5–9 µm in length and 3–9 µm in width) and the number of pits per group (10–22) fall well within the variability reported for this group.

Taken together with the other evidence presented in this chapter, the material provides secure evidence for *Callixylon* and therefore for anatomically preserved *Archaeopteris* in Svalbard. This demonstrates that the Svalbard flora included not only compression fossils of archaeopterid branches but also coalified woody tissues, strengthening whole-plant reconstructions and extending the known anatomical record of *Archaeopteris* into the palaeotropical Devonian. Having established the presence of *Callixylon* in Svalbard, the following section examines the rooting systems that provide further insight into the growth habit and ecology of these trees.

Feature	Plantekløfta Specimen	Trifilievi Group	Erianum Group	Newberryi Group	Arnoldii Group
Tracheid diameter (µm)	21 – 41	10 - 70	22 - 60	23 - 68	44
Number of pits per group	10 – 22	3 - 40	1 - 34	8–20	4 - 30
Rows of radial pits	2	1–4	1 - 5	1 - 4	1 - 3
Ray height (in cells)	NA	1 - 80	1 - 97	1 - 90	1 - 9
Ray width (in cells)	NA	1 - 2	1 - 2	1 - 5	1 - 2
Radial tracheids	NA	Absent	Present	Rare or absent	Absent
Number of pits in cross field	NA	2–12	2–10	4–10	2–6
Age	Frasnian	Frasnian - Missipian	Frasnian - Famennian	Frasnian - Famennian	Famennian - Missipian

Table 16. Comparison of anatomical features between the Plantekløfta specimen and established *Callixylon* species groups (Trifilievi, Erianum, Newberryi and Arnoldii groups). Features compared include tracheid diameter, number of pits per group, number of rows of radial pits, ray height and width (in cells), presence of radial tracheids, number of pits in cross fields and stratigraphic age range. NA = data not available.

5. *In situ* rooting systems

Material used in description

There were at least three sites where *in situ* *Archaeopteris* trees were seen, two of which had rooting systems significant enough to allow description of the rooting systems (AF22B and NARCHF).

Tree 1 (Plate 28A-B), locality NARCHF

Description

The tree, with *Callixylon* wood (Plate 28A, B - see previous section), appears more or less vertical within the horizon and is preserved in red-grey sandstone, below a conglomeritic layer (Davies *et al.* 2021, Figures 13B-F). The trunk has been compressed to coalified material. The preserved height of the trunk is 62 cm, with a maximum basal width of 11 cm. Above the level of lateral root divergence the trunk narrows to 8 cm in width.

Several lateral roots are present, the most conspicuous being two robust laterals extending from opposite sides of the trunk. These diverge at an angle of approximately 150° relative to the main axis. The lateral roots extend up to 10 cm horizontally into the surrounding palaeosol and penetrate to a depth of 35 cm below the palaeosol surface. The maximum preserved spread of the root system is 42 cm. Individual lateral roots are up to 6 cm wide and taper gradually to 10 mm wide into the sediment. Smaller lateral root traces (0.5 cm) are also preserved adjacent to the larger roots, although these are more fragmentary (Plate 28B - white arrow).

The contact between the base of the trunk and the palaeosol is gradual, with the enclosing mudstone showing subtle disturbance along the course of the roots. No external bark features or surface ornamentation are preserved due to compression.

Amy's tree (Plate 28C-F), locality AF22B

The specimen is preserved in an upright orientation within a significant grey mudstone horizon, with the plant material represented by a thin coalified compression (Plate 28C). The trunk has a preserved height of 46 cm. The maximum width of the trunk is 9 cm near its upper surface. Towards the base, the trunk widens abruptly into the sediment, extending into a basal rooting structure 11 cm in width

(Plate 28D), from which lateral roots diverge into the surrounding palaeosol (Plate 28E).

The lateral roots range in width from 0.6 cm to 2 cm. On the right hand side of the specimen, one larger lateral root is preserved, with a second smaller root extending beneath it into the palaeosol (Plate 28D - white arrow). The two roots are separated vertically by approximately 2 cm. The maximum preserved lateral spread of the root system is 39 cm. In addition to the lateral roots, coalified traces suggest the presence of roots extending vertically into the palaeosol (Plate 28D - black arrow).

The palaeosol is a grey mudstone, fine-grained and compact, with a sharp boundary to the overlying grey mudstone. Around several of the root traces, orange-coloured halos are visible, extending a few millimetres into the surrounding sediment and marking disturbance along the path of the roots. The root surfaces are otherwise featureless due to compression, with no evidence of bark structures or ornamentation preserved.

Discussion (Part II: Trunk and Root Material)

1. Introduction: Scope and Evidence for *Archaeopteris*

The results presented in this chapter illustrate a wide range of material which can be attributed to *Archaeopteris* from across the entire Mimerdalen Subgroup. This includes collections from the lower to the upper beds, with material including leafy branches, anatomically preserved wood, medium- to large-diameter trunks, branched trunk specimens and *in situ* root systems. This makes it possible to address whether the taxa which has been historically treated as distinct (*Svalbardia polymorpha*, *Caulopteris*, *Callixylon*, and *Actinopodium nathorstii*), can be integrated into a single, coherent whole-plant concept in Devonian Svalbard.

2. *Caulopteris* Specimens: Morphotypes and Organotaxy

Caulopteris morphotypes range widely in size, preservation and stratigraphic position, yet all exhibit branch scars arranged in a regular helical sequence around the trunk. In one specimen, where it can be demonstrated, a Fibonacci organotaxy is found, specifically 5:8, yielding a $3/8$ organotactic fraction.

Beck (1979) showed that in his specimen of *Callixylon brownii* the traces leave the eustele in a regular spiral sequence, starting directly from the pith as primary strands, and are all about the same size at the point where they separate. He interpreted the traces as branch traces, not leaf traces. Beck's specimen, with a pith of about 12 mm across, can also be interpreted to have a $3/8$ organotactic fraction (Beck, 1979, Figure 4). On this basis, the Svalbard *Caulopteris* specimens can be interpreted as consistent with the external form of small *Callixylon* trunks. Beck also suggested that some trunks of *Archaeopteris* may have borne only lateral branch systems and no leaves. This is an important architectural framework for interpreting the Svalbard material, where all preserved scars are of comparable size across the specimen and show a consistent organotaxy. Taken together, this pattern is more readily explained as the insertion of branches rather than leaf traces on the trunk.

Trivett's (1993) study of a large trunk of *Callixylon whiteanum* showed that lateral traces followed a predictable helical sequence but increased in complexity up the trunk: traces extended up to 16 cm and supplied progressively larger and more

complex branches distally. This demonstrated that the helical insertion recognised by Beck (1979) could generate a spectrum of lateral organs as the tree matured.

Both leaves and branches were borne in the same ontogenetic helix. Trivett also formalised growth into a continuum of phases, governed by size thresholds in the primary body. Small axes (Types I–II) produced leaves and a few ranks of branches, whereas larger axes (Types IV–V) produced only branches. The Svalbard *Caulopteris* trunks, which show only small branch scars, are therefore consistent with axes in which leaf production from the main stem had ceased and the trunk bore lateral branch systems, probably equivalent to penultimate branches. However, because attached higher-order branching is rarely preserved, the number of further branch orders produced by these laterals cannot be determined with confidence.

Another feature observed in Trivett's specimen was the absence of organised abscission layers: many branch traces terminated passively within the wood, suggesting mechanical self-thinning rather than active shedding. This process would have left a temporary helical record of branch scars on trunk surfaces, comparable to those seen in *Caulopteris*. Unlike Trivett's specimen, however, the Svalbard material shows no evidence of adventitious traces, i.e. irregular insertions outside the helical sequence that she interpreted as regenerative axes formed opportunistically after damage or in specific environmental conditions. Their absence may reflect the smaller size of the trunks examined, since Trivett reported adventitious traces most frequently in larger Type IV–V axes. Alternatively, the absence of adventitious traces may reflect taphonomic limits of compression preservation, or genuine architectural variation within early archaeopterid trees. It should therefore not be used alone to place the Svalbard material into a single developmental stage.

Chaloner (1999) noted that trunks of *Archaeopteris* in the Middle Devonian could already reach 20–80 mm in diameter, based on material described from localities in Europe and North America. He used this size range to show that by the Givetian the genus had developed a true woody habit and was already forming tree-sized individuals. The *Caulopteris* specimens described from Svalbard fall into the same range, with several examples overlapping Chaloner's values. Subsequently, Cornet et al. (2012) described a 15 cm wide partly permineralised trunk of *Callixylon* from the mid–late Givetian of Belgium, with a 25–29 mm wide pith, matching the largest

trunk from Svalbard. This shows that *Archaeopteris* of similar size was also present in palaeotropical Laurussia, extending the distribution of early tree-sized individuals beyond the mid-latitude records on which Chaloner's observations were based.

Chaloner (1999) described a small *Archaeopteris* specimen from the Famennian of Kiltorcan, Ireland. It preserves the apex of a trunk approximately 20 mm in diameter, bearing a crown of penultimate branches inserted within a short length of axis.

Chaloner also argued that the architecture of these axes was consistent with a tree growth form, with regularly spaced lateral insertions supporting planate branches. The Svalbard *Caulopteris* material agrees with this: the scars are arranged helically, as in anatomically preserved *Callixylon*, and the diameters indicate sufficient secondary wood to sustain upright growth. However, Chaloner also noted that in young plants penultimate branches could appear crowded at the probable crown. By contrast, the Svalbard trunks display the helical organisation more clearly, suggesting that they represent larger axes where the branch bases, which may have been crowded at small diameters, are more separated on the surface.

A second example of a large axis with attached penultimate branches was illustrated by Beck (1960), in which several sterile and fertile branching systems are attached to the distal end of a 2–3 cm axis in a lax spiral, though the details were not mapped. Beck interpreted this as a branch, although no supporting evidence was provided. Both this specimen and the smaller Svalbard examples may show helical insertion of branch systems onto 2–3 cm woody axes, without the pronounced planation expected in major lateral branches of large trees, suggesting that these axes may represent young trunks, upper trunk/crown regions of larger trees or relatively small mature archaeopterid axes.

Medium-sized trunks with possible attached lateral branches from the Mimerdalen Subgroup (Plate 24) provide the first Svalbard evidence of archaeopterid axes preserving attached branches rather than isolated fragments. Although fragmentary, their size and organisation suggest derivation from substantial trees attributable to *Archaeopteris*. These specimens bridge the gap between isolated branches and large unbranched trunks, indicating that attached lateral organs were present in the Svalbard material and reflecting variation in archaeopterid growth architecture.

Meyer-Berthaud et al. (2000) described a long but slender trunk of *Archaeopteris/Callixylon erianum*. This was interpreted as a young axis, providing new detail on the organisation of vascular traces during early trunk development. Type A traces departed from the stele in a regular helical sequence, diverging steeply and terminating after a short course. These were interpreted as short-lived ultimate branches. In contrast, Type B traces were larger, regular and developed in association with Type A insertions. These were interpreted as long-lived perennial branches. Type H represented small, short-lived adventitious traces with no fixed identity, thought to be latent primordia capable of producing either roots or shoots depending on conditions.

Although 5 m in length, the Moroccan trunk had a diameter of only 5–9 cm, indicating that it represents an immature stage compared with the massive axes known from later Famennian forests. The Svalbard *Caulopteris* specimens may represent a comparable or smaller developmental stage, with diameters typically between 2–6 cm but up to 10 cm. Unlike the Moroccan material, no irregular adventitious traces are apparent in the Svalbard specimens. This difference could be attributed to the smaller size of the trunks, the taphonomic limits of compression preservation or genuine architectural variation within early archaeopterid trees. Taken together, the Moroccan and Svalbard evidence reinforces that the helical organotaxy of *Caulopteris* represents the same developmental framework identified in anatomically preserved trunks and that these scars record the insertion of lateral branching systems.

Several interpretations therefore remain possible regarding the position of the Svalbard *Caulopteris* axes within the whole plant. The regular helical organotaxy, comparable scar size and similarity to anatomically preserved *Callixylon* support their interpretation as archaeopterid woody axes bearing lateral branch systems, most likely penultimate branches. However, it remains uncertain whether these axes represent young trunks, upper trunk or crown regions of larger trees, or relatively small mature archaeopterid trees that retained helically arranged lateral branches along much of the stem. The branch bases are not as crowded as might be expected in a compact crown, but the material also lacks direct evidence for the larger adventitious or long-lived branch systems described in some younger *Archaeopteris* specimens. The available evidence therefore supports an *Archaeopteris*-type trunk

interpretation, while leaving the precise developmental or architectural position of these axes unresolved.

The Svalbard *Caulopteris* specimens show that even relatively small trunks expressed the same helical organotaxy as seen in anatomically preserved *Callixylon*. Comparisons with Beck (1979), Chaloner (1999), Trivett (1993) and Meyer-Berthaud et al. (2000) demonstrate that the scars are best explained as the insertions of branches, that by the Givetian–Frasnian these axes had already developed a persistent woody framework and that they extend the known variation within archaeopterid trunk architecture rather than contradicting an *Archaeopteris*-type interpretation.

An underlying issue in the *Archaeopteris* literature is whether these trees produced a distinct crown or simply bore laterals along the trunk. Beck (1979) and Trivett (1993) emphasised that a continuous helical series of laterals could generate trunk form without invoking a sharply defined crown, whereas Chaloner (1999) and Meyer-Berthaud et al. (2000) argued that long-lived branches provided the structural basis of one, particularly in younger axes. The Svalbard material sits between these interpretations. It supports the presence of helically arranged lateral branches on relatively small archaeopterid woody axes, but does not demonstrate whether these axes formed part of a discrete crown, an upper trunk region of a larger tree or the mature architecture of a smaller archaeopterid form. This variation suggests that existing models of *Archaeopteris* architecture should be applied flexibly, allowing for regional or developmental variants that may not have produced, or may not preserve, the same adventitious or long-lived branch systems seen in better-known younger material.

Presence of pith-like cavity cast

The discovery of a very large trunk preserved as an external mould but incorporating a longitudinal internal cast represents the largest plant yet found from the Mimerdalen Subgroup. Notably, no external branch scars are visible.

Archaeopteris/Callixylon is known to possess a relatively large central pith, reaching at least 30 mm in diameter in some specimens. This feature is relevant because decay of the pith and adjacent tissues could allow water, sediment and agents of decay to enter the centre of the trunk, producing distinctive taphonomic signatures in

non-anatomically preserved fossils. Two trunk specimens described above, both preserved in sandstone, preserve longitudinal internal features that are interpreted here as possible casts of a central pith region.

Caulopteris specimen PMO.250.220 A/B (Plate 22) preserves a rounded, cylindrical structure running longitudinally beside the main axis. This structure is tentatively interpreted as a sediment-filled pith-like cast. Its off-centre position may reflect gravitational settling of sediment during decay in a fluvial setting, although displacement during compaction cannot be excluded. Several features support an internal origin: the sediment fill is continuous with the trunk fill, branch bases partially enclose the cylindrical structure, its surface texture resembles branching vascular/sympodial patterns described in *Archaeopteris* eusteles (Beck, 1971), and its dimensions are broadly comparable with the pith region of *Archaeopteris/Callixylon*. These observations suggest that the cast may have originated within the trunk, although the poor preservation means this interpretation must remain cautious.

Comparable but less certain features are present in the large trunk recorded from the Estheriahaugen Member, which preserves more than a metre of axis with a continuous longitudinal ridge interpreted here as a possible displaced pith-like cast (Plate 25). Its off-centre position and associated longitudinal deformation may reflect sediment infill of a weakened or partially hollow central region during decay. Associated shrinkage cracks are comparable to features reported in large *Callixylon* and *Archaeopteris* trunks from North America (Arnold, 1934, 1936; Cross & Hoskins, 1951). Taken together, these features are consistent with the presence of large axes containing a prominent central pith region, but they do not provide anatomical proof of a preserved *Archaeopteris* eustele.

The Svalbard material therefore suggests that some large trunks may have developed around a prominent central pith region, comparable with that of *Archaeopteris/Callixylon*. This interpretation strengthens the possible association between *Caulopteris*, the large trunk material and archaeopteridalean trees in the Mimerdalen assemblage, but it should be regarded as a taphonomic and morphological argument rather than a definitive anatomical identification.

3. Presence of *Callixylon*

Alongside the Fibonacci organotaxy and evidence for central pith cavities, the assemblage also includes anatomically preserved wood that can be confidently assigned to *Callixylon*, the structurally preserved wood of *Archaeopteris* (Plates 26–27). Although preservation is limited, the material preserves key features of secondary xylem, including radially arranged tracheids and biseriate bordered pits organised into distinct groups, which align with the diagnostic characters of *Callixylon* (Beck, 1960), the wood of *Archaeopteris*.

4. Presence of *in situ* rooting systems

At least two sites (ARC22A, NARCHF) preserve *in situ* rooting systems (Plate 28) with laterally extending roots directly comparable in form to other mid–Late Devonian *Archaeopteris* (Algeo & Scheckler, 1998; Stein et al., 2020). One specimen includes coalified wood identified as *Callixylon*. In the Svalbard specimens, lateral roots extend up to ~39 cm across the palaeosol and penetrate ~35 cm vertically, with root diameters ranging from 0.6–2 cm. These dimensions are based on trunk sizes up to 67 cm in height and 11 cm in width, considerably smaller than those documented from better-preserved *Archaeopteris* elsewhere. At Cairo Quarry (mid-Givetian), root networks extended radially up to ~11 m and penetrated 1.2–1.6 m into palaeosols, with primary roots 6–16 cm wide tapering distally to 1–1.5 cm and fine rootlets as small as 1–2 mm (Stein et al., 2020). No equivalent fine rootlets are preserved in the Svalbard material. Later Famennian occurrences, such as Waterloo Farm (Gess & Berry, 2024) and the Donbass Basin (Snigirevskaya, 1994), preserve basal diameters of ~30 cm with roots 10–14 cm wide, scaling to trees ~25 m in height based on comparison to living *Araucaria* (Stein et al. 2020). The smaller size of the Svalbard roots and trunks therefore most likely reflects either juvenile growth stages or their earlier stratigraphic position relative to the larger Frasnian–Famennian forests.

Conclusions

The main findings from this chapter are summarised below, outlining the evidence that unites the Svalbard material within the genus *Archaeopteris*.

1. Leafy branches assigned to *Svalbardia polymorpha* and anatomically preserved material referred to *Actinopodium nathorstii* were redescribed and united, demonstrating the typical characteristics of *Archaeopteris*.
2. Trunk material, previously attributed to *Caulopteris nodosa*, exhibits a Fibonacci organotaxy consistent with that observed in small *Archaeopteris/Callixylon* trunks. The dimensions of the branch bases on these trunks correspond closely to those of the newly identified bases of leafy *S. polymorpha* branches and some preserve evidence of attached lateral branches. Taken together, this supports a stem plus penultimate plus ultimate branch organisation, in which *Caulopteris*-type trunks bore lateral branch systems comparable to the leafy *Svalbardia* axes described above.
3. The largest trunk, 18 cm in diameter trunk lacking branch bases, contains a large pith cavity cast consistent in size with *Archaeopteris–Callixylon*. A smaller trunk also appeared to have a pith cavity cast. The presence of a large pith cavity may have led to a distinctive taphonomic pathway for *Archaeopteris* trunks.
4. Smaller *in situ* trees display coalified wood with grouped pitting and robust structural roots, both diagnostic features of *Archaeopteris/Callixylon*.
5. Leafy *Svalbardia polymorpha* branches occur throughout all fossiliferous horizons of the Mimerdalen Subgroup, encompassing the stratigraphic levels from which all *Archaeopteris*-type material is recorded (Text Figure 38). This supports the interpretation that the Svalbard specimens represent an integrated *Archaeopteris*-type plant preserved in multiple taphonomic forms.

The suite of new material described here significantly extends knowledge of *Archaeopteris* in Svalbard. For the first time, leafy branches (*Svalbardia polymorpha*), anatomical axes (*Actinopodium nathorstii*), *Caulopteris* trunks, *Callixylon* wood, medium-sized trunks with attached branches, *in situ* rooting systems and large pith-cavity boles can be considered together as part of an *Archaeopteris*-type whole-plant interpretation. Importantly, these remains span the mid Givetian to early Frasnian interval of the Mimerdalen Subgroup, suggesting that *Archaeopteris*-type plants were a persistent component of equatorial vegetation in Laurussia during this time.

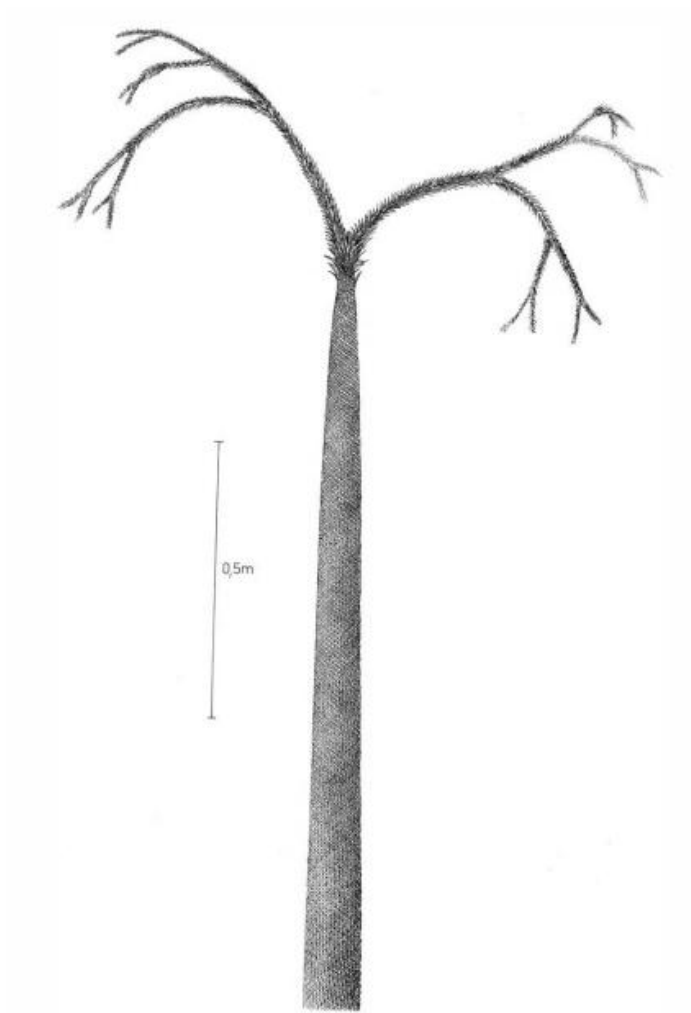
These findings emphasise that by the mid–late Givetian, tree-sized *Archaeopteris* with woody trunks, helically inserted branches and spreading crowns were already established in palaeoequatorial Laurussia (Svalbard). This places the Svalbard material broadly coeval with the earliest records of *Archaeopteris* from the mid-latitudes (e.g. Cairo, New York: Stein et al., 2020), but crucially extends its known distribution into equatorial regions. It also complements and predates the better-known Frasnian–Famennian forest assemblages of Laurussia (e.g. Oklahoma: Trivett, 1993; Belgium: Fairon-Demaret & Leponce, 2001; Ireland: Chaloner, 1999) and Gondwana (Morocco: Meyer-Berthaud et al., 2000).

Together, these findings demonstrate that by the mid–late Givetian, *Archaeopteris* had already established structurally complex and ecologically significant trees in equatorial environments. The presence of medium-sized branching trunks, *in situ* root systems, *Caulopteris* axes, *Callixylon* wood and leafy branches provides one of the most complete whole-plant records of *Archaeopteris* yet described. Their occurrence across multiple horizons of the Mimerdalen Subgroup confirms that *Archaeopteris* formed a persistent component of the Late Devonian vegetation of Svalbard.

However, direct evidence for large, persistent woody lateral branches, such as those depicted in Beck’s (1971) reconstructions and predicted by the architectural models of Trivett (1993) and Meyer-Berthaud et al. (2000), remains absent from the Svalbard material. The limited anatomical preservation within the Mimerdalen Subgroup means that this question is unlikely to be resolved through conventional anatomical analysis alone. Future work integrating field mapping of branching orientations, quantitative organotaxy and comparison with anatomically preserved material from coeval localities may help determine whether early *Archaeopteris* in Svalbard developed long-lived woody laterals or maintained a more pole-like habit with ephemeral penultimate branches.

Regardless of this uncertainty, the integration of *Svalbardia polymorpha*, *Caulopteris nodosa*, *Callixylon* and *Actinopodium nathorstii* establishes *Archaeopteris* as a previously unrecognised tree component of the low-latitude Devonian landscape, expanding the palaeogeographical and ecological range of early forest ecosystems.

Chapter 3.2: Lycopsid Trees from the Mimerdalen Subgroup - *Protolepidodendropsis pulchra*



Text Figure 53. *Protolepidodendropsis pulchra* as reconstructed by Schweitzer, 1965

Introduction

The emergence of arborescent lycopsids in the Devonian marks a pivotal stage in the evolution of terrestrial ecosystems and the appearance of forested landscapes. Distinct from contemporaneous euphyllophytes, lycopsids developed an independent set of structural and developmental traits including determinate aerial growth, shoot-derived rooting systems and microphyllous leaves (Kenrick & Crane, 1997; Hetherington & Dolan, 2016). By transforming plant structure and physiology, these innovations also reshaped Earth's surface processes by amplifying silicate weathering, facilitating carbon burial and reinforcing substrate stability in Devonian ecosystems (Algeo & Scheckler, 1998; Gibling & Davies, 2012). Within this evolutionary framework, *Protolepidodendropsis pulchra* as here presented, represents one of the earliest well-documented examples of the lycopsid tree habit, offering insight into the structural and ecological foundations of arborescence in the group of Devonian lycopsids.

Arborescence in lycopsids evolved independently of other vascular plant lineages and represents a distinct solution to achieving height and mechanical stability. Unlike contemporaneous progymnosperms, which relied heavily on extensive secondary xylem, arborescent lycopsids achieved support through different combinations of cortical tissues, periderm, limited secondary vascular tissues and shoot-derived rooting systems (Wang et al., 2005; Hetherington & Dolan, 2016, 2017). However, the extent to which these features were developed in Devonian forms varies between taxa and is often difficult to assess because many specimens are preserved as external casts, impressions or incomplete organs. In waterlogged floodplain environments, shoot-derived rooting systems would also have provided anchorage and stability in soft substrates. For this reason, Devonian lycopsid architecture is best treated as a series of partly overlapping growth strategies rather than a single model.

The lycopsid lineage has a long evolutionary history, with dispersed trilete spores providing evidence for early vascular plant diversity by the Silurian (Richardson & Lister, 1969; Strother, 1991; Wellman et al., 2003; Kenrick & Crane, 1997). However, dispersed spores alone are difficult to assign confidently to particular lycopsid orders without associated macrofossils or additional diagnostic characters. The earliest

widely recognised lycopsid macrofossil record includes *Baragwanathia*, which shows clear vascular organisation by the Late Silurian to Early Devonian (Lang & Cookson, 1935; Hueber, 1981; Kraft & Kvaček, 2017). These early lycopsids were relatively small, herbaceous and simply branched, forming the foundation for later diversification. During the Middle to Late Devonian, several plant groups developed tree-like growth independently, including cladoxylaleans, progymnosperms and lycopsids (Scheckler, 1986; Niklas & Speck, 2001). In lycopsids this transition produced a range of early tree forms with elongated stems, limited secondary vascular development and shoot-derived rooting systems, although the anatomy of these structures is not equally well known across Devonian taxa (Wang et al., 2005; Hetherington & Dolan, 2017).

By the Middle to Late Devonian, arborescent lycopsids displayed a range of architectural forms rather than a single uniform growth habit. Taxa including *Chamaedendron*, *Guangdedendron*, *Omprelostrobus* and *Sublepidodendron* suggest variation in trunk size, crown organisation, rooting systems and reproductive structures, including differentiated crowns and larger strobili (Schweitzer & Li, 1996; Gao et al., 2022; Liu et al., 2022). However, many of these plants remain incompletely known and direct comparison is limited by differences in preservation and by the fact that not all organs are known for each taxon. This variation indicates that tree-sized lycopsids had developed multiple structural configurations for maintaining upright growth and mechanical stability. The presence of these forms by the Frasnian suggests that several features later characteristic of Carboniferous arborescent lycopsids were already established in earlier Devonian taxa.

Rooting systems were central to this evolutionary transition, but their evolutionary relationships are not straightforward. Early tree lycopsids developed a variety of basal organs and rooting structures, including horizontally spreading roots or root-like axes from the base of the stem, cormose rhizomorphs with dichotomising roots, and lobed rhizomorphic systems with dichotomising roots (Rothwell & Erwin, 1985; Phillips & DiMichele, 1992; Hetherington & Dolan, 2017; Thomas & Cleal, 2018). This variation reflects both the experimental nature of Devonian plant construction and the wet, unstable substrates in which many of these plants grew. These forms may represent different solutions to anchorage, water uptake and substrate

stabilisation rather than a simple linear sequence leading directly to the stigmarian systems of Carboniferous lycopsids. In *Protolapidodendropsis pulchra*, the anatomy of the rooting structures is not known, so the terms used here are morphological rather than anatomical.

Fossil forests from the Middle to Late Devonian record this shift in plant form and ecology. Sites such as Gilboa New York, Xinhang China and Plantekløfta in Svalbard, show that early forests were structurally diverse, containing a mixture of cladoxylaleans, archaeopterids and lycopsids (Stein et al., 2007; Berry & Marshall, 2015; Gao *et al.*, 2022). Within these communities, lycopsids formed dense stands of slender trees that helped stabilise floodplain sediments and promoted soil development. Cormose, lobed and later more extensively branched rhizomorphic rooting systems are commonly associated with growth in waterlogged or unstable substrates, where they provided anchorage and helped stabilise the sediment (Berry & Marshall, 2015; Hetherington & Dolan, 2017; Gao *et al.*, 2022).

The Plantekløfta Formation in Svalbard preserves the oldest known *in-situ* lycopsid forests, dominated by *Protolapidodendropsis pulchra*. These trees formed dense, monospecific stands with stems exceeding one metre in preserved height and up to 20 cm in basal diameter (Berry & Marshall, 2015). Their uniform size and close spacing suggest short-lived, rapidly colonising individuals adapted to high sedimentation rates and periodic flooding. Repeated forest horizons at Plantekløfta record successive colonisation events, demonstrating the ecological resilience of these arborescent plants within dynamic basin environments. Morphologically, *P. pulchra* is characterised by a swollen cormose basal region, a slender upright stem and narrow ribbon-like rooting structures. This combination bridges the gap between small herbaceous forms such as *Leclercqia* (Banks et al., 1972) and the later stigmarian-based trees of the Carboniferous (Phillips & DiMichele, 1992; Thomas & Cleal, 2018). The association of these bases with palaeosol horizons, dense in situ stands and shallow spreading rootlets suggests growth on soft, periodically waterlogged floodplain substrates.

Despite an abundance of collected material and ecological importance as one of the earliest arborescent lycopod forms, *Protolapidodendropsis pulchra*, remains poorly understood in terms of its overall morphology and growth architecture. Earlier

descriptions (Høeg, 1942; Schweitzer, 1965, 1999) and later field work (Berry & Marshall, 2015) established its general form but left open questions about crown organisation, phyllotaxy and the structure of the cormose base and rootlets. These aspects are central to understanding how early lycopsid trees achieved mechanical stability and maintained upright growth in soft, waterlogged substrates.

Høeg (1942) described trunk material with diamond-shaped leaf cushions as the new species *Bergeria mimerensis* and narrower, leafy axes under *Protolepidodendropsis pulchra*. Schweitzer (1965) combined these under the name *P. pulchra*, providing the first reconstruction of the tree trunk and crown (Text Figure 53: Schweitzer, 1965, fig. 14; 1999, fig. 29). The new material described here allows this reconstruction to be reassessed in light of more-complete specimens from Svalbard.

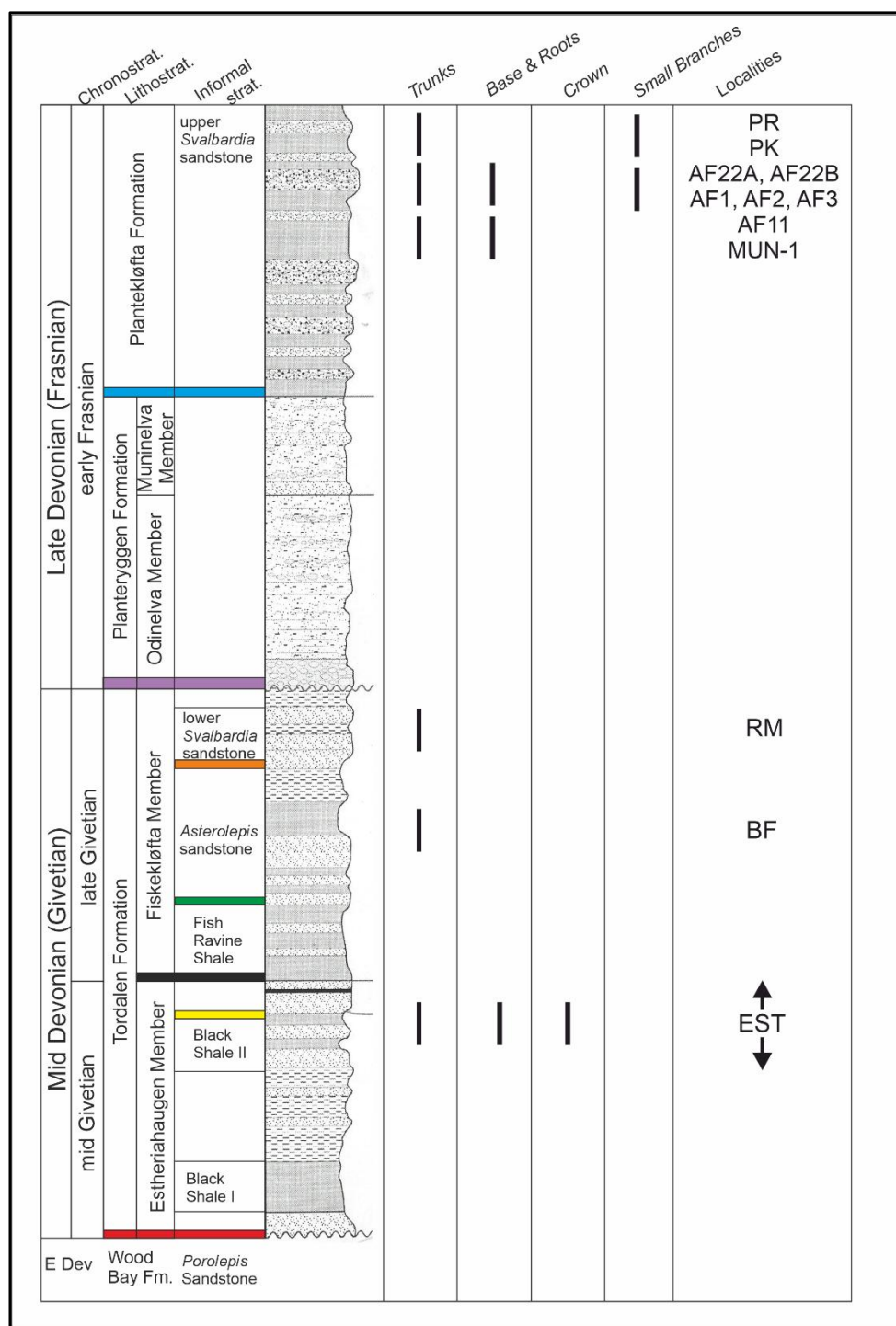
The new material described, provides the first evidence of an attached complete crown and the first documentation of the narrow ribbon-like rootlets that extend from the base. Together with new information on leaf-cushion organisation and phyllotactic pattern, these observations clarify the architecture of *P. pulchra* and refine its position within the evolutionary development of the lycopsid tree habit. They also allow discussion of the early development of the young plant, a recurring topic in Palaeozoic lycopsid biology.

Objectives of this chapter:

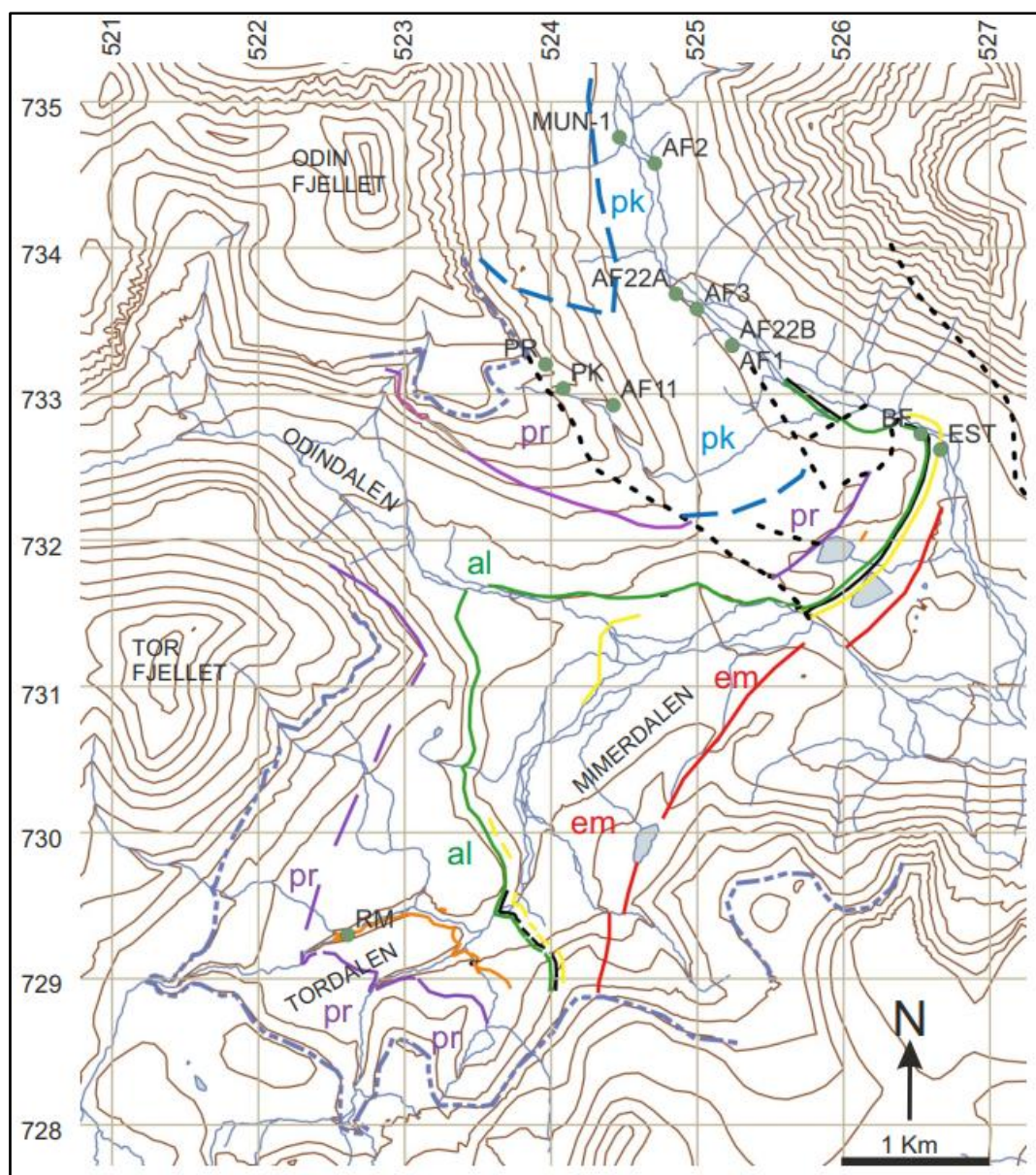
1. Redescribe the morphology of *Protolepidodendropsis pulchra* from new and existing Svalbard material, clarifying the form of its trunk, crown and rooting system.
2. Reconstruct its overall growth architecture using crown and bases to interpret developmental organisation and mechanical support.
3. Refine the stratigraphic context of *P. pulchra* forests within the Mimerdalen Subgroup.
4. Compare the structure of *P. pulchra* with coeval arborescent lycopsids to evaluate its transitional significance in the evolution of the tree lycopsid habit.

Collection of Material

Fossil material assigned to *Protolapidodendropsis pulchra* was collected from multiple localities within the Mimerdalen Subgroup of central Spitsbergen, including Planteryggen (PR), Plantekløfta (PK), ArcForest 2022A–B (AF22A–B), Arc Forests 1–3 (AF1–3), Arc Forest 11 (AF11), Munindalen 1 (Mun-1), River's Meet (RM), Before Forest (BF) and Estheriahaugen (EST) (Text Figures 54, 55). These occur within the upper Plantekløfta Formation and Tordalen Formation of the Mimerdalen Sub-Group, this includes the main plant-bearing localities (AF1, AF2 & AF3) described by Berry & Marshall (2015). The assemblage includes four categories of fossils: (1) upright trunks, (2) cormose bases with attached roots, (3) smaller vegetative branches and (4) a single crown specimen



Text Figure 54. Stratigraphic column showing the occurrences of plant fossils associated with *P. pulchra* in Svalbard. These include collections of trunks, base & roots, small branches and a single crown. The stratigraphic columns illustrate the chronostratigraphy, lithostratigraphy and informal stratigraphy, following Piepjohn & Dallmann (2014). In the localities column: PR = Planteryggen, PK = Plantekløfta, AF22A = ArcForest2022A, AF22B = ArcForest2022B, AF1 = Arc Fores 1, AF2 = Arc Forest 2, AF3 = Arc Forest 3 (from Berry & Marshall, 2015), AF11 = Arc Forest 11, Mun-1 = Munindalen 1, RM = River's Meet, BF = Before Forest, EST = Estheriahaugen (Includes Shale II and yellow sandstone).



Text Figure 55. Geological map of Munindalen and Mimerdalen showing the distribution of the Mimerdalen Subgroup. Localities yielding *Protolapidodendropsis pulchra* are labelled, key is given in Text Figure 54. Map created by Berry and Marshall (unpublished) based on field observations from 2010–2023, with stratigraphic units modified from Piepjohn & Dallmann (2014). Colours correspond to the base of stratigraphic units shown in Text Figure 54. Grid = UTM zone 33N.

Tree bases

Terminology

In this section, the term tree base refers to the swollen, cormose basal region of *Protolapidodendropsis pulchra*. This structure is interpreted as a basal rooting organ or rhizomorphic stem-base region, rather than as a root in the strict anatomical sense. It formed the transition between the upright stem and the finer rooting structures preserved in the palaeosol. Leaf cushions preserved on the surface of the base indicate that at least part of this organ retained stem-like morphology. The term rootlet is reserved here for the narrow, ribbon-like structures preserved beneath and around the bases. These are interpreted as rooting structures on the basis of their position, morphology and radiating arrangement, although their anatomy is not sufficiently preserved to demonstrate that they are true roots sensu strictu.

Material Used for Description:

Two new bases of *Protolapidodendropsis pulchra* were collected by Berry and Marshall in 2016 from the AF2 locality, Plantekløfta Formation, a site that forms part of one of the fossil forests described by Berry and Marshall (2015). Both specimens were recovered as casts weathered out from the palaeosol that hosts the fossil forest horizon (Text Figure 56).

The specimens are interpreted as the basal regions of *P. pulchra* because they are expanded relative to the overlying stem region and occur in direct association with the fossil forest horizon. However, the degree of basal expansion should be interpreted cautiously. The broader lower region may represent a genuinely swollen cormose base, but its apparent width may also have been enhanced by flattening, compaction or weathering during preservation. The preserved lower surface is mostly smooth and does not show clear lobes; therefore, the term “cormose” is used here in a broad morphological sense to describe an expanded basal region, rather than to imply a lobed stigmarian-type rhizomorph.

Descriptions

AF-Base-1 (Plate 29, Text Figure 56A-B, Text Figure 57)

AF-Base-1 is the more informative of the two specimens, preserving key morphological features including phyllotaxy. Although the basal section is partially missing (Plate 29B - black arrows), it retains a clearly recognisable cormose form, with a flattened lower surface that would have sat on or within the palaeosol (Plate 29B) and a swollen cormose appearance in side view (Plate 29A, B). No rootlet attachment scars are visible.

The specimen measures 250 mm in height and 226 mm in maximum diameter at the basal surface, tapering to 182 mm at the top (Plate 29A, B; Text Figure 56A-B). Width reduction is gradual, with a slightly concave profile forming at mid-height (Plate 29A, B - white arrows).

Leaf Cushion Morphology

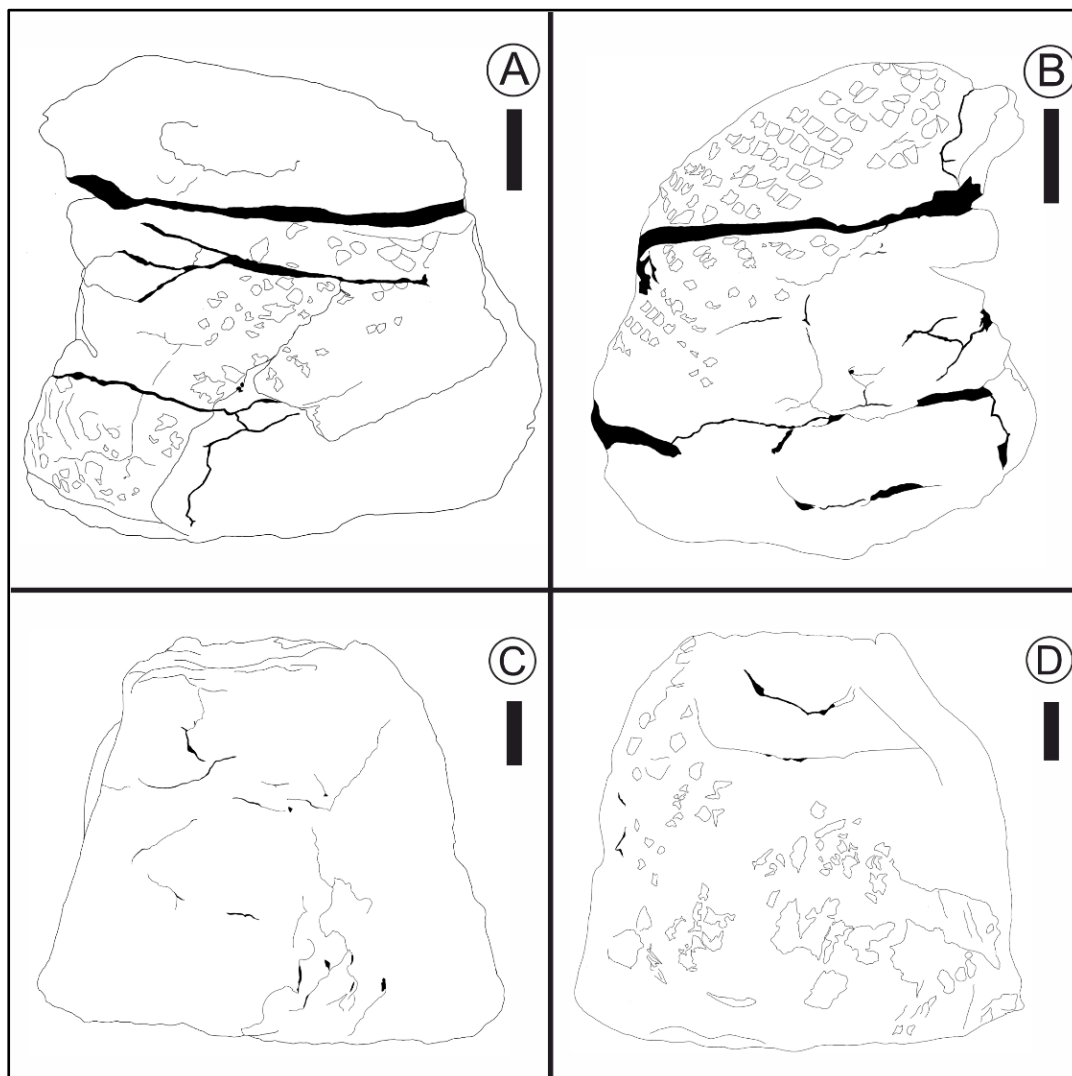
Leaf cushions are arranged in two visible helical sets on the preserved surface of AF-Base-1: one clockwise and one counter-clockwise. To avoid confusion, the term helix is used here for the observed phyllotactic pattern. The numbered lines in Text Figure 57C–D refer only to the better-preserved counter-clockwise helices that were selected for measurement; they should not be interpreted as complete vertical rows or orthostichies.

The white bars in Text Figure 57B show the measured spacing between adjacent counter-clockwise helices. These measurements were taken only where the leaf cushions were sufficiently clear to identify the same helical trend across the preserved surface. Toward the basal part of the specimen, especially in the lower region shown in Text Figure 57C–D, the surface appears vertically compressed and locally distorted. This distortion may have altered the apparent spacing and shape of the leaf cushions, so the measurements are treated as descriptive rather than as evidence for a precise developmental change.

Longitudinal grooves and indentations are also present on parts of the base. These are interpreted cautiously. They may reflect compression, sediment infill along collapsed tissue zones, or the preservation of internal cortical/cushion-related relief

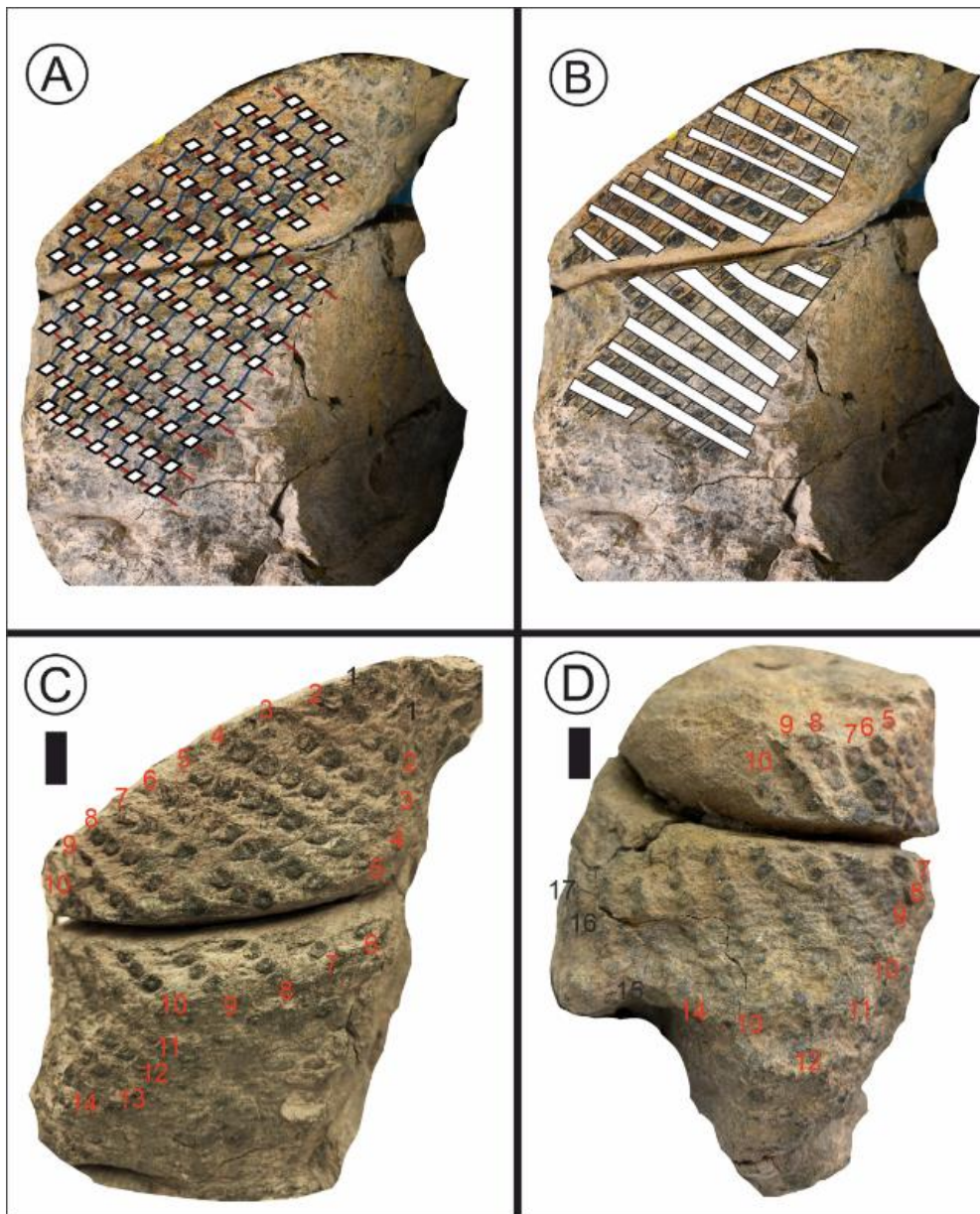
rather than true external surface features. They are not interpreted here as definite rootlets.

Phyllotaxy



Text Figure 56. Line drawings of *Protolpidodendropsis pulchra* swollen cormose bases. A. Side profile of AF-Base-01, corresponding to Plate 29A. Scale bar 50 mm. B. Reverse side of AF-Base-01. Scale bar 50 mm. C. Side profile of AF-Base-02. Scale bar 25 mm. D. Reverse side of AF-Base-02. Scale bar 25 mm.

Spacing between adjacent counterclockwise rows increases from an average of 2 mm in Rows 1–2 to 6 mm in Rows 13–14, across a vertical distance of 65 mm (Text Figure 57B). Counterclockwise helices are more widely spaced (average 7 mm, range 3–12 mm), compared to clockwise helices which have less distance between leaf cushions (average 2 mm, range 1–3 mm) (Text Figure 58).



Text Figure 57. Phyllotactic arrangement of scars on Base-1. A. Clockwise (blue) and anticlockwise (red) spirals of leaf bases. B. Interpretive drawing showing spacing between clockwise rows. C. Labels of clockwise rows. Row numbers in red were used to calculate the morphometric measurements of leaf cushions in Table 2; those labelled in black were too poorly preserved to be used in quantitative analysis. D. Same as C, but the base has been rotated 90° to show the final rows more clearly. Scale bar: 20 mm.

Position on the base	Row Number	Average Length	Average Width
Higher	2	7 (n=4)	6 (n=4)
	3	7 (n=5)	6 (n=5)
	4	7 (n=6)	6 (n=6)
	5	7 (n=5)	5 (n=5)
	6	6 (n=9)	5 (n=9)
	7	6 (n=9)	5 (n=9)
	8	6 (n=7)	4 (n=7)
	9	5 (n=11)	4 (n=11)
	10	5 (n=5)	4 (n=5)
	11	5 (n=11)	4 (n=11)
	12	5 (n=7)	4 (n=7)
	13	5 (n=7)	4 (n=7)
Lower	14	5 (n=7)	4 (n=7)

Table 17. Rows of leaf cushions in *P. pulchra* and their measurements. The table lists row numbers illustrated in Text Figure 57, along with the average length and width of leaf cushions in each row. N indicates the number of sufficiently preserved leaf cushions used for measurements in each row. Note that lower row numbers (e.g., row 2) correspond to higher positions on the base, whereas higher row numbers (e.g., row 14) correspond to lower positions on the base (see column “Position on the base”).

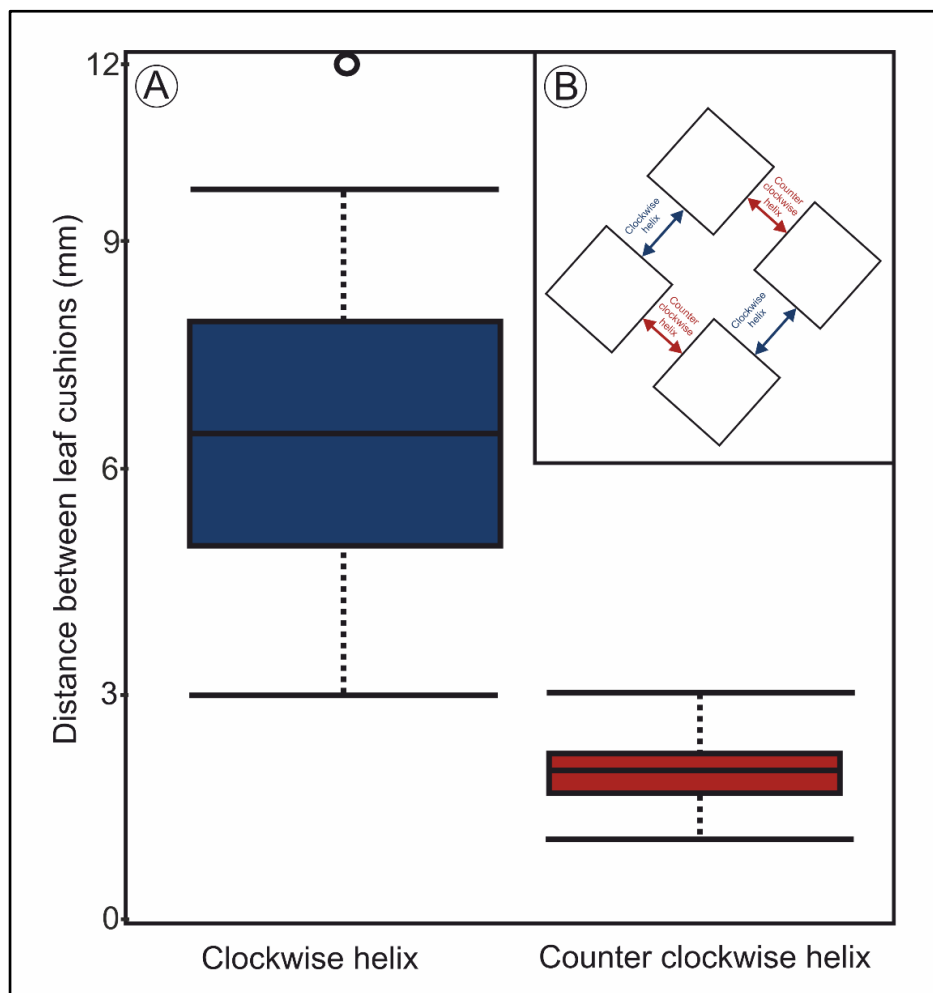
AF-Base-2 (Plate 30, 31A, Text Figure 57C-D).

Base 2 is less well preserved than Base-1 but retains a similar cormose shape (Text Figure 56C, D). It tapers gradually from 185 mm at the base to 160 mm at the midline (Plate 30A - white arrow), before narrowing sharply to 85 mm at the top. Around 129 mm from the base, the tapering angle steepens, resulting in a distinctly concave profile (Plate 30A, B - asterisk). It is unclear whether this morphology reflects original growth form or taphonomic deformation.

The basal surface is only partially preserved (Plate 30F). Its half-oval outline likely results from weathering along natural planes of weakness (Plate 30F - white arrow; Plate 30F - black arrow). Erosion is also visible on the upper surface (Plate 30E). Unlike Base-1, no clearly preserved leaf cushions are present.

Surface Features

- **Circumferential Grooves:** Two shallow grooves encircle roughly one-third of the mid-lower portion of one lateral side (Plate 30A - grey and white arrows). Their origin is uncertain but may result from taphonomic compression or post-depositional erosion, or soil surface.
- **Longitudinal Indentations:** A series of vertical linear indentations are present on the lower third of the base (Plate 31A - white arrows), averaging 30 mm in length and 2.7 mm in width. These may represent former rootlet traces or attachment scars, though they may also be preservation artefacts.



Text Figure 58: (A) Box and whisker plot showing the distances between leaf cushions in the clockwise helices (blue) and anticlockwise helices (red) of a *P. pulchra* tree base. Each box represents the interquartile range (IQR), with the horizontal line inside the box indicating the median. Whiskers extend to the minimum and maximum values within 1.5× the IQR, and individual points beyond this range are plotted as potential outliers. All measurements are in millimetres (mm). (B) Diagrammatic representation of the orientation of clockwise (blue) and anticlockwise (red) helices on the tree base.

Rooting structures

Terminology

The term “rooting structure” is used here descriptively for the narrow, ribbon-like structures preserved in the palaeosol beneath and around the cormose bases of *Protolepidodendropsis pulchra*. The term “rootlet” is avoided because no internal anatomy is preserved in sufficient detail to confirm these structures as true roots *sensu stricto*, or as stigmarian rootlets in the strict anatomical sense. They are interpreted as rooting structures because they occur beneath or adjacent to in situ bases, are preserved within palaeosol surfaces, have a flattened ribbon-like morphology and occasionally bifurcate. However, their exact point of origin and anatomical relationship to the swollen basal organ cannot be demonstrated in all specimens. The terminology used here is therefore morphological rather than anatomical.

Material Used in Description

The morphology of the ribbon-like rooting structures was described primarily using two specimens collected from palaeosol layers beneath fossil forest localities: Specimen 1, AF22B-roots, found directly beneath an in situ tree base, and Specimen 2, AF-2-roots, from a similar palaeosol horizon but without direct association with a tree base. Specimen 1 preserves numerous ribbon-like structures extending across the palaeosol surface beneath the associated tree base and forms the primary basis for this description. Specimen 2 provides supplementary morphological details.

Rooting structures within the palaeosol

Observations before the removal of debris from the palaeosol revealed partially preserved, horizontally orientated ribbon-like structures within the palaeosol layer (Text Figure 59B - black *). Several prominent structures were initially visible, including one section where a structure appears to bifurcate. Subsequent clearing of debris exposed additional distal fragments. Corresponding fragments were also preserved within the palaeosol counterpart (Text Figure 59C-D), including additional fragmentary carbonised structures.

The predominantly horizontal orientation of these structures is interpreted cautiously. It may reflect shallow growth through a wet, fine-grained substrate close to the

sediment surface. However, compaction of a muddy palaeosol may also have flattened originally three-dimensional structures into a more horizontal plane. It is therefore not possible to determine whether these structures originally grew horizontally, emerged from the base and bent, or were reoriented during burial and compaction.

Morphological Features

The rooting structures are fragmentary and incompletely preserved. Their position on the specimen and in the field suggests that they extended away from the basal region of the plant within the palaeosol (Text Figure 59A, B - green arrows).

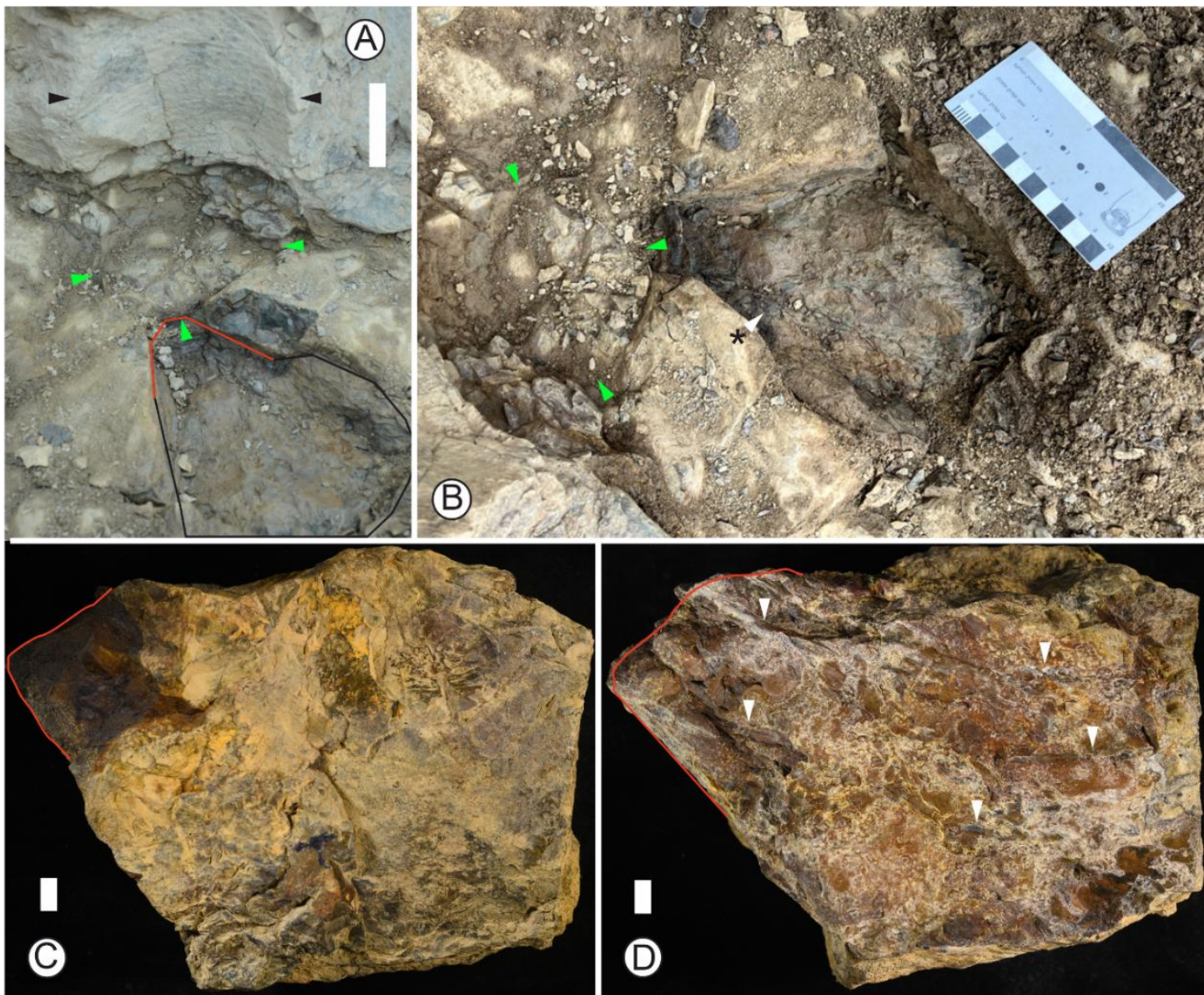
However, the available material does not clearly demonstrate a single central point of origin, a regular row arrangement or a consistent rhizotactic pattern. For this reason, they are described as spreading around or away from the base, rather than as radiating from a central region.

The structures occur either as compressions (Plate 31D, G; Plate 32B, C, E, F) or as impressions where the carbon has been removed (Plate 32A, D, G). They vary in incomplete length from 13 to 173 mm (mean = 45 mm) and in width from 2 to 9 mm (mean = 3 mm), with longer structures generally being wider.

Individual structures frequently exhibit gentle ribbon-like undulations and occasionally display parallel surface striations (Plate 32A, C, G). A distinctive tip was identified in one specimen (Plate 32H, I - white arrow). A possible central strand is visible in some examples (Plate 32A - white arrow), although this cannot be confirmed anatomically. Occasional isotomous bifurcation is observed (Plate 32E).

Overall, the material indicates an expanded basal region associated with shallow, ribbon-like rooting structures preserved within the palaeosol. However, it does not preserve enough anatomical or positional detail to confirm these structures as true roots, stigmarian-type rootlets or a formally organised rhizotactic system.

Text Figure 59. Palaeosoil associated with an *in situ* *Protolepidodendropsis pulchra* tree base at locality AF22B. **A.** Tree base showing a horizontal impression in the palaeosoil (green arrows) and an upright cast preserved in the overlying conglomerate (black arrows). The black and red outline marks the area from which the palaeosoil specimen shown in C–D was collected. Scale bar = 50 mm. **B.** Plan view of the same tree base after removal of overlying debris. The black asterisk marks a horizontal rootlet and green arrows indicate the outer extent of the tree base. **C.** Top surface of the palaeosoil specimen. The red line corresponds to the position indicated in A. Scale bar = 10 mm. **D.** Bottom surface of the palaeosoil specimen showing rootlet impressions (white arrows). The red line corresponds to the position indicated in A. Scale bar = 10 mm.



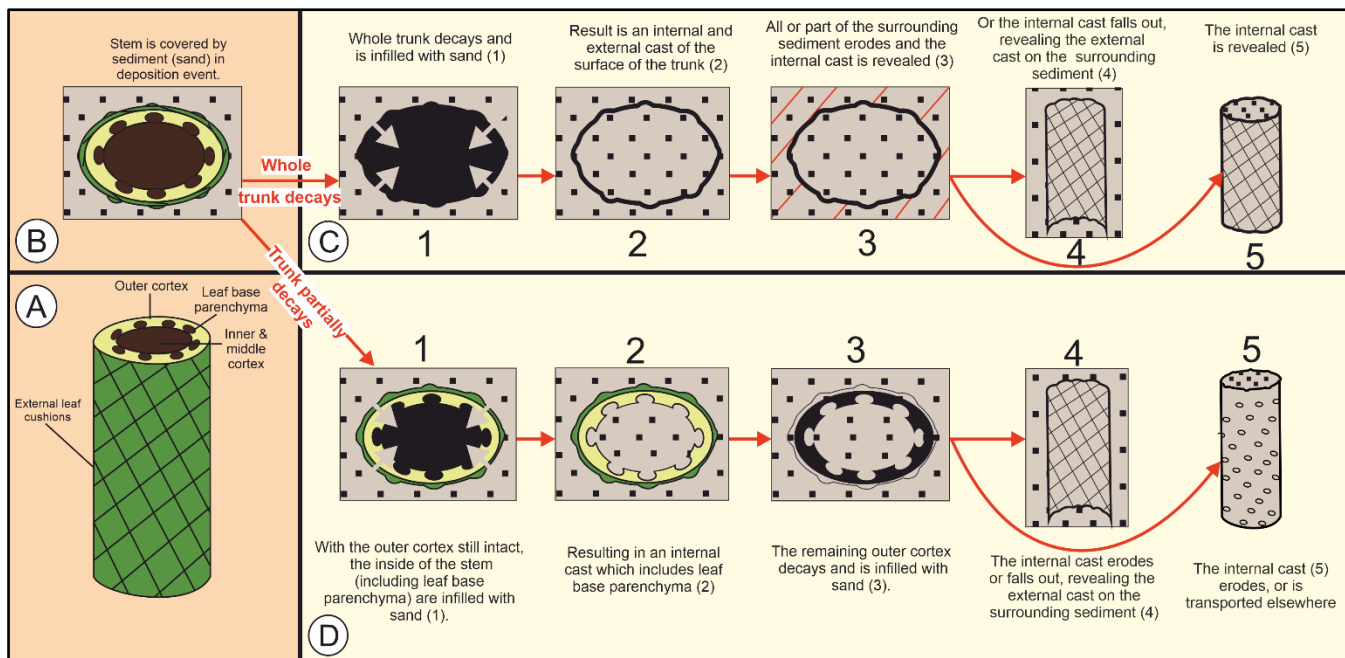
Robust Middle Portion of the Trunk

Material Used in Description

A large quantity of fragmentary trunk material assigned to *P. pulchra* was examined, comprising both previously described specimens (Høeg, 1942; Schweitzer, 1968, 1999) and new material collected during the 2010 - 2023 field seasons. The new specimens were recovered from the Lower *Svalbardia* Sandstone in Tordalen and the Plantekløfta Conglomerate, including material from the AF forest localities and the Plantekløfta type locality (Text Figures 54, 55). While much of the material consists of small fragments (Plates 33, 36), approximately 15 medium to large trunk specimens provide key insights into overall size, surface morphology and tapering (Plates 34, 35). One, photographed in the field, preserved the tapering profile and provides insights into the dimensions of the trunk (Text Figure 61). Additional information is derived from upright bases and partial trunks preserved at the *in-situ* forest sites.

Taphonomic Considerations: Sediment Type

Trunk preservation and preserved detail varies depending on sediment type and taphonomy. Most informative specimens occurred as internal casts or external impressions within coarse-grained sediment, these occur in yellow Lower *Svalbardia* Sandstone and sandstones in the Plantekløfta Fm. Internal casts frequently exhibited clear leaf cushion arrangements in parastichies around the external portion of the trunk (Plate 33). Some specimens had preservation which included leaf base parenchyma or intrafoliar bladders (sensu Meyen, 1976; Berry & Edwards, 1997), which formed rounded protrusions beneath the cortical surface (Plates 33A, B; 34). Preservation quality of rhombic leaf cushions varied considerably within and among specimens (Plate 34), sometimes preserving both the leaf cushion and intrafoliar bladders together (Plate 34G-J), while in other cases only one feature was preserved (Plate 34A-F).



Taphonomic Pathways Leading to Trunk Preservation Variability

The differences in preservation across trunk specimens can be attributed to variation in the level of cortical tissue preserved, combined with decay, sediment infill, compaction and later exposure (Text Figure 60). The specimens do not necessarily preserve the true external surface of the original stem in all cases. Instead, different specimens may expose different levels within the cortex, ranging from surfaces close to the outer leaf-cushion-bearing region to deeper cortical levels associated with the internal region of the leaf base.

In cases where leaf cushions are preserved but leaf base parenchyma is absent, the initial burial event (Text Figure 60B) likely led to the decay of much of the trunk tissue, which was then infilled with sediment. This process resulted in a cast of the trunk or stem surface, capturing relief associated with the leaf-cushion-bearing cortical region (Plate 36A, C, J; Text Figure 60C). This surface is interpreted as close to the outer leaf-cushion-bearing region, but it is not necessarily the true outside of the original stem.

In contrast, trunks preserving features such as the leaf base parenchyma likely experienced a different taphonomic sequence. After initial burial (Text Figure 60A), part of the outer or middle cortical region associated with the leaf-base complex may have remained intact, while the internal tissues, including the xylem and deeper cortical tissues, decayed or collapsed. This internal space was then infilled with sediment during a subsequent depositional event, producing a cast surface with raised protrusions that reflect the position of leaf-base parenchyma and probable intrafoliar bladders (Text Figure 60D-2). The term intrafoliar bladder is used here for a recurring rounded or inflated feature within the leaf-cushion region, but it should be understood as a morphological interpretation of sediment-filled relief rather than a cellular anatomical diagnosis. Following this, the remaining cortical tissues decayed. A mould or cast of the surrounding sediment may therefore preserve the inner side of the outermost remaining cortical region, rather than a simple external cast of the true outer trunk surface (Text Figure 60D-4).

In both scenarios, erosion of the surrounding rock would have been necessary to expose the preserved cast and mould surfaces (Text Figure 60C-3 and D-5). In some cases, these cast surfaces were later removed or eroded away completely, leaving behind moulds in the surrounding sediment (Berry & Marshall, Fig. 4L; Text Figure 60C-4, D-8). Preserved surfaces may show leaf cushions and probable intrafoliar bladders together (Plate 33B, F, I, K), probable intrafoliar bladders alone (Plates 33A; 34C, D, I), or solely the leaf-cushion scars (Plate 33C, D, G, L), depending on the level of cortex preserved, degree of decortication, sediment infill and subsequent erosion of surface features.

Overall, these preservational pathways suggest that variation in leaf-cushion and intrafoliar-bladder expression may reflect different cortical levels being exposed, rather than a single uniform external surface preserved across all specimens.

Morphology and Dimensions of Robust Trunk Sections

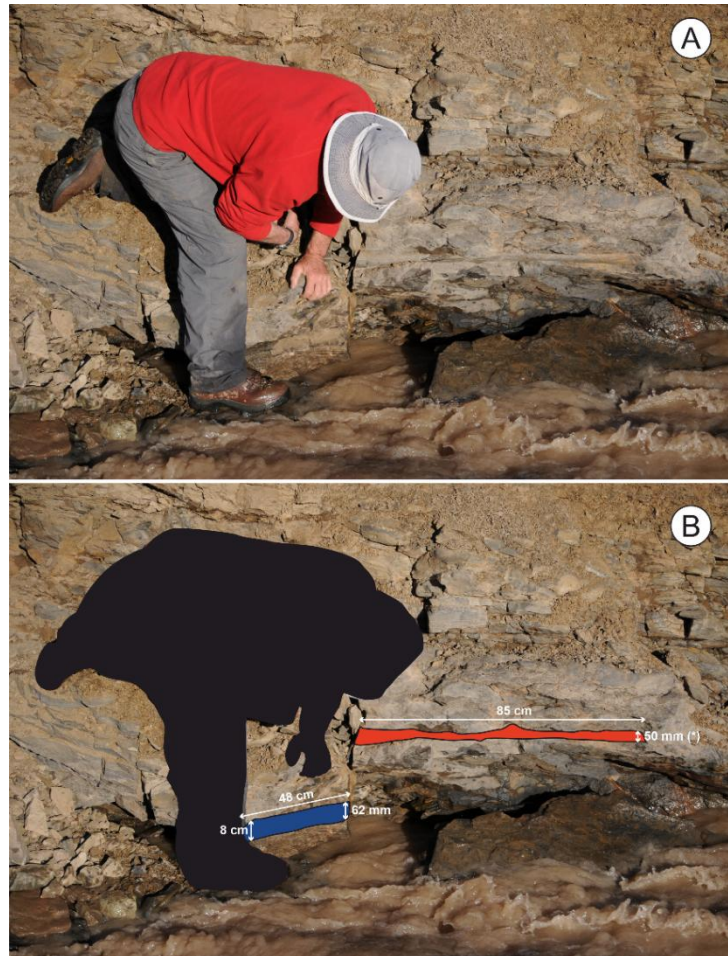
Field observations show that in situ trunks are visible for up to 73 cm above the ground before becoming obscured by overlying Devonian mudslide/conglomerate debris. The largest observed trunk was horizontally preserved within palaeosol, measuring 133 cm in total length and divided into two segments of 85 cm (Text Figure 61 - red trunk) and 48 cm (Text Figure 61 - blue trunk). Its diameter gradually decreased from 8 cm to 5 cm, tapering along the length of the trunk, with field observations suggesting a slight hint of branching before the remainder of the trunk disappeared into the outcrop (Berry; field notes 2010). Other robust trunk fragments ranged in length from 142–410 mm and width from 48–137 mm (Plate 34).

Small, medium and large trunks were commonly compressed during preservation (Plates 34–36). Sediment infill occurs within longitudinal fissures and central depressions of some larger trunk specimens (Plate 34 - black arrows). These features are interpreted as the result of post-mortem decay and collapse of internal tissues, followed by sediment infiltration and compaction during early diagenesis. This process produced surface deformation, including longitudinal depressions and fissures visible on preserved cast or mould surfaces.

Leaf Cushions

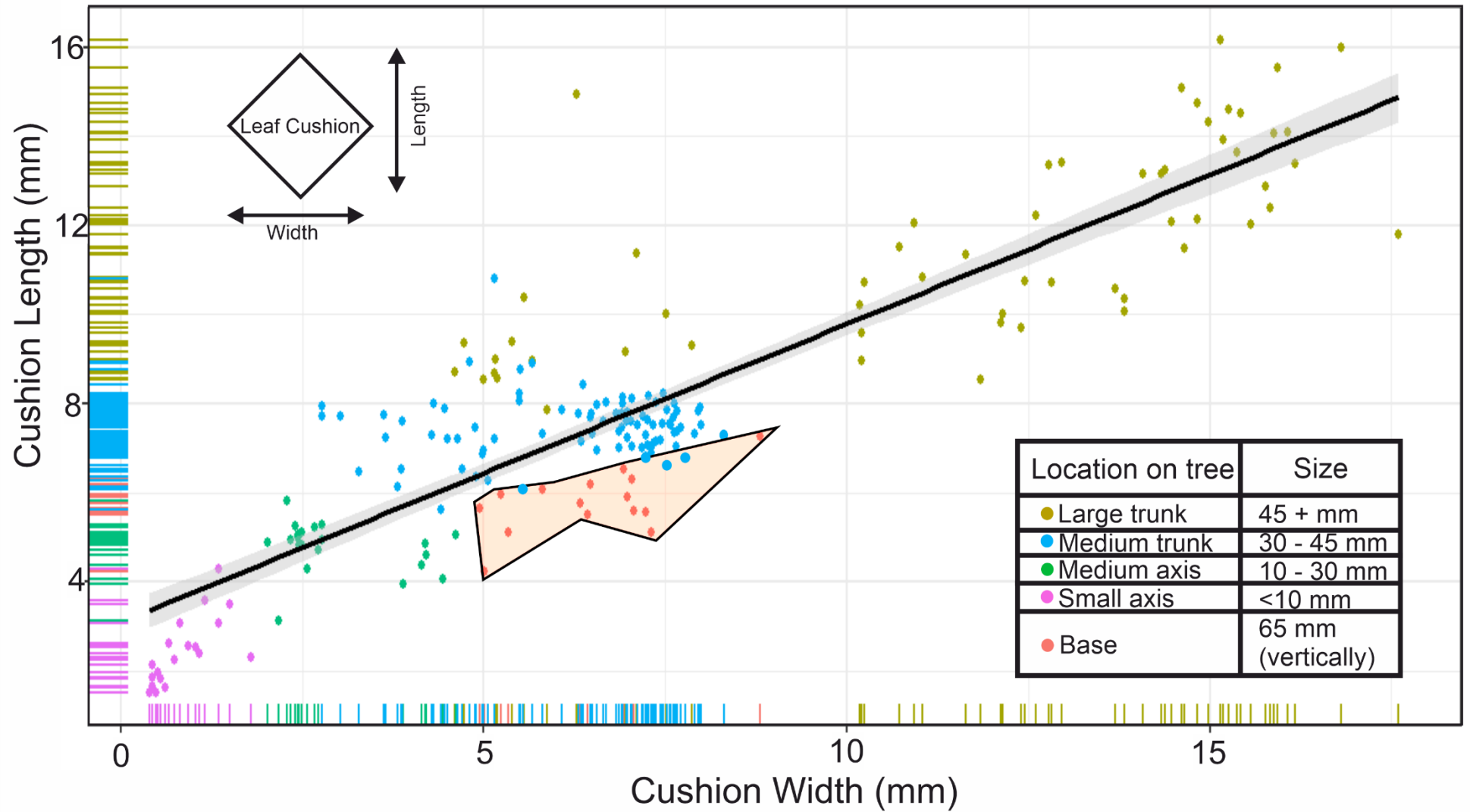
The leaf cushions of medium to large trunks were described in detail by Schweitzer (1968, 1999), including their ontogenetic arrangement into orthostichies and parastichies, preservation variability of both leaf cushions and leaf base parenchyma and quantitative measurements of cushion dimensions. Schweitzer also documented differences between the leaf cushion patterns on the middle portion of the trunk and the leaf scars on the bifurcating upper portion, noting transitional forms between the two (Schweitzer, 1968, Plate 34, Fig. 4; see also Plate 35A–C, this study). This study adds new quantitative data, comparing leaf scar and cushion size across individuals of varying sizes.

For consistency throughout this study, small axes are defined as those <10 mm in width, medium-sized axes between 10–30 mm, medium-sized trunks between 30–45 mm and large trunks as those >45 mm in width. These size classes are based on the width of the preserved organ on which the leaf cushions occur. They are not intended as formal organ categories, but provide a practical proxy for relative position within the plant, from distal leafy axes to larger trunk and basal regions. This allows changes in cushion size to be assessed across the reconstructed growth architecture of *P. pulchra*.



Text Figure 61. Large trunk of *P. pulchra* preserved in sandstone at locality AF2. A. Field photograph showing the main portion of the trunk preserved in the outcrop before extraction, with a smaller fragment that had fallen into the underlying river channel. B. Annotated image of the same trunk, highlighting the segment preserved in the outcrop before extraction (red) and the dislodged segment in the river channel (blue). The total preserved length is 133 cm. The asterisk (*) indicates the truncated end of the trunk, where subtle evidence of possible branching was observed

Variation in Leaf Cushion Dimensions in *P. pulchra*



Text Figure 62. Variation in leaf cushion dimensions in *P. pulchra* across different stem, trunk and basal regions. Specimens are grouped by the width of the organ on which the cushions occur, with width used as a proxy for position within the plant. Small axes (<10 mm wide) represent distal leafy axes, medium axes (10–30 mm) represent larger branch or upper stem fragments, medium trunks (30–45 mm) and large trunks (>45 mm) represent increasingly robust trunk material, and the base represents cushions measured across a 65 mm vertical section of the cormose basal region. The plot shows that cushion length and width generally increase with organ size, supporting a developmental gradient from small distal axes to larger trunk and basal regions. Data points from the base are enclosed within a convex hull to show their grouping. The schematic diagram in the top left illustrates how leaf cushion length and width were measured.

Leaf Cushion Dimensions

There is a positive relationship between cushion length and cushion width with clear groupings based on the size of the trunk or axis (Text Figure 62). The smallest leaf cushions are found on the smaller axes while the largest leaf cushions are located on large trunks (Table 18). The average cushion length for small axes is 2.4 mm, for medium sized axes is 4.8 mm, for medium-sized trunks is 7.5 mm, for large trunks is 11.6 mm, and for cushions at the tree base is 5.8 mm (Table 18). Small axes also have the thinnest leaf cushions and large trunks have the widest leaf cushions.

Measurement Type	Quantitative Measurement	Position on Tree				
		Small Axis	Medium Axis	Medium Trunk	Large Trunk	Base
Length	Lowest Value	1.5 **	3.1	5.6	7.9*	4.3
	Average Value	2.4**	4.8	7.5	11.6*	5.8
	Highest Value	4.3**	5.8	10.8	16.1*	7.3
	Range	2.8**	2.7	5.2	8.3*	3
Width	Lowest Value	0.4**	2	2.8	4.6	4.9*
	Average Value	0.9**	3	6.3	11.7*	6.5
	Highest Value	1.4**	4.6	8.3	17.6*	8.8
	Range	0.9**	2.6	5.5	13.0*	3.9

Table 18. Summary statistics for the length and width of leaf cushions and leaf scars from *P. pulchra*. For each measurement, the minimum (**), maximum (*), mean and range are reported. Small axes are defined as any axis <10 mm in width; medium-sized axes 10–30 mm; medium trunks 30–45 mm; and large trunks >45 mm. All measurements are in millimetres (mm).

The data points for the leaf cushions at the tree base (Text Figure 62 - orange data points) differ from the main trend. Although the base represents the widest preserved region of the plant, its cushions are comparatively small relative to those on large trunk fragments. If cushion size simply increased with organ width, the base would be expected to plot further towards the upper right of the graph. Instead, the base cushions occupy a lower field, overlapping more closely with medium trunk values. This suggests that the cormose basal region followed a different developmental pattern from the more cylindrical trunk and branch regions, consistent with its interpretation as a specialised basal organ.

Phyllotaxy

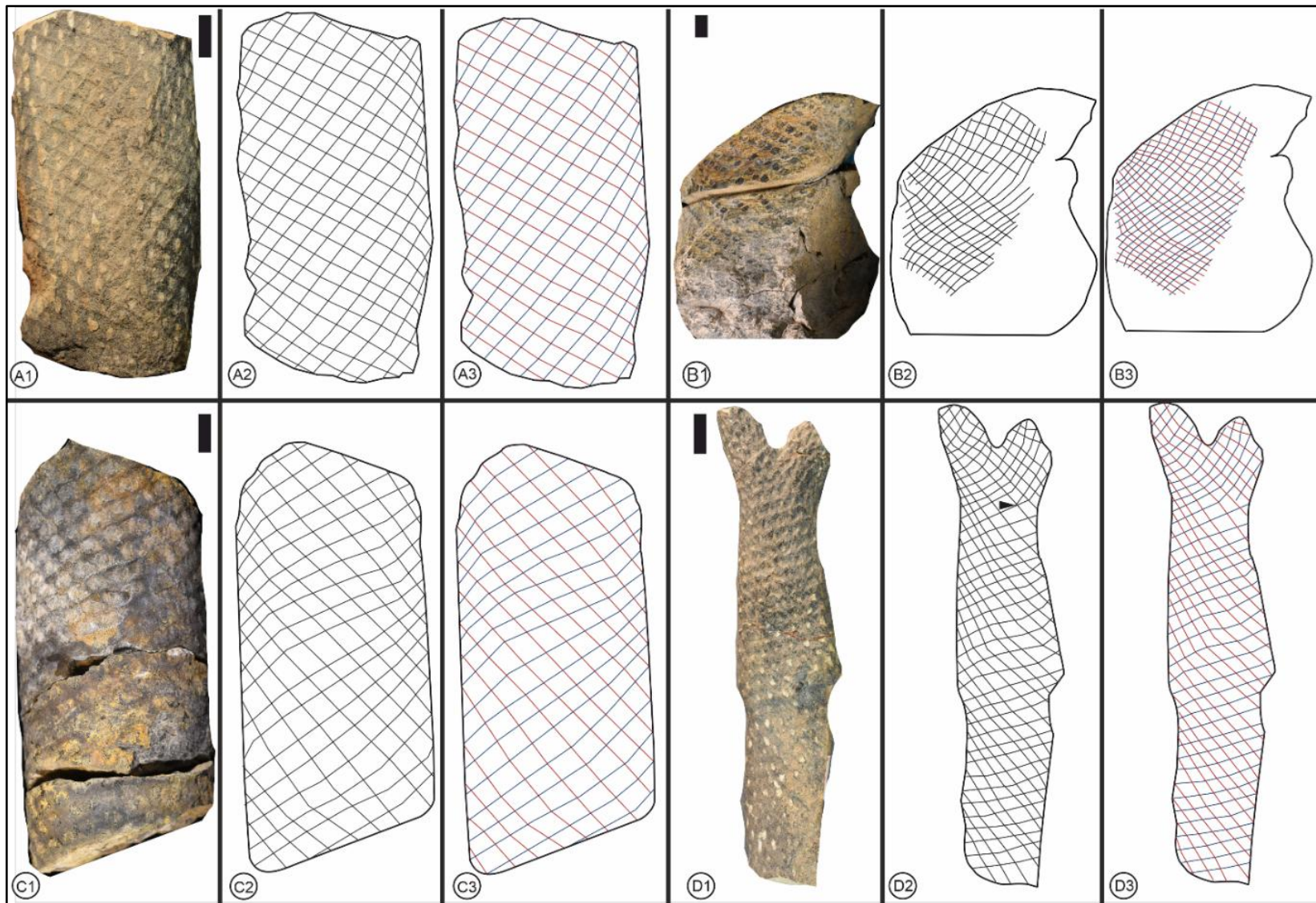
As observed at the base, leaf cushions on the trunk are arranged in both clockwise and anticlockwise helical patterns (Text Figure 63). In most specimens, complete phyllotactic patterns could not be determined due to poor or incomplete preservation. Two specimens where complete phyllotactic patterns could be determined will be discussed below (Text Figure 64). Nevertheless, some informative morphometric measurements were obtained by examining the insertion points of leaf-cushion helices, revealing variation in leaf-cushion spacing across different portions of the tree. Compared to leaf cushion phyllotaxy on the base (Text Figure 63B), where distinct spacing and divergence between anticlockwise helices occurs across the expanded basal region, the arrangement along the trunk remains relatively consistent (Text Figures 63A, C). However, apparent differences in leaf-cushion size, shape or spacing toward the lower part of the trunk and base should be interpreted cautiously. These regions are more likely to have been affected by compaction, decortication or distortion during preservation, and may not represent a primary developmental gradient. In one specimen, an additional clockwise helix is inserted just below the point of bifurcation near the upper portion of the trunk (Text Figure 63D - black arrow), possibly reflecting a local change in phyllotactic organisation close to the bifurcation.

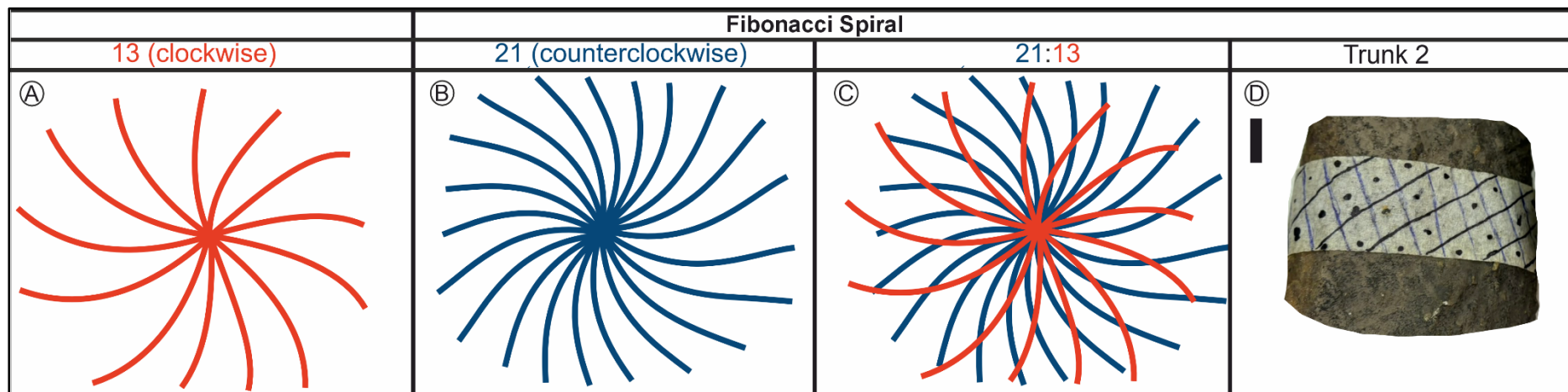
Two trunk specimens preserve phyllotactic patterns around the whole stem clearly enough to determine helical arrangements. These were traced onto a paper collar before phyllotaxy was evaluated (Text Figure 64D). Trunk 1 is 76 mm wide and 80 mm in diameter (locality AF-11), while Trunk 2 is 56 mm wide and 65 mm in diameter (locality RM – Plate 34G, H). Both display a 21:13 Fibonacci phyllotactic pattern.

Angles between successive leaf cushions were calculated by measuring angular displacement of the centre of the leaf cushion along helices on the trunk surface. This was done for both clockwise and anticlockwise helices. In Trunk 1, angles ranged from approximately 30–50°, while in Trunk 2, they ranged from 50–70°. These angles reflect the spacing of leaf cushion insertions along individual parastichies.

Inter-cushion distances also varied between specimens. This was calculated by measuring the distance between centre points of leaf cushions in successive clockwise or anticlockwise helices. In Trunk 1, spacing between adjacent leaf cushions was 6–10 mm along the anticlockwise helices and 4–7 mm along the clockwise helices. In Trunk 2, spacing varies less, ranging from 7–9 mm anticlockwise and 7–8 mm clockwise.

Text Figure 63. Phyllotactic patterns of clockwise (red) and counterclockwise (blue) spirals in the mid-trunk (A, C), base (B) and upper trunk (D) of *Protolpidodendropsis pulchra*. Each panel includes: (1) a macrophotograph of the specimen, (2) an interpretative outline of the leaf-cushion arrangement and (3) the same interpretation with clockwise and counterclockwise helices distinguished by colour. Clockwise helices are shown in red and counterclockwise helices in blue. Black arrows in D2 indicate the insertion of an additional clockwise helix immediately below the point of bifurcation. Scale bars = 20 mm. **A.** Specimen 36 of Schweitzer (1965, Plate 34, Fig. 1). **B.** AF-Base-01. **C.** AF-Stem-01. **D.** Specimen 34 of Schweitzer (1965, Plate 34, Fig. 4).





Text Figure 64. Fibonacci phyllotactic patterns in a *P. pulchra* trunk specimen. A. Clockwise helices in trunk 2. B. Counterclockwise helices in trunk 2. C. Combined phyllotactic diagram illustrating parastichy pairs with 21:13 phyllotaxy. D. Trunk 2 with marked cushions to trace helices.

Upper Portion of Trunk and First Basal Dichotomy of Trunk

Material used for description

Three specimens collected by Schweitzer and Berry are used to describe the upper portion of the trunk, including the first dichotomy. Two specimens from the Lower *Svalbardia* Sandstone (locality RM) were collected and described by Schweitzer (1965) and further detailed in Schweitzer (1999). The first specimen (Schweitzer, 1965, Plate 34, Figure 4) shows an isotomously bifurcating trunk, while the second (Schweitzer, 1965, Plate 39, Figure 1) captures similar morphological details. A third specimen, collected by Berry in 2016 from the same River's Meet locality, provides additional insights into branching patterns after the first basal dichotomy (Plate 11A, B, E, F, H, I).

Previously described material

Specimen 1 (Specimen 34 in Schweitzer, 1965, Plate 35, Figure 4; Schweitzer, 1999, Plate 20, Figure 5). **S017224**

Preservation and morphology

One of the most significant specimens described by Schweitzer captures the upper portion of the trunk preserved as an internal cast, measuring 225 mm in length and up to 48 mm in width (Plate 35A–C). This specimen shows an isotomous bifurcation with an angle of approximately 70°, resulting in two branches of nearly equal size (~23 mm in width). Each branch terminates shortly after the dichotomy.

Leaf cushions

On the lower half of the specimen, rhombic leaf cushions are present (Plate 35A, B - black arrow), transitioning to three-dimensional, fusiform cushions in the upper portion, immediately before the first basal dichotomy (Plate 35A, B - white arrows). A transitional form with intermediate features appears between the two patterns of leaf cushions. Notably, the trunk width narrows by about 10 mm immediately before bifurcating (Plate 35A, B - white arrow), marking the point where fusiform cushions become dominant.

Specimen 2 (Specimen 46 in Schweitzer, 1965, Plate 39, Figure 1; Schweitzer, 1999, Plate 22, Figure 1).

Preservation and morphology

The second specimen also briefly described by Schweitzer, shows another bifurcating trunk preserved as both an internal cast and an external cast in the surrounding sediment. It measures 233 mm in length and 54 mm in width (Plate 37C, D) and bifurcates at an angle of 60°, producing two branches of similar width (~17 mm). One branch terminates immediately after the bifurcation, while the other extends 74 mm from the bifurcation with a gentle curve. When comparing the width of the external impression (53 mm, Plate 37C - white arrow) with the width of the internal cast immediately before the bifurcation (26 mm, Plate 37C - black arrow), the width of the trunk is halved in size.

Leaf cushions

Surface preservation on the internal cast is relatively poor, but faint fusiform cushions are discernible after the bifurcation (Plate 37, C, D - blue arrow), more clearly visible to the naked eye. On the lower portion of the internal cast (Plate 37C, D - red arrow) and clearly visible on the external impression (Plate 37C, D - white arrow) are flattened, rhombic leaf cushions.

New material

Specimen 3: Upper portion of trunk with two dichotomies (RM-01, Plate 37A, B, E, F, H, I). **S017227-01**

Preservation

A specimen (RM-01) preserves details of the proximal two dichotomies along the trunk. This includes both an internal cast and an external cast (Plate 37A), though only the internal cast was transported to Cardiff. Despite partial damage during transport (Plate 37B - red arrow), field photographs retain all details of the branching pattern (Plate 37A, B).

Leaf cushions

Rhombic leaf cushion are visible on the external mould (Plate 37A - red arrow) and lower portion of the internal cast. Approaching the bifurcation, the fusiform leaf

cushion becomes dominant (Plate 37A - blue arrow), with a somewhat intermediate form existing between the two patterns.

First Dichotomy

The trunk fragment measures 145 mm in length and 46 mm in width. It bifurcates isotomously at a 60° angle, producing two axes of nearly equal width (21–22 mm). At the base of the trunk, the width is 38 mm (Plate 37A, B - green arrow), which narrows to 30 mm before widening to 48 mm just prior to the trunk bifurcating. Distal to the dichotomy, the left branch measures 22 mm in width and the right branch 21 mm.

Second Dichotomy: Right Branch

After the initial isotomous dichotomy, the right branch extends 59 mm before terminating. Its width narrows from 21 mm near the basal bifurcation to 12 mm at its distal end. Approximately 22 mm along the length of this branch, an incipient dichotomy is visible from the basal transverse plane (Plate 37A - black arrow, H, I), though the surrounding sandstone matrix obscures further external morphology (Plate 37H, I - white arrow). Further preparation was avoided to prevent potential damage because the sandstone is very hard.

A second isotomous bifurcation is inferred based on the similar size and morphology of the two emerging branches (both 12 × 16 mm in cross-section), each showing early signs of individual branch development. This incipient bifurcation, occurring shortly after the first, aligns perpendicularly to the initial dichotomy (Plate 37A - white arrow). Following this split, the axes widen slightly (Plate 37I), although further morphological details are obscured by the sandstone matrix (Plate 37I - white arrow).

Second Dichotomy: Left Branch

After the first basal dichotomy, the left branch extends 37 mm in length, maintaining a consistent width until it terminates. Notably, there is no indication of further bifurcation along its length, and it appears more flattened than the right axis. Surface details on the left branch begin to fade 22 mm after the first basal dichotomy—the same point at which an incipient dichotomy is observed in the right branch (Plate 37A - black arrow). It is likely that the left branch has not been preserved in sufficient

length and detail to reveal a corresponding dichotomy, and due to the poorer preservation quality, any incipient dichotomy is obscured.

Crown and distal axes

Material Used and Preparation Details

Høeg (1942) described small, occasionally leafy axes, attributing these specimens either to *P. pulchra* or as a "lepidophyte, likely the same species as *Bergeria mimerensis*" (1942: Plate LI, Figures 3–5; Plate LII, Figures 8–10; Plate LVI, Figures 5–6). Current evidence indicates these specimens likely represent fragmentary portions of smaller axes belonging to the distal regions of an arborescent lycopod crown. Schweitzer (1965) reconstructed this crown as sparsely branched with four total dichotomies and drooping overall crown morphology (Schweitzer, 1965, Figure 14).

Additional specimens collected by Berry (2016) and Wyatt (2022, 2023) have provided new insights into the branching architecture of the crown, clarifying how these branching elements fit together (Plates 38–41). The most notable specimen includes an almost intact densely branching crown recovered from the Estheriahaugen Member. Fragmentary axes were also recovered from the Estheriahaugen Member and various localities within the Plantekløfta Formation.

Field Collection of Crown Specimen

A relatively intact crown of *P. pulchra* was collected from Shale Unit 2 of the Estheriahaugen Member during the 2022 field season (Plate 38). The specimen was encased within an ironstone concretion measuring approximately 50 cm (length) × 40 cm (width) × 19 cm (depth). Preliminary examination in the field revealed additional fossil material on the surface of the nodule, including something that resembled *Pachytheca* and probable fragments of *Archaeopteris* branches. Upon splitting the concretion into two large slabs with a chisel and hammer, unidentifiable plant material requiring further laboratory preparation was exposed. Subsequent careful reduction of the slabs using hammer and chisel generated smaller counterpart fragments, ultimately revealing a well-preserved lycopod crown as a thin carbonaceous compression. Identification as *P. pulchra* was confirmed by leaf-base morphology typical for this species. Three large slabs containing the majority of the

crown (Plate 38), along with at least 26 smaller corresponding fragments (Text Figure 65B), were transported to the university for detailed analysis.

Preparation of Crown Specimen

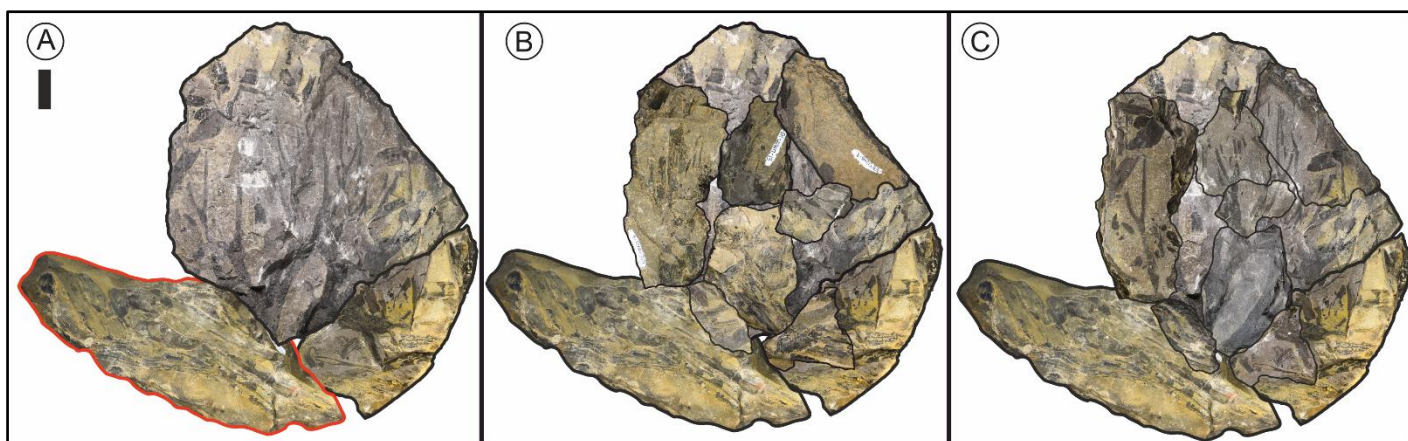
Following transport to the university, preparation commenced on the crown specimen. The ironstone matrix proved exceptionally resistant, making it difficult to prepare with standard serial *dégagement*. As the proximal part of the crown was not exposed (Text Figure 65A), a hammer and chisel were used to carefully remove the surface layer which exposed the upper portion of the trunk (Plate 38 - black arrows; Text Figure 66A - white arrows) and the first basal dichotomy (Plate 10 - white arrows; Text Figure 66A - black arrow).

Morphological description of crown and upper trunk

Overall appearance and size of crown

The crown is exceptionally well preserved, providing a near-complete view of its overall morphology. A prominent basal dichotomy is followed by successive branching events, with the two halves of the crown slightly overlapping. Each branching point is marked by a progressive reduction in axis diameter, terminating in slender, sub-parallel distal axes. The abundance of distal branches suggests a series of closely spaced sequential dichotomies that contribute to the observed branching density. Although compaction has obscured finer details in some regions, the branching architecture remains clearly discernible. The entire three-dimensional crown has been squashed into a fossil that is approximately 2-3 cm thick.

The preserved portion of the crown measures approximately 40 cm from the base to the tips of the most distal axes (Text Figure 66C - blue dotted line). The exposed trunk segment measures 65 mm in length. Its maximum preserved width near the base of the slab is 37 mm, though complete the diameter is closer to 54 mm (Text Figure 66C - black dotted line). Just prior to bifurcation, the trunk narrows to a visible width of 26 mm (Plate 38 - black arrows).



Text Figure 65. Pieces of ironstone nodule containing an almost intact crown of *P. pulchra*.

A. The three largest slabs of the nodule, which contain the bulk of the crown. The slab with red edging was further prepared to reveal the first-order bifurcation and the upper portion of the tree trunk (see Text Figure 11A; white arrows). **B.** Nodule fragments with corresponding counterparts placed face down, as found in the field. **C.** Image showing the counterparts reversed to illustrate the organisation of the crown. Scale bar = 40 mm. Locality EST.

Crown Branching Architecture

Basal Dichotomy

A basal dichotomy divides the trunk into distinct left (Plate 38 - red arrow; Text Figure 66A - red arrow) and right (Plate 38 - blue arrow; Text Figure 66 - blue arrow) crown branches. The angle of divergence between these two branches is unclear due to compression of the crown and slab incompleteness above the bifurcation. The two branches form the base of structurally distinct yet partially overlapping crown halves, with overlap most evident distally (Plate 38 - black asterisk). The total preserved crown width is approximately 16 cm (Text Figure 66C - orange dotted line), although the lateral branches are clearly incomplete. The basal division is interpreted as an approximately isotomous dichotomy because the two primary branches are similar in preserved width, but compression prevents confident reconstruction of their original three-dimensional angle.

Secondary Branching Distal to the Basal Dichotomy

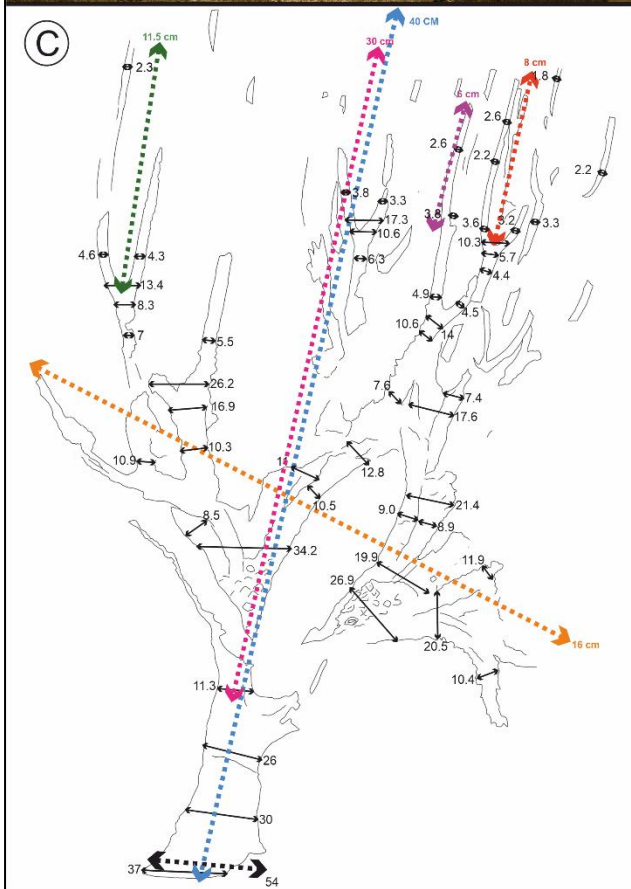
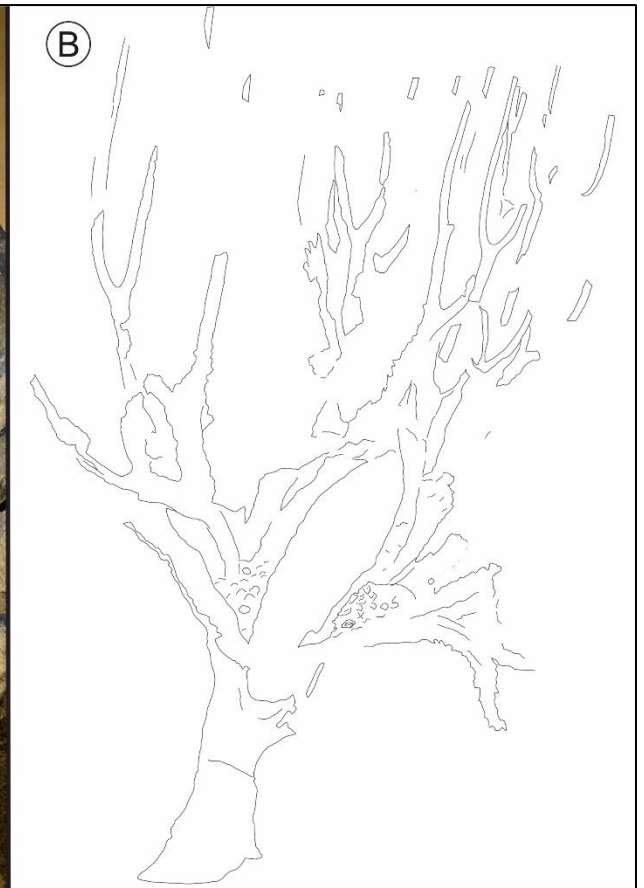
Both the left and right primary crown branches undergo further division, each dividing approximately in half into two prominent sub-units. Where visible, these secondary divisions also appear broadly isotomous, with daughter axes of similar preserved width. However, the orientation of successive dichotomies is not consistent enough to demonstrate a fixed branching rule. Some divisions appear to occur obliquely or in slightly different planes relative to the preceding dichotomy, while others may have been compressed into the same bedding plane during preservation. Therefore, the crown is interpreted as having repeated isotomous to near-isotomous dichotomies, but not as showing a regular pattern in which each dichotomy occurs at right angles to the previous one.

On the left side, the main axis is split along a medial line, forming two distinct branching subunits. The left subunit descends beneath the surface layer and disappears from view at the edge of the slab, while the right subunit is exposed and preserved at the surface. This suggests that at least part of the crown had a three-dimensional arrangement before compression, rather than all branches originally lying within a single plane.

Similarly, the right crown branch divides medially into two approximately symmetrical subunits. The left subunit preserves three axes of similar width, while the right subunit contains comparable axes but with less morphological detail preserved. These sub-branches will be described in detail below. Overall, the preserved crown architecture is best described as a compressed, repeatedly dichotomising system with broadly equal divisions, but the exact angular relationship between successive dichotomies remains uncertain.

Text Figure 66. Whole crown specimen of *P. pulchra* following preparation, showing the upper trunk and crown architecture.

A. Macrophotograph of the crown specimen. White arrows indicate the outer edges of the trunk, black arrow indicates first dichotomy in the trunk. Red arrow depicts right side of crown and blue arrow depicts the left side of the crown. The red box highlights an area with closely spaced sequential bifurcations, critical for interpreting branching organisation seen in Text Figure 67. Scale bar: 30 mm. **B.** Interpretive line drawing of the specimen. **C.** Annotated line drawing with crown dimensions: Black dotted line: estimated width of the unpreserved upper trunk. Blue dotted line: total crown length. Pink dotted line: crown length following the initial trunk bifurcation. Orange dotted line: total crown width. Green dotted line: axis length after a distal bifurcation (left side). Purple dotted line: axis length after a distal bifurcation (right side). Red dotted line: length of a terminal axis following a distal bifurcation. **D.** Interpretive diagram showing axis positions relative to the sediment. The key indicates whether distal tips are above, below, level with, or indeterminate relative to the bedding surface. Scale bar: 30 mm. Locality EST.



Terminology for Crown Description

Due to the complexity of the crown structure, specifically the closeness of dichotomies in the proximal part of the crown, it is divided into clearly defined units to facilitate interpretation. Each segment is labelled according to Text Figures 67 and 70, and these labels are used consistently throughout the morphological description.

Following the initial basal dichotomy, the crown separates into left (Plate 38 - red arrow) and right (Plate 38 - blue arrow) primary branches, designated as 'L' (Text Figure 67A, B) and 'R' (Text Figure 70A, B), respectively.

Each primary branch ('L' and 'R') is further divided medially into two subunits:

- The left half is given the suffix 'L' (e.g. L-L, R-L; red axes in Text Figures 67B and 70B)
- The right half is given the suffix 'R' (e.g. L-R, R-R; blue axes in Text Figures 67B and 70B)

For example, 'R-L' refers to the left half of the right crown branch.

Each subunit is then split into two parts of roughly equal size, each containing one or two visible axes (Text Figures 67C, D; 14C, D).

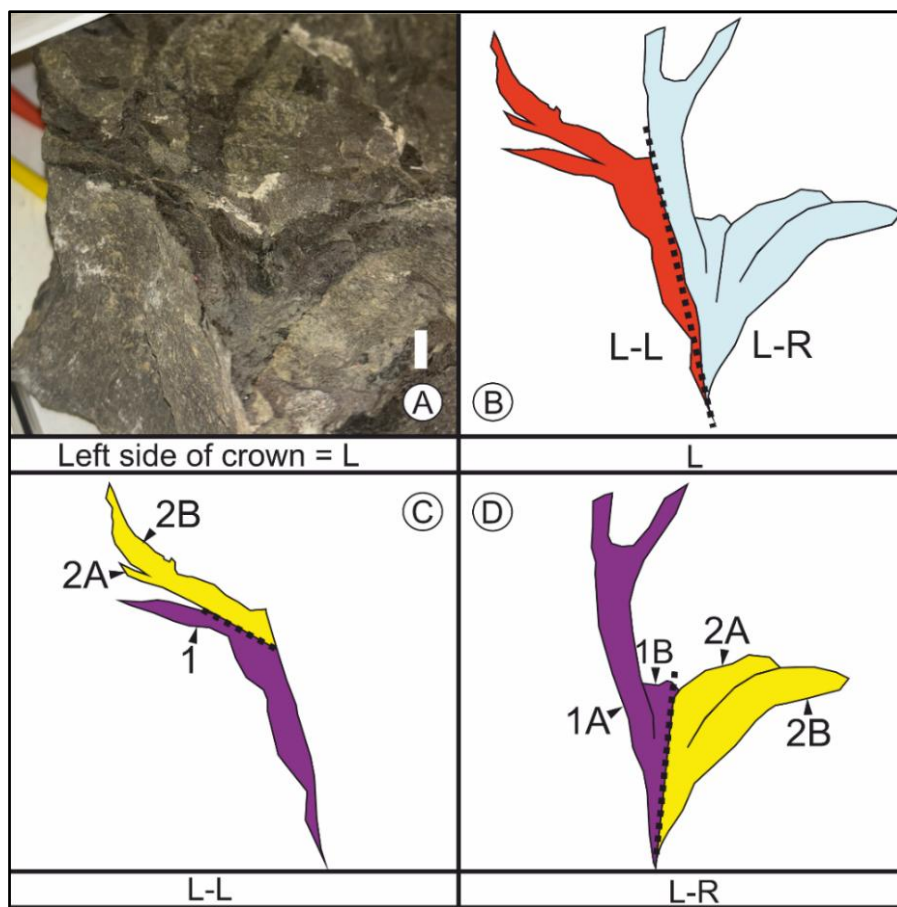
- Axes on the left are assigned the suffix '1' (purple axes)
- Axes on the right are assigned the suffix '2' (yellow axes)
- When more than one axis is present, an additional 'A' or 'B' is added to distinguish them

For example, 'R-L-1A' refers to an axis on the right branch ('R'), in its left subunit ('L'), in the left grouping ('1'), and identified as axis A. The collective unit comprising R-L-1A and R-L-1B is referred to simply as R-L-1.

Left Primary Branch

Overall Morphology

The left primary branch of the crown (Plate 38 - red arrow, Plate 39) is very informative, revealing a highly three-dimensional branching architecture that has been compressed against the surface of the concretion. The branch is divided into two distinct segments, a L-L and L-R segment separated by a clear medial margin (Text Figure 67A, B). These undergo a series of dichotomous divisions (Text Figure 67C,D; Plate 39), ultimately producing the sub-parallel distal branches on the left side of the crown.



Text Figure 67. Subdivision of the left primary branch of the *P. pulchra* crown into discrete branching units.

A. Photograph of the left primary branch. Scale bar = 30 mm. B. Line drawing of the left section of the crown, showing subdivision along the medial plane into left (L-L; red axes) and right (L-R; blue axes) subunits. C. Line drawing of L-L, further subdivided along the medial plane into two segments: L-L-1 (purple axis) and L-L-2, which in turn bifurcates into L-L-2A and L-L-2B (yellow axes). D. Line drawing of L-R, subdivided along the medial plane into two segments: L-R-1 and L-R-2, each of which is further divided into two axes, designated A and B.

Detailed Morphology of the Left Primary Branch (L-L and L-R)

L-L Segment: Three-Dimensional Axis Arrangement (See Text Figure 67C)

The portion of the crown labelled L-L demonstrates that it is a complex, spatially layered system preserved in depth through the matrix. Within this segment, at least three visible divisions are present, expressed as compressed carbonaceous layers separated vertically by approximately 30 mm.

Along its medial line, L-L is further subdivided into two main segments: **L-L-1** and **L-L-2** (Text Figure 67C).

L-L-1 (See Text Figure 67C; *purple axis*)

The L-L portion extends for 32 mm (Plate 39B - white *) before dividing into 2, an upper axis (2- Text Figure 67C - yellow axes) and a lower axis (1- Text Figure 67C - purple axes), demonstrating a third dichotomy distal from the trunk (Text Figure 68E2 - blue *). The lower axis, L-L-1, diverges from L-L-2 at an angle of 22° and continues for 67 mm until it reaches the edge of the slab (Plate 39C - white *; Plate 39A - purple arrow).

In side profile (Plate 39A), L-L-1 is seen to descend much deeper into the matrix, disappearing approximately 30 mm below the surface (Plate 39A - black arrow). This vertical extension further supports the interpretation of the crown as a compressed three-dimensional, complex branching structure.

L-L-2A & L-L2B (See Text Figure 67C; *yellow axes*)

The segment L-L-2, with a total preserved length of 123 mm, bifurcates into two layers: an upper axis (L-L-2B) exposed at the surface (Text Figure 67C - L-L-2B), and a lower axis (L-L-2A) that diverges at an angle of ~13° and quickly disappears into the matrix (Plate 39A; Text Figure 67C - 2A). This bifurcation point (Text Figure 13E2 - green asterisk) lies 64 mm distal to the previous branching event. L-L-2A descends to a depth of approximately 12 mm below the surface, while L-L-2B remains entirely exposed.

L-R Segment: Axis Arrangement (See Text Figure 67D)

L-R provides the clearest view, with four slightly overlapping axes of similar width (8–11 mm) lying flat on the nodule surface. Along its medial line, L-R is subdivided into two segments: L-R-1 and L-R-2 (Text Figure 67D). Each segment further divides into two axes, designated A and B, resulting from closely spaced sequential dichotomies (Text Figure 67D).

L-R-1 (See Text Figure 67D; purple axes)

L-R-1A displays a distinct bifurcation near its distal end (Text Figure 68D2; purple asterisk, Text Figure 67D - 1A), occurring approximately 56 mm beyond the previous branching point. This represents the fifth observed dichotomy in the crown distal to the trunk. Prior to bifurcation, the axis widens from 10 mm to 17 mm, after which only the right-hand branch remains visible, tapering to 5 mm.

L-R-1B is partially obscured by adjacent axes and best viewed under cross-polarised light (Plate 40E - black arrow). Its distal end extends below the surface where it becomes concealed.

L-R-2 (See Text Figure 67D; yellow axes)

L-R-2A and L-R-2B form a closely paired set of axes, each approximately 11 mm wide. Both curve gently to the right in contrast to the leftward curvature observed in the L-R-1 pair. L-R-2B extends slightly further than L-R-2A but the distal ends of both axes descend below the surface of the nodule.

Observed Sequence of Dichotomies in Left Primary Branch

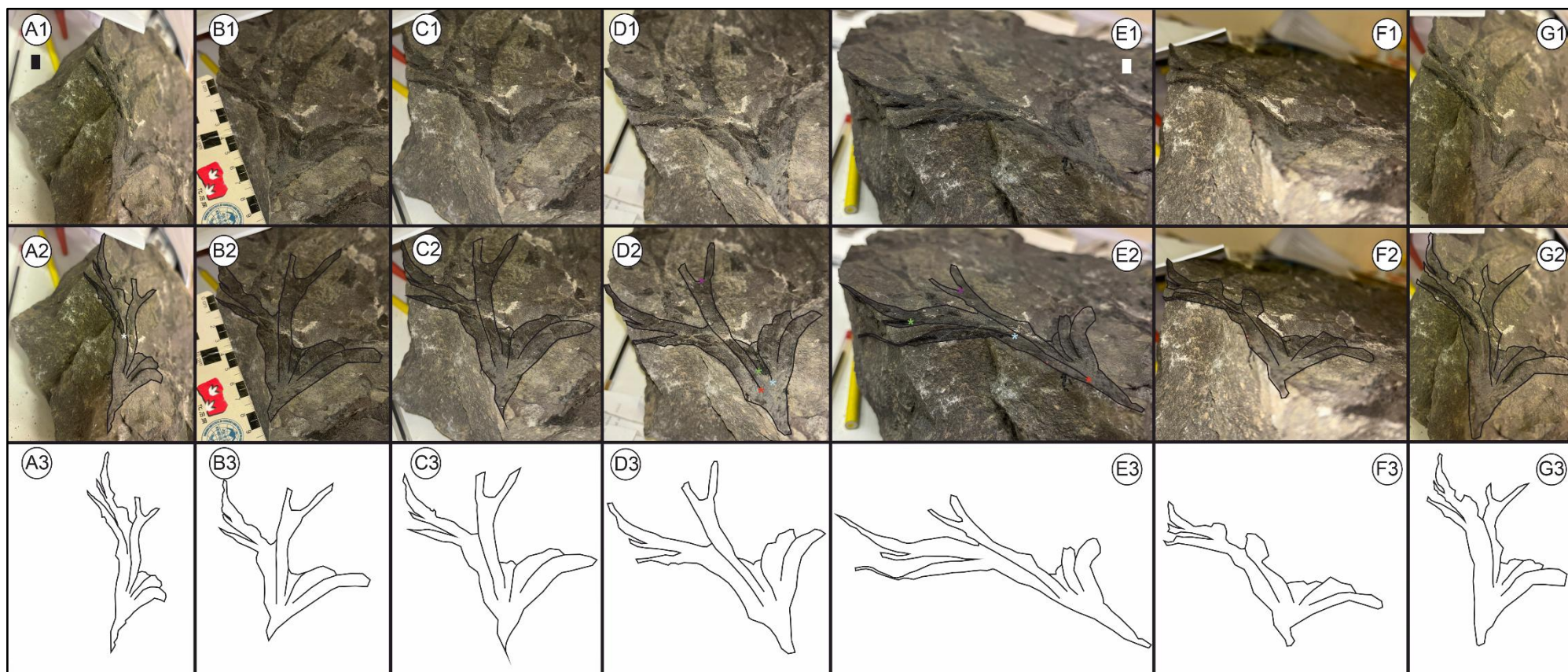
The L-R portion of the crown preserves at least three closely spaced, sequential dichotomies, with a fourth identified approximately 56 mm beyond the previous branching point, located at the distal end of axis 1A (Text Figure 68D2; purple *). When including the initial basal bifurcation of the trunk, the total number of directly observed dichotomies within the crown is five in this part of the specimen.

Additional Paired Axes in the Counterpart of L-R

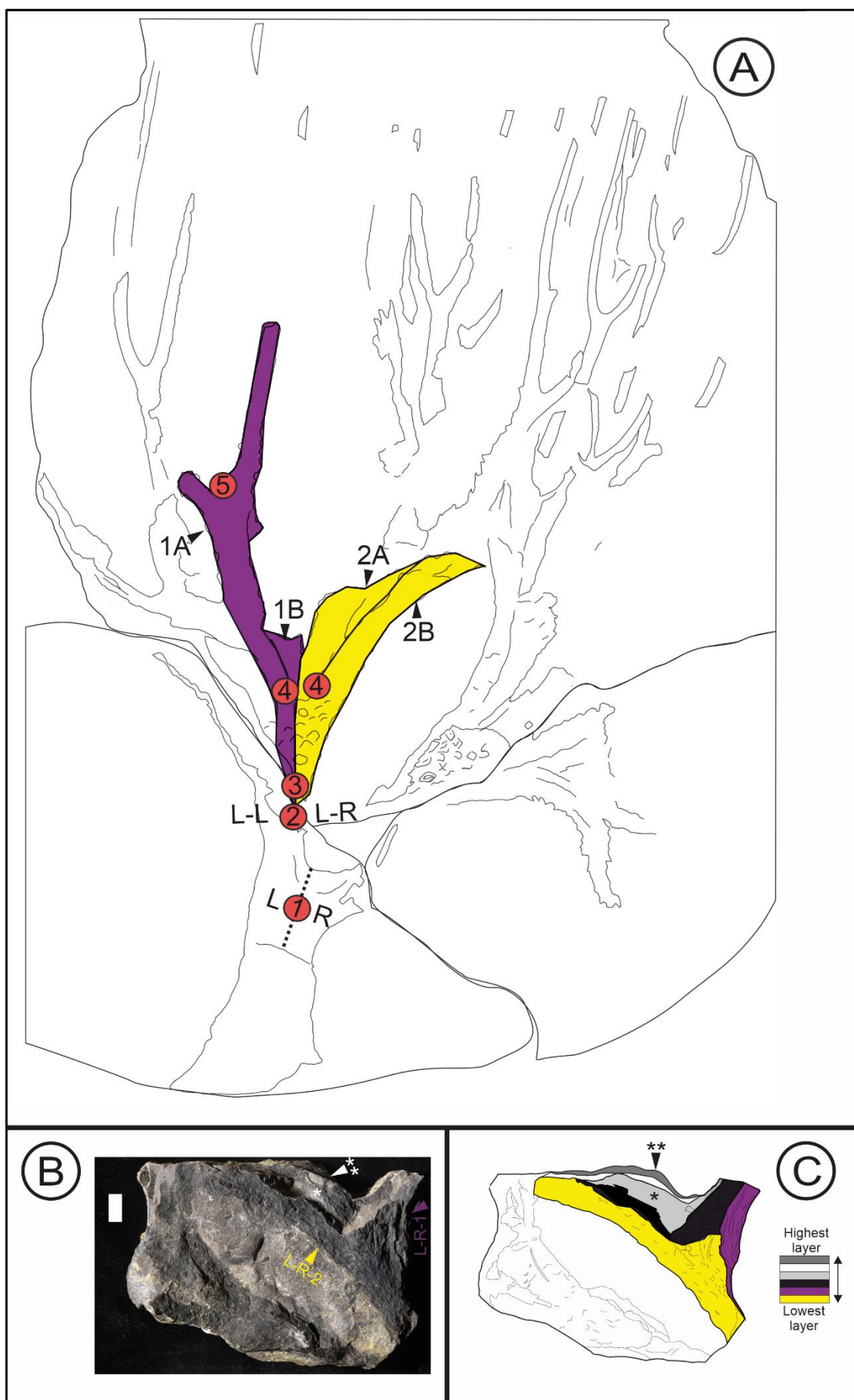
The counterpart of the L-R segment reveals an additional paired set of axes. A thin compression, corresponding to the counterpart of L-R-2, preserves portions of both axes, including the bifurcation between L-R-2A and L-R-2B (Text Figure 69B - yellow arrow, Plate 40A–B). In addition, a partial fragment of the counterpart to axis L-R-1A is visible near the slab edge (Text Figure 69B; purple arrow).

Two additional axes are preserved in the upper layer of the counterpart, separated from axes L-R-1 and L-R-2 by an intervening sediment layer up to 15 mm thick (Text Figure 69C; black shading). The first axis (Text Figure 69C - * light grey shading) is preserved as a substantial portion of an axis, separated from the L-R counterpart by a wedge of sediment (Text Figure 69C - black shading). The second axis lies above the first, separated by a thin sediment layer (Text Figure 69C - white) and is only partially preserved, appearing as a narrow compression at the slab edge (Text Figure 69C - ** dark grey shading).

The presence of a substantial axis, or pair of axes, directly beneath the L-R segment suggests that an additional dichotomy may have occurred in a plane perpendicular to those visible on the slab surface. This would raise the number of divisions in this part of the crown to six, though their presence is only assumed from the paired axes preserved in the upper layer of the counterpart, with no conclusive evidence to map them confidently onto the crown.



Text Figure 68. Photographs, interpretative overlays, and line drawings of the left primary branch of the *P. pulchra* crown. The material was viewed from different angles in order to develop the understanding of the 3D arrangement of branches. Panels A–G show different perspectives and angles used to photograph the left primary branch, highlighting the various axis layers within the crown. Images labelled **1** show the original macrographs of the fossil; **2** presents interpretative line drawings overlaid on the fossil images; **3** displays the interpretative line drawings in isolation, illustrating the branching system. Coloured asterisks in D2 and E2 correspond to bifurcation points as seen in Text Figure 14. The red * = 2, blue = 3, green = 4, purple = 5. Scale bar = 10 mm.



Text Figure 69. Interpretative line drawing of the part and counterpart of the left primary branch of the *P. pulchra* crown. **A.** Interpretative line drawing of the three largest slabs of the concretion, which together preserve the entire crown of *P. pulchra*, illustrating section L–R of the left primary branch with illustrative labels and visible dichotomy numbers circled in red. Axis labels and colours correspond to those described in Text Figure 67C–D. **B.** Macrophotograph of the counterpart of the crown, with colours and labels corresponding to the axes shown in A. * refers to the first paired axis, which is separated from L-R-2 by 15 mm of sediment. ** refers to the second paired axis, which terminates at the edge of the slab. **C.** Light grey shading and (*) refer to the first paired axis, which is separated by sediment from the axes on the counterpart (yellow and purple) and those present only on the counterpart and separated by a thick wedge of sediment (black shading). Dark grey shading (**) refers to the second paired axis, which lies above the first and is separated by a thin layer of sediment (white shading). The shading colour key highlights the relative depth of the layers.

Right Primary Branch:

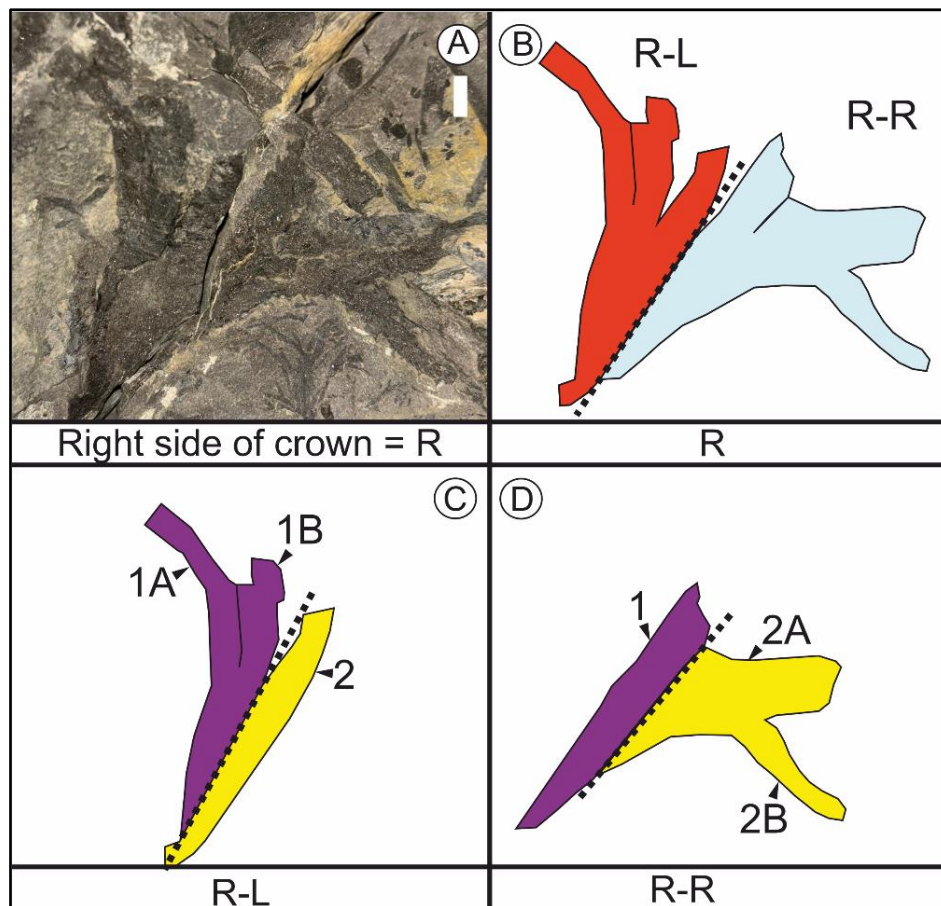
Overall Morphology

The right primary branch is more splayed than the left, with at least six similarly sized axes diverging radially in a fan-like arrangement (Text Figure 70; Plate 38 - blue arrow; Plate 41E). These axes originate from a common point approximately 48 mm distal to the first basal dichotomy. The branch is preserved across two slabs, with a medial margin separating it into R-L and R-R segments (Text Figure 70B). Part of this margin is obscured at the slab junction (Plate 41B - white *). R-R lies flat on the surface, while R-L is offset lower into the matrix, with its right margin descending ~35° (Text Figure 71C1-3). A wedge of sediment separates the two halves (Plate 41A - white arrow), marking a bifurcation.

Detailed Morphology of Right Primary Branch (R-L and R-R)

R-L Segment: Three Dimensional Axis Arrangement (See Text Figure 70C)

The R-L segment is better preserved in terms of overall morphology and further supports the interpretation of a three-dimensional branching system within the crown of *P. pulchra*. It comprises three axes of similar width (7–9 mm), with two leftmost axes lying flat on the surface with a slight overlap and a third axis on the right which descends into the matrix at an angle of ~35°.

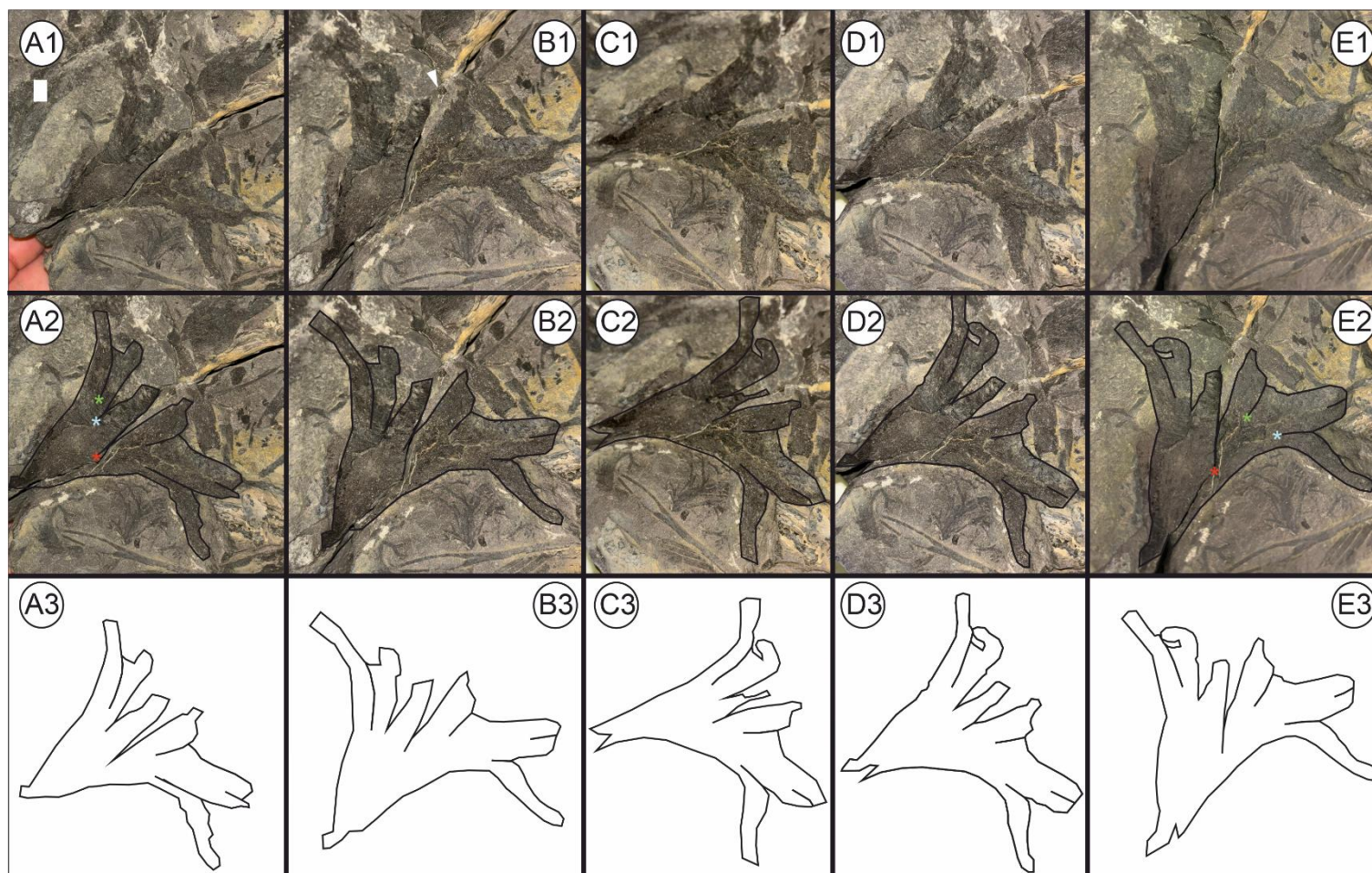


Text Figure 70. Subdivision of structural units within the right primary branch of the *P. pulchra* crown. **A.** Photograph of the right primary branch. Scale bar = 30 mm. **B.** Line drawing of the right section of the crown, showing subdivision along the medial plane into left (R-L, red axes) and right (R-R, blue axes) subunits. **C.** Line drawing of the R-L subunit, further divided along the medial plane into two segments: R-L-1 (purple axis) and R-L-2. R-L-1 is further subdivided into R-L-1A and R-L-1B (purple axes). **D.** Line drawing of the R-R subunit, subdivided along the medial plane into R-R-1 (purple axis) and R-R-2 (yellow axis). R-R-2 is further divided into R-R-2A and R-R-2B.

A medial division (Text Figure 70C - black dotted line) separates R-L into R-L-1 (Text Figure 70D - purple axes) and R-L-2 (Text Figure 70D - yellow axis). The two left axes of R-L-1 (R-L-1A and R-L-1B) are paired and slightly overlapping, curving gently to the left, while the right-hand axis (R-L-2) exhibits a gentler leftward curve.

R-L-1A & R-L-1B (Text Figure 70C; purple axes)

R-L-1 is composed of two overlapping axes of similar size, diverging at a bifurcation point visible on the surface (Text Figure 71E2 - blue asterisk). R-L-1A extends for 44 mm beyond the bifurcation (Plate 41F - white *), while R-L-1B extends for 36 mm (Plate 41F - black asterisk) and lies atop R-L-1A. The distal tip of R-L-1A is



Text Figure 71. Photographs, interpretative overlays, and line drawings of the right primary branch of the *P. pulchra* crown. Panels A–G show different perspectives and angles used to photograph the branch, highlighting the multiple axis layers within the crown. Images labelled **1** show the original macrographs of the fossil. **2** presents interpretative line drawings overlaid on the fossil and **3** shows the interpretative line drawings in isolation, illustrating details of the branching system. Coloured asterisks in A2 and E2 correspond to bifurcation points. The red * = 2, blue = 3, green = 4,. Scale bar = 10 mm.

obscured by overlapping material from the left primary branch (Plate 38 - black *), while R-L-1B terminates below the nodule surface.

R-L-2 (See Text Figure 70C; *yellow axis*)

R-L-2 is a single axis, 9 mm in width, diverging from R-L-1B at an angle of $\sim 29^\circ$. It curves gently to the left before descending sharply into the matrix at $\sim 35^\circ$. Its distal tip is obscured by overlying sediment, which separates it from the R-R segment (Plate 41A - *white **). The very distal portion of R-L-1 lies approximately 18 mm below the surface (Plate 41A - black asterisk), indicating a clear vertical offset between the R-L and R-R segments.

Three-Dimensional Branching in R-L: Axes Beyond the Surface

Side profile imaging of the slab containing R-L (Plate 41C) reveals multiple layers of compressed carbon (Plate 41C - arrows), interpreted as branches preserved at different depths relative to those described above. These additional axes range from 12 to 26 mm in preserved length, distally. Two upper axes are preserved 20 mm and 30 mm above the surface, respectively (Plate 41C - white arrows), while a third axis lies ~ 30 mm beneath the surface (Plate 41C - black arrow).

The orientation of these axes reinforces the three-dimensional organisation of the crown. The deepest axis projects downward, nearly perpendicular to the nodule surface while the upper two descend at angles of $\sim 115^\circ$ and $\sim 125^\circ$, emphasising spatial divergence across multiple planes.

R-R Segment: Detailed Morphology (See Text Figure 70D)

The R-R segment is less well preserved than other regions of the crown with some of the surface detail degraded. However, it still forms a spatially distinct unit which is separated from R-L by a substantial wedge of sediment (Plate 41A - white arrow). It consists of at least three axes lying relatively flat on the surface of the nodule, the boundary between the first two is indistinct (Plate 41F - black arrow), but a clear 45° bifurcation is seen between the second and third axes (Plate 41F - white arrow). R-R is also positioned slightly higher on the nodule than the axes of R-L (Plate 41A, E).

A medial division (Text Figure 71E2 - green *) separates R-R into two segments: R-R-1 (Text Figure 70D - purple axis) and R-R-2 (Text Figure 70D - yellow axes). R-R-2 is further subdivided into R-R-2A and R-R-2B (Text Figure 71E2 - blue *). Both axes curve rightward, with R-R-2B diverging at a near-perpendicular angle to the main axis of the right branch (Plate 41F - white arrow).

R-R-1 (See Text Figure 70D; purple axis)

R-R-1 is a single axis measuring 11 mm in width (Plate 41A - black arrow), emerging vertically from the main branch and aligned with the plane in which the rest of the right branch is preserved. It lies slightly higher than R-R-2 and is bordered on its left margin by the sediment wedge separating it from R-L (Plate 41A - white arrow).

The left margin of R-R-1 features tooth-like projections, likely representing attached or partially preserved leaves (Plate 42A, B - black arrows). These measure 2–3 mm in length and extend at an angle of ~30° from the axis surface.

R-R-2A & R-R-2B (See Text Figure 70D; yellow axes)

R-R-2 is composed of two axes: R-R-2A (14 mm wide) and R-R-2B (9 mm wide). R-R-2A maintains a gentle rightward curve, while R-R-2B emerges at an almost perpendicular angle to the main axis (Plate 41F - white arrow), showing a more pronounced rightward curvature. A faint central line visible along the length of R-R-2A may indicate an additional bifurcation, though this may alternatively result from surface distortion due to overlapping material and poor preservation and cannot be conclusively confirmed.

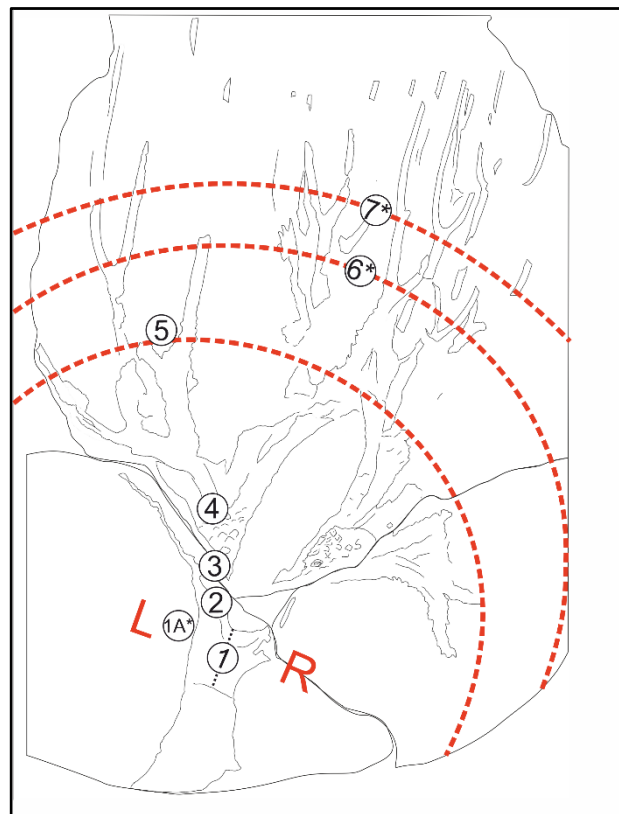
Distal Branching in Crown

The left and right portions of the crown preserve evidence for at least five visible dichotomies which are clearly visible on the left side (Text Figure 72 - 1–5). These are indicated either by direct observation of an axis splitting into two or, where the bifurcation itself is not preserved, inferred from the presence of the corresponding number of daughter axes. If the crown underwent five successive dichotomies, the total number of distal axes would reach 64 (Text Figure 18).

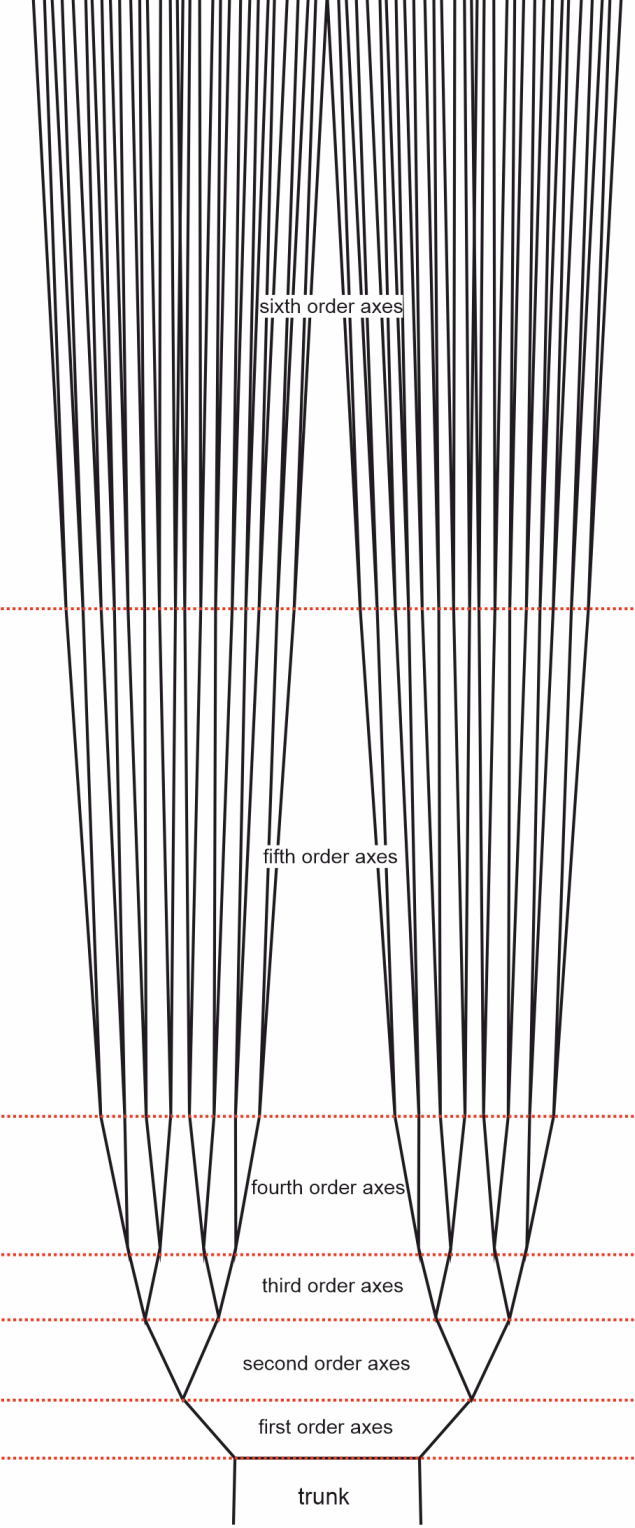
In the counterpart to the left portion of the crown, multiple paired axes above those preserved on the nodule indicate an additional bifurcation (Text Figure 69B–C). This

split must have occurred soon after the initial trunk bifurcation, as the extra axes overlie the preserved crown layer on the nodule surface (Text Figure 72 - 1A*).

In addition to the five definite bifurcations, the distal portions of the crown preserve at least two further levels of branching axes (Text Figure 72 - 6*, 7*). Some are clearly attached and represent consecutive bifurcations. Their position well beyond the fifth bifurcation makes it unlikely that they correspond to the fourth and fifth divisions on the right side of the crown. Instead, they most likely represent additional distal dichotomies. However, because these axes are not fully attached and cannot be traced continuously, they cannot be numbered with complete certainty though their presence is inferred.



Text Figure 72. Schematic diagram of bifurcations in the crown of *P. pulchra*, based on the line drawing in Text Figure 69A. Labels 1–5 indicate observed dichotomies mapped directly from the crown. Label 1A* marks a presumed dichotomy, inferred from paired axes preserved in the upper layer of the counterpart to the left branch. Labels 6* and 7* denote additional dichotomies inferred from extra branching in the distal tips of the right side of the crown; although these cannot be directly mapped, their presence is assumed.

Branching organization	dichotomy number	total number of axes
		64
	6	
		32
	5	
		16
	4	
		8
	3	
		4
	2	
		2
	1	
		1

Text Figure 73. Branching organisation of the first six sequential dichotomies in the crown of *P. pulchra*. The first column illustrates the branching pattern, the second column indicates the dichotomy number, and the third column shows the corresponding number of distal axes produced.

2. Distal Crown Morphology: Evidence from Fragmentary Axis Material

Material

Whilst the crown specimen remains the most informative example for reconstructing the overall architecture of *P. pulchra*, other specimens provide additional morphological data of variation. This includes material collected from the Plantekløfta type locality (Plates 42F, 43A, E), Estheriahaugen (Plate 43B), Munindalen (Plate 43D, E), AF22B (Plate 43C, D) and Planteryggen (Plate 43F, G).

Summary of Crown Material

The organisation of the first few dichotomies in the crown is difficult to establish because of their close spacing, which leads to crowding and overlapping of axes. Further distally, the axes are more widely separated and spread outward in the nodule, making their arrangement easier to map. As the crown opens out beyond the earliest bifurcations, the axes become narrower and more widely spaced which allows their relative positions to be traced with greater clarity (Text Figure 72, 73).

Across the ~40 cm preserved length of crown, from the first basal bifurcation in the trunk to the most distal tips (Text Figure 66C - blue dotted line), there is a marked reduction in axis width. After the first and second bifurcations, the corresponding left and right crown segments, located ~15 cm from the trunk base, measure approximately 34.2 mm and 26.9 mm in width, respectively. Two more bifurcations occur shortly after this point, producing axes that are 9–11 mm wide by ~20 cm along the crown. By the outer edge of the slab, the most distal axes have narrowed to just 1.8–2.6 mm in width. This represents an almost tenfold decrease in axis diameter over a 20 cm stretch of the crown.

A notable feature of the distal tips in the crown is that, beyond the presumably final bifurcation, the axes gently recurve and become sub-parallel to one another. As a result, the distal axes appear aligned, corresponding to the direction of growth observed in the trunk. This recurvature is particularly evident in one of the outermost axes on the left primary branch (Plate 38 – top left, Plate 40F). The left-hand axis, positioned near the outer margin of the crown, shows a more pronounced upward

curve post-bifurcation than its paired axis on the right, which emerges from the same bifurcation. The right-hand axis remains relatively straight, likely due to its position already lying within the shared growth direction.

Other specimens

Several specimens comprise small bifurcating axis fragments morphologically consistent with those in the distal portions of the crown. Some are incomplete, preserving only short segments before or after the bifurcation (Plate 43B, D), while others retain more extensive portions of axis on both sides of the bifurcation (Plate 43A, F, G).

The most complete example is shown in Plate 43A, with a total preserved length of 211 mm. The axis below the bifurcation is 9 mm wide, expanding to 11 mm before dividing isotomously into two axes of ~6 mm width each, with a bifurcation angle of ~30°. The daughter axes extend for 130 mm and 111 mm, respectively, before terminating at the slab edge. Post-bifurcation, both axes curve gently leftward and upwards, displaying the same upward recurvature and sub-parallel orientation seen in the distal tips of the axes of the crown specimen (Plate 40F - white arrow).

Interestingly, this specimen does not have the same dramatic reduction in width as seen in the distal axes of the crown, there is only a 1 mm reduction in axis width across 165 mm of axis.

A notable preservation feature is the presence of internal casts distally (Plate 43A - white arrows), with external moulds beneath (Plate 43A - black arrows). In both left and right axes, the internal cast preserves a continuous central depression possibly representing the vascular strand along much of the distal length (Plate 15A - black *), which is not visible in the external impression.

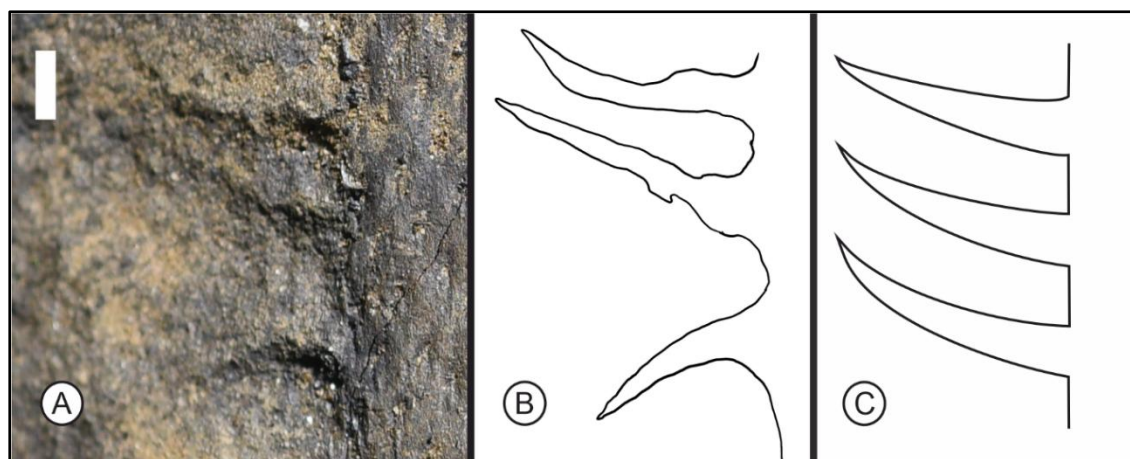
Other, less well-preserved specimens do not display the same upward recurvation in the distal axes as seen in Plate 43A (Plate 43B–G). These examples also exhibit a much wider bifurcation angle between the daughter axes, ranging from 40° to 70°. The axis fragments are notably smaller than those in Plate 43A, which may contribute to the observed morphological differences. Alternatively, this variation could be taphonomic in origin, smaller axes may have lacked sufficient structural

rigidity or may have been more prone to distortion during burial and preservation, particularly if already fragmented.

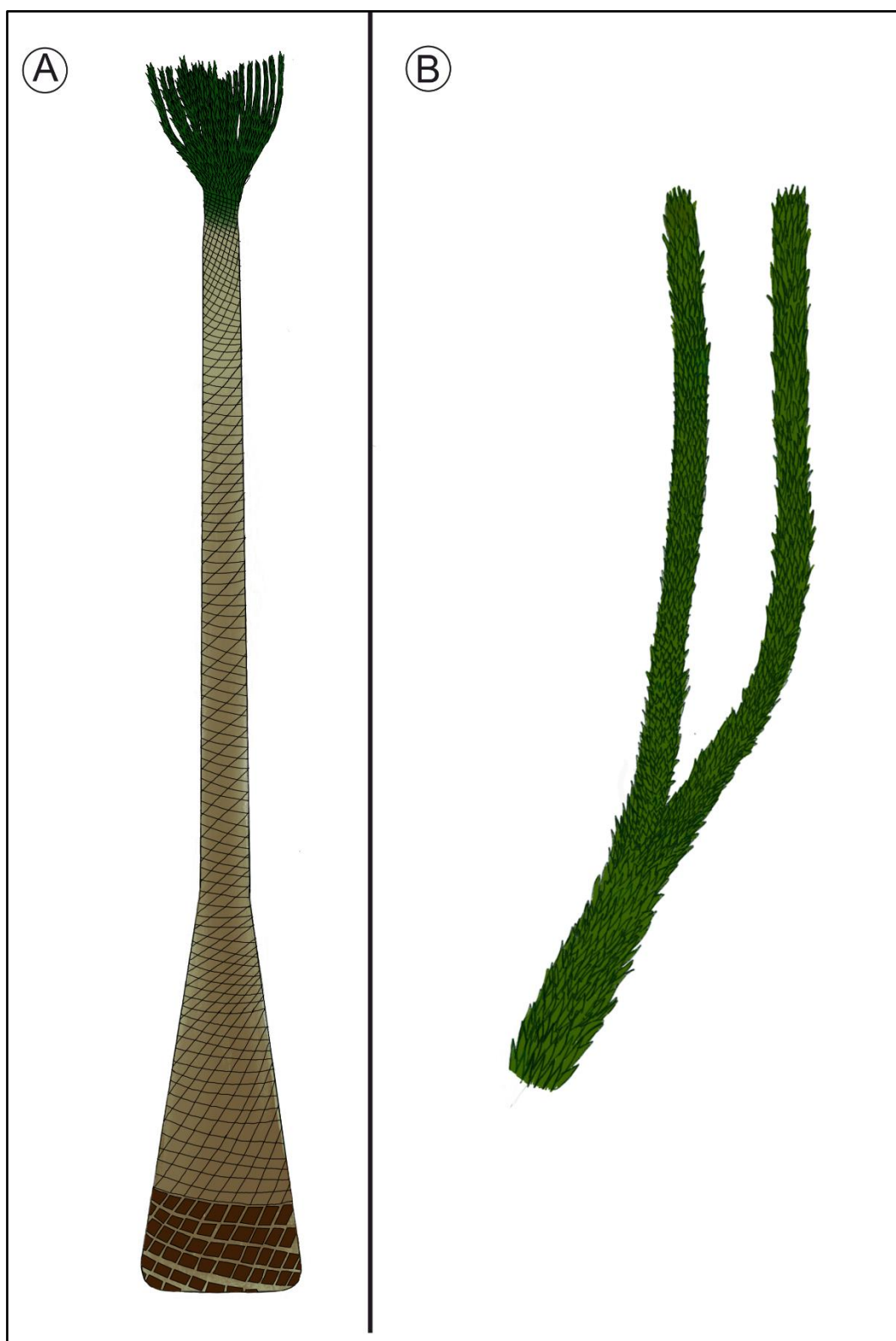
Leaves Associated with the Distal Crown

A small number of specimens preserve leaves, including those described by Høeg (1942; Plate LII, Fig. 8; Plate LV, Figs 9–12; Plate LVI, Figs 1–6) and Schweitzer (1968, Fig. 13; 1999, Fig. 28), as well as additional material collected by Berry.

When present, leaves are borne on small axis fragments either found in isolation or associated with the terminal crown region of the tree. In the large crown specimen, foliage is only observed beyond the first and possibly the second visible bifurcation point (Plate 43A–C). Leaves emerge at a near-perpendicular angle to the growth direction of the supporting axis (Text Figure 74). Leaf blades average 3 mm in length, with a range of 2–4 mm. The average basal width is 1 mm, ranging from 0.9 to 1.4 mm. The distal tips of the leaves frequently curve upwards, orienting in the direction of axis growth.



Text Figure 74. Leaf blades preserved on a small distal axis of *P. pulchra*, likely representing the distal portion of a crown (see Plate 14D–E). A. Photograph of three leaf blades. B. Interpretative line drawing of leaf blades. C. Reconstruction of leaf blades. Scale bar = 10 mm.



Text Figure 75. A Reconstruction of *Protolpidodendropsis pulchra*. A. Whole-tree reconstruction showing overall habit and scale. B. Reconstruction of a pair of distal axes illustrating branching pattern and leaf arrangement.

Discussion

1. Summary and Reconstruction

The new material of *Protolepidodendropsis pulchra* described in this chapter provides evidence to reconstruct the morphology of an early arborescent lycopsid from the rooting structures to the distal crown. Although the absence of internal anatomy and fertile organs limits full interpretation, the preservation of a complete crown, substantial portions of trunks and well-defined bases offers a rare insight into the growth form and architecture of one of the earliest tree-sized lycopsids. *P. pulchra* is one of the few Devonian arborescent lycopsids for which a near-complete morphological reconstruction can be achieved, allowing direct comparison with contemporaneous taxa from Euramerica and South China, as well as with later Carboniferous forms. As for *Archaeopteris*, fossils conforming to the trunk and branches have been found at all fossiliferous levels within the Mimerdalen Subgroup, from the Estheriahaugen Member to the Planetkløfta Formation (Text Figure 54).

The Svalbard material indicates that *P. pulchra* was a small tree, the overall architecture comprised three main elements: a cormose rooting base, a straight columnar trunk and an isotomously branched crown, an organisation typical of the earliest arborescent lycopsids. The trunk was narrow and gradually tapered upwards, with helically arranged rhombic leaf cushions following Fibonacci phyllotaxis where known. The base was cormose and preserved *in situ* in some specimens showing small dichotomising rootlets. The crown divided isotomously several times. The first few dichotomies were close together, with greater spacing distally and the overall crown architecture formed a stiff vertical crown. No evidence of pseudomonopodial differentiation is present, suggesting an entirely dichotomous growth habit.

The absence of evidence of extensive secondary thickening indicates that mechanical support was likely provided largely by cortical tissues rather than secondary xylem, consistent with the “peridermal support” model proposed for later lycopsids (Thomas, 2018). The reconstruction in Text Figure 75 illustrates this compact, pole-like growth form, representing one of the earliest expressions of the arborescent lycopsid body plan (see Hueber, 1992; Wang et al., 2005, for architectural terminology).

2. Comparisons

***Longostachys latisporophyllus* (Text Figure 21D)**

Longostachys latisporophyllus from the Givetian of South China represents one of the earliest bipolar lycopsids to be described in detail (Cai & Chen, 1996). The fossils are dominated by fragmentary material, comprising only eight partially complete stems and few specimens showing clear dichotomous branching. Reconstruction indicates a relatively small, heterosporous tree lycopsid reaching heights of up to ~1.5 m. The most complete trunk measures 70 cm in length and 2 cm in preserved width, with the largest basal fragments up to 3.5 cm in diameter.

Only a few bifurcating axes are known for *L. latisporophyllus*, attributed to ultimate or distal crown branches. These resemble some of the fragmentary distal axes and perhaps equivalent to the second bifurcation within the *P. pulchra* crown. In both taxa, there is a morphological shift in leaf cushion shape around where the trunk bifurcates into the crown. In *L. latisporophyllus*, the cushions become broader and shorter. Fertile structures are presently unknown for *P. pulchra*, preventing direct comparison with the well-preserved cones of *L. latisporophyllus*.

The roots of *L. latisporophyllus* are well documented and preserved with attached trunks (Text Figure 21). There is variability in diameter and branching complexity in *L. latisporophyllus* roots, which could be a result of differing ontogenetic stages or represent intraspecific variation within the species, with mature individuals developing a funnel-shaped, dichotomising system. The largest reach 3.5 cm in diameter, producing two or three primary roots from the base that dichotomise two to three times within a short distance (1–2.5 cm). Following the terminology of Hetherington and Dolan (2017), these dichotomising structures may be comparable to the rooting structures associated with *P. pulchra*, although the taxon lacks the swollen cormose basal region seen in the Svalbard material.

***Chamaedendron multisporangiatum* (Text Figure 75E)**

Chamaedendron multisporangiatum from the Frasnian of South China represents another distinct experiment in bipolar lycopsid architecture (Schweitzer & Li, 1996a). At only ~50 cm tall and with a trunk diameter of 7 mm, it was far smaller than either *P. pulchra* or *L. latisporophyllus*, yet it developed an upright stem, a crown with at

least four bifurcations and dichotomous roots lacking an expanded base. For such a diminutive plant, this produced a surprisingly complex, bushy canopy less than half a metre high.

Beyond its overall form, *Chamaedendron* is notable for its reproductive structures. Leaves were borne in pseudoverticillate parastichies along repeatedly dichotomising axes, with fertile regions distributed across the branches rather than condensed into strobili according to Schweitzer & Li (1996). Each sporophyll carried multiple sporangia (4–6 megasporangia or up to 12 microsporangia) according to the authors, which are widely considered to actually be megaspores.

Anatomically, *Chamaedendron* possessed a simple protostelic xylem with exarch maturation and no secondary tissues, consistent with its small size and limited stature.

***Lepidosigillaria primaeva* (the Naples Tree) (Text Figure 21B)**

The Naples Tree from the Frasnian of New York represents one of the earliest large arborescent lycopsids, with a preserved trunk over 3.25 m long and an estimated unbranched height of at least 5 m based on field evidence (White, 1905; Grierson & Banks, 1963). Its base was cormose, reaching ~38.5 cm in width before tapering to 12 cm at the preserved top of the base, a growth strategy comparable with the cormose base of *P. pulchra*. Both trees also had ribbon-like rooting structures.

The surface of the Naples Tree varied considerably along its length. At the base, leaf cushions were widely spaced and arranged in vertical rows on longitudinal ribs, producing a sigillarioid appearance. Cushion separation has been associated with secondary growth and is broadly comparable to the wider spacing seen in parts of *P. pulchra*. However, as with the Svalbard material, some variation in cushion shape and spacing may also reflect different levels of decortication, with specimens preserving either the outer leaf-cushion-bearing surface or deeper cortical levels associated with the leaf-base region. Above the base, development between the two trees diverges: in the Naples Tree, cushions become progressively elongated and spirally arranged up the trunk, passing through Knorria-type decortication into lepidodendroid forms that combine features of *Sigillaria* and *Lepidodendron*. In contrast, *P. pulchra* retains rhombic cushions along the trunk, with fusiform forms

appearing only near the first bifurcation of the trunk, a region which is not preserved in the Naples specimen. This comparison therefore supports morphological similarity between the two taxa, but cushion-shape variation should not be interpreted solely as developmental because taphonomic and decortication-related effects may also contribute.

The leaf cushions of the Naples Tree were obovate and bore ligular pits with vertically elongate parichnia, features that link it to *Bothrodendron* and early sigillarioid forms (White, 1905; Phillips & DiMichele, 1992). Small, persistent leaves were retained down to approximately 70 cm above the base of the trunk. This extended foliage likely increased the photosynthetic surface area along the stem. In contrast, *Protolapidodendropsis pulchra* concentrated photosynthesis within its broad, fan-shaped crown at maturity, although the leaf cushions along the trunk may also have retained photosynthetic function whilst the tree grew. *L. primaeva* represents a parallel experiment in Devonian lycopsid morphology, similar in basal construction yet distinct in leaf base morphology.

Leptophloeum rhombicum (Text Figure 76C)

New material of *Leptophloeum rhombicum* from the Famennian of South Africa reveals a simpler rhizomorphic organisation than previously recognised (Prestianni & Gess, 2014). The specimens comprise straight stems bearing contiguous rhombic leaf bases and an unlobed, slightly flared cormose base with circular rootlet scars and a short, smooth transition to the leafy axis. The base is only marginally wider than the stem and lacks any sign of distinctive lobing or a fully developed stigmarian system. Although the crown remains unknown, the preserved morphology indicates a small tree with limited differentiation between base and stem. This configuration reflects an early, less integrated stage of rhizomorphic development among Late Devonian lycopsids.

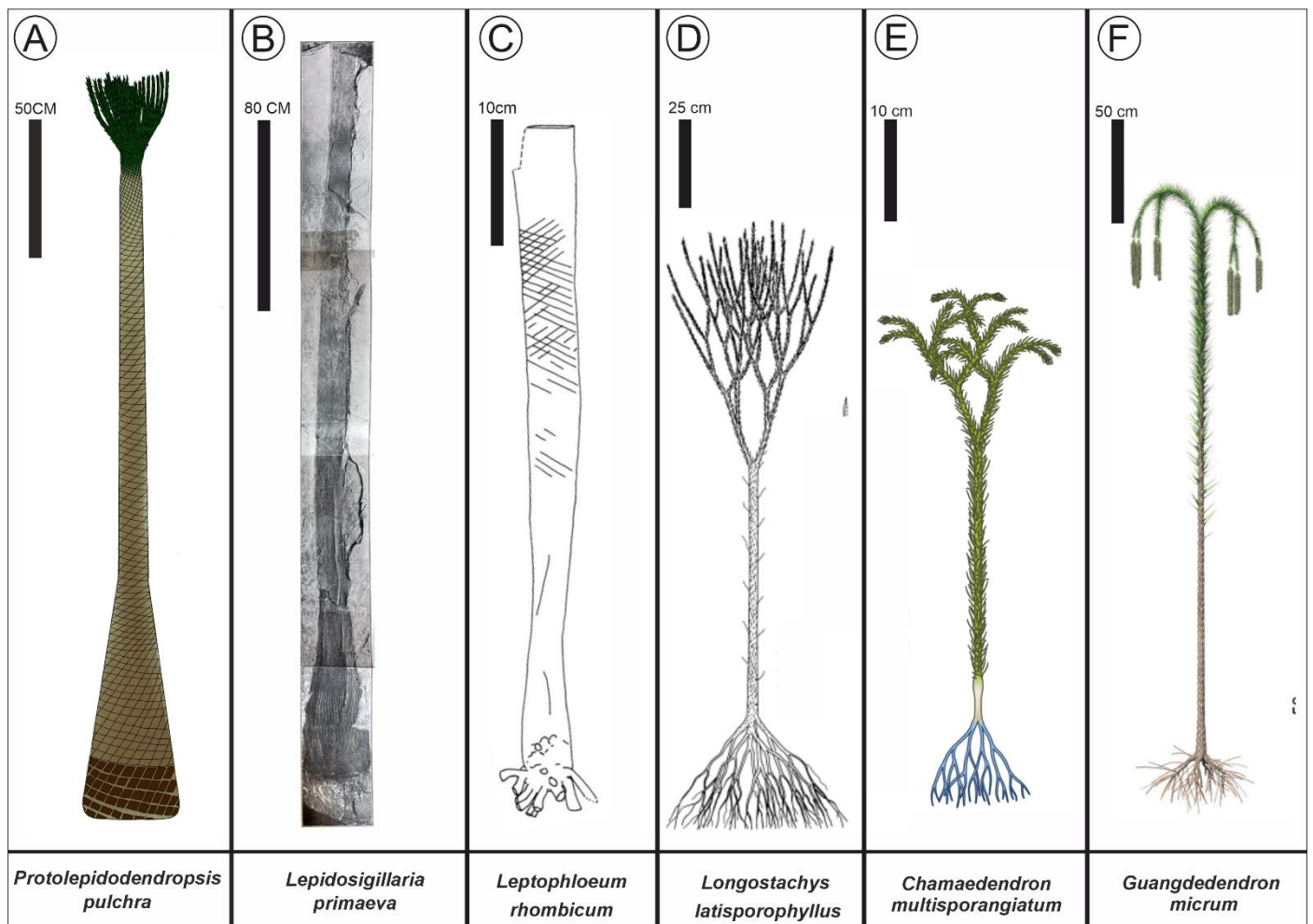
Guangdedendron micrum (Text Figure 76F)

Guangdedendron micrum is a Late Devonian bipolar lycopsid from the Famennian of South China and represents one of the most complete examples of a small Devonian tree lycopsid known to date. The reconstruction presented by Gao *et al.* (2022) combines a well-developed stigmarian rooting system, a straight trunk and a fertile crown which together illustrate the emerging characteristics of the isoetalean body

plan. This refers to the fully integrated tree architecture typical of Late Devonian and Carboniferous arborescent lycopsids, in which a stigmarian rooting system, determinate trunk and reproductive crown are organised around a dominant central axis. *G. micrum* displays one of the earliest expressions of this configuration, whereas *P. pulchra* retains a simpler organisation that precedes this integrated form.

The well-developed stigmarian-type rhizomorph was composed of four primary axes that dichotomised, with helically arranged roots. This configuration produced a stable, radiating root system similar in organisation to that of Carboniferous *Lepidodendron* but appearing at least 10 million years earlier. The trunk of *G. micrum* was covered with narrow fusiform leaf cushions bearing the distinctive features of a well-advanced lycopsid: prominent leaf scars, ligular pits and vertically elongate parichnos grooves (Gao *et al.*, 2022). These cushions exhibit a degree of cortical differentiation and vascular specialisation not seen in the stem of *P. pulchra*, where the rhombic cushions remain relatively uniform and simple along the trunk until the first dichotomy into the crown, where they become fusiform. The regular alignment of cushions and the presence of pronounced parichnos grooves in *G. micrum* indicate a higher level of tissue organisation, implying an increased separation between photosynthetic and mechanical functions within the stem. This structural differentiation likely reflects the development of a more robust, mechanically supported and physiologically integrated trunk, a crucial step toward the coordinated hydraulic and mechanical systems characteristic of Carboniferous tree lycopsids (Bateman, 1994; Phillips & DiMichele, 1992; Boyce & DiMichele, 2016; Hetherington & Dolan, 2016).

At the crown, *G. micrum* displays a dichotomous branching pattern with terminal, pendulous monosporangiate strobili borne singly or in pairs (Gao *et al.*, 2022). These large reproductive organs provide rare evidence for fertile crown organisation among Late Devonian tree lycopsids, marking a clear step toward the more extensively reproductive crowns characteristic of giant Carboniferous forms.



Text Figure 76. Comparative growth forms of Middle–Late Devonian arborescent lycopsids. A. *Protolapidodendropsis pulchra* — reconstruction showing full tree habit, based on material from Plantekløfta and Munindalen, Svalbard (Berry & Marshall, 2015). B. *Lepidosigillaria primaeva* — trunk specimen with rhombic leaf cushions (White, 1905). C. *Leptophloeum rhombicum* — reconstruction illustrating slender trunk and rhizomorphic base (Prestiani & Gess, 2020). D. *Longostachys latisporophyllus* — reconstruction showing branching habit and terminal strobili (Cai & Chen, 1996). E. *Chamaedendron multisporangiatum* — reconstruction showing dichotomous crown and basal rooting system (Schweitzer & Li, 1996; Hetherington & Dolan, 2016). F. *Guangdedendron micrum* — reconstruction of small tree form with stigmarian rhizomorph (Wang et al., 2019). Scale bars as indicated.

3. Development of the base and trunk

Leaf cushions on the base

In this section, the term leaf cushion is used for the persistent, rhombic to fusiform raised or impressed areas on the stem surface that mark the position of former leaves. These structures are interpreted as leaf cushions because they are repeated, helically arranged, have a consistent rhombic outline and occur as discrete surface units rather than as isolated leaf scars. The term leaf base is used more generally for the leaf-bearing region, including the cushion and any associated internal tissues, such as parenchymatous or sediment-filled areas. Therefore, “leaf cushion” refers specifically to the external morphological unit, whereas “leaf base” is used only where the broader leaf-bearing structure or internal tissue region is being discussed.

In *Protolpidodendropsis pulchra*, both bases and trunks preserve helically arranged leaf cushions that reflect the organisation of the shoot apex at the time the leaves were initiated. Because leaf cushions are produced during apical growth, their arrangement provides useful information about phyllotaxis and relative changes in stem expansion. However, cushion size and spacing cannot be treated as a simple direct record of apical activity, because they may also have been modified by secondary growth, decortication, compaction and differential preservation. The interpretations below therefore treat leaf-cushion dimensions as an approximate developmental signal, rather than as a direct measurement of apex size.

In other arborescent lycopsids, changes in cushion dimensions along the trunk have been linked to changes in apical organisation and radial growth. In *Leptophloeum rhombicum*, for example, variation in cushion dimensions has been interpreted as reflecting progressive widening and contraction of the apical dome during determinate growth (Wang et al., 2005), while Carboniferous taxa such as *Lepidodendron* and *Lepidophloios* preserve helically arranged cushions that have been used to infer aspects of apex geometry and growth history (Phillips & DiMichele, 1992; Boyce & DiMichele, 2016). These comparisons provide a useful framework for interpreting *P. pulchra*, but the Svalbard material must also be considered in light of taphonomic alteration and possible preservation at different cortical levels.

The cormose bases (Plate 29) are swollen, measuring up to 226 mm across at the basal surface and tapering to 182 mm at 250 mm height. Four key observations were made:

1. The leaf cushions on the base are smaller than expected given that the base is the widest part of the plant (Text Figure 62).
2. Leaf-cushion size appears to increase from the lower part of the base to the upper part (Table 17).
3. The distance between leaf cushions decreases from the lower part of the base to the upper part (Text Figure 57B).
4. The phyllotaxis of the base appears to remain constant despite the upward narrowing of the base (Text Figure 57A).

Taking these observations into account, leaf-cushion size may provide an approximate indication of the size and organisation of the apex at the time of leaf initiation, but it cannot be used as a direct proxy for apex size without qualification. Apparent cushion dimensions may also have been affected by decortication, compaction and the level of cortex preserved. Similarly, spacing between leaf cushions may reflect a combination of primary spacing at initiation and later modification by radial expansion or limited secondary growth. Wider spacing near the lower part of the base may therefore indicate some basal expansion after cushion initiation, but it may also have been enhanced by compression or distortion of the cormose base. This interpretation is consistent with the expected developmental position of secondary tissues in arborescent lycopsids. Secondary or reinforcing tissues would have developed behind the actively growing apex, meaning that older, lower regions of the plant would have had more time to undergo radial expansion than younger, more apical regions. Greater spacing between cushions near the lower part of the base may therefore reflect post-initiation expansion of the stem surface after the cushions had formed, whereas the more closely packed cushions higher on the base and trunk may indicate less subsequent radial expansion.

Leaf cushions are rhombic impressions 4–7 × 5–9 mm in size, arranged in helices spaced approximately 6 mm apart near the lower part of the base and narrowing to 2 mm toward the upper part. The number of helices appears to remain constant,

suggesting that the broad phyllotactic pattern was maintained as the base narrowed upwards. This pattern is consistent with early basal expansion and limited secondary thickening concentrated toward the lower part of the base. However, because the base is compressed and may preserve different cortical levels, the preserved cushion size and spacing should be interpreted as evidence for relative growth pattern rather than a precise reconstruction of apical geometry.

Comparable patterns are seen in *Leptophloeum rhombicum*, where leaf cushions increase in size upward and secondary thickening was interpreted as being limited to the lower stem (Wang et al., 2005). This suggests that *P. pulchra* may have followed a broadly similar developmental strategy, combining early apical widening with basal reinforcement. However, in contrast to *Leptophloeum*, which developed a more differentiated cormose rhizomorph, *P. pulchra* retained a leaf-bearing basal swelling from which fine ribbon-like rooting structures extended. This morphology may represent a less integrated form of rhizomorphic organisation and could capture an earlier stage in the structural evolution of the arborescent lycopsid body plan.

The combination of apparently smaller, more widely spaced cushions at the base and larger, more closely packed cushions above is consistent with early basal expansion followed by more uniform axial growth. However, this pattern may also have been influenced by secondary thickening, decortication and compaction of the expanded base. The interpretation of early apical enlargement and localised basal reinforcement is therefore proposed cautiously, rather than treated as a direct developmental sequence.

A comparable organisation is seen in the Naples tree (*Lepidosigillaria primaeva*; White, 1905), where the lower cortex is distended and the original rows of cushions are stretched apart during basal enlargement, while the phyllotactic order is retained. As in *P. pulchra*, cushion spacing appears to contract upward as growth becomes more axial. However, in both taxa, some variation in cushion shape and spacing may reflect different levels of decortication as well as biological growth. The transition from separated to more contiguous helices is therefore interpreted as evidence for changing growth conditions along the base and lower trunk, but not as a precise marker of the point at which radial expansion ceased.

Leaf Cushions on the Trunk

The trunks of *Protolepidodendropsis pulchra* are slender and straight, tapering from 75 mm above the base to approximately 50 mm upward and bear helically arranged rhombic leaf cushions that continue the pattern established on the cormose base. Cushions are well defined, measuring 5–8 mm in width and 7–10 mm in height, with their long axes inclined slightly upward. They are contiguous along the trunk surface, forming continuous, evenly spaced helices without visible gaps between rows. Phyllotactic analysis indicates stable patterns of 21:13, corresponding to Fibonacci spirals, with 21 counter-clockwise and 13 clockwise helices.

Phyllotactic analysis of *P. pulchra* therefore provides the earliest evidence for a stable Fibonacci pattern in a tree-sized Lycopsid and demonstrates a highly regulated apical meristem. Similar regular phyllotactic systems have been described in *Leptophloeum rhombicum* (Wang et al., 2005) and Carboniferous forms such as *Lepidodendron* and *Lepidophloios* (Phillips & DiMichele, 1992; Boyce & DiMichele, 2016), where cushion arrangement directly reflects the geometry and stability of the apical dome. This consistency across the trunk of *P. pulchra* confirms that phyllotaxy was tightly controlled and maintained throughout growth, in accordance with the pole-like, determinate growth model characteristic of arborescent lycopsids (Thomas, 2018).

The regular 21:13 spirals contrast sharply with the non-Fibonacci series (7:8, 8:9) described in the Early Devonian *Asteroxylon mackiei* (Turner et al., 2023), where leaf initiation was developmentally flexible and often shifted between whorled and spiral arrangements. The presence of a true Fibonacci pattern in *P. pulchra* indicates a more stable and centrally organised apical meristem, reflecting a higher level of developmental regulation than that seen in early herbaceous forms. This transition from variable to fixed phyllotaxis marks a key stage in the evolution of lycopsid shoot architecture, corresponding with the establishment of determinate, pole-like growth.

Comparable patterns occur in other Devonian arborescent lycopsids. *Leptophloeum rhombicum* displays similarly regular rhombic cushions arranged in close helices, decreasing in size upward along a tapering trunk, with secondary cortex restricted to the basal few centimetres (Wang et al., 2005). *Chamaedendron* (Schweitzer, 1996) exhibits continuous vertical cushion rows that taper gradually toward the crown,

while *Guangdedendron micrum* (Gao et al., 2022) and *Omprelostrobus gigas* (Liu et al., 2022) show more advanced differentiation between trunk and rhizomorph. Within this evolutionary continuum, *P. pulchra* represents an earlier, simpler stage of trunk organisation: a uniformly leafed, narrow stem produced by a single phase of primary apical growth. Its consistent Fibonacci phyllotactic ratios and the regularity of cushion insertion reflect a highly stable apical meristem, preserving the developmental precision characteristic of determinate, pole-like growth in early arborescent lycopsids.

Transition from Trunk to Crown

Toward the upper part of the trunk, *Protolapidodendropsis pulchra* narrows gradually and the leaf cushions become smaller and more closely spaced before the first dichotomy. Phyllotaxy remains consistent through this zone, with helices continuing uninterrupted from the trunk into each daughter axis, indicating that both axes were derived from a single apical meristem. The reduction in cushion size and spacing reflects apical tapering as elongation slowed before division, consistent with determinate growth terminating in isotomous branching.

In one specimen (Text Figure 63D₂; Plate 35A-C), an additional set of small leaf bases occurs immediately below the point of dichotomy, forming a narrow band of closely packed cushions that overlie the regular trunk pattern. These bases appear to have been inserted late in development, representing a short phase of increased leaf initiation as the apical dome widened prior to splitting. Additional support for this interpretation comes from the material originally described by Schweitzer (1965) under *Bergeria mimerensis* and *P. pulchra*, which includes the same specimen. His figures show a clear reduction in cushion size and relief toward the upper part of the trunk, from c. 10 mm wide in the lower regions to <4 mm near the dichotomy, followed by elongate orthostichous scars on the distal axes (Schweitzer, 1965, Taf. 37 Fig. 1–2). Schweitzer interpreted this as the onset of cushion development restricted to the upper trunk, but re-examination of the same specimen demonstrates that it records the opposite process: progressive contraction and loss of cushions as the apex narrowed and reorganised before division. The narrow zone of densely inserted cushions beneath the fork therefore represents a transient phase of

intensified apical activity, marking the final stage of elongation immediately prior to dichotomy.

The isotomous nature of the first dichotomy also distinguishes *P. pulchra* from some other Devonian arborescent lycopsids such as *Longostachys*, where anisotomous division produced more hierarchically ordered axes (Cai and Chen, 1996). However, isotomous dichotomies are also known in material attributed to *Lepidodendropsis* by Gensel and Pigg (2010), although that material bears ligules and may require taxonomic revision. For this reason, *Lepidodendropsis* is treated here cautiously as a broad comparative form rather than as a tightly defined architectural model. The branching in *P. pulchra* therefore appears to retain a simple pattern of broadly equal apical division, consistent with the symmetrical organisation of some early arborescent lycopsids, but it should not be assumed to represent the only primitive condition among Devonian tree lycopsids.

Crown Organisation

The crown specimen (Plate 38) represents an unusually complete crown of a Devonian lycopsid and provides rare evidence for the distal architecture of *Protolepidodendropsis pulchra*. It records a compact series of closely spaced dichotomies: the first four occur within ~10 cm of vertical height, and the crown extends ~38 cm from the first fork to the distal tips. Counterparts preserve axes on multiple depth planes, indicating that the crown was three-dimensional and tiered rather than planar, although the major basal dichotomy appears to have had the strongest influence on the overall architecture. Distal axes emerge from successive forks and gently recurve upward. This recurvature may reflect re-orientation of axes to maintain upward growth within a densely branched crown, although compaction and the original three-dimensional position of the branches may also have influenced their preserved orientation.

The younger Plantekløfta specimen (Plate 43A) preserves a single dichotomy followed by a 13 cm undivided axis before termination, suggesting longer internodes and a more elongate distal crown than the Estheriahaugen material. Separated by ~3–4 Myr, these differences may reflect several possible factors, including ontogenetic stage, ecological conditions, preservation, specimen position within the crown or evolutionary change through time. Schweitzer's second specimen (Plate 37C, D) also suggests that not all crowns had such closely spaced basal branching. Crown size and branching density may therefore have varied between individuals or through development.

The overall crown architecture is best described as a repeatedly dichotomising system in which the visible divisions are broadly isotomous. However, the branching pattern should not be described as invariant. Some axes are incomplete, overlapping or preserved on different bedding planes, and compression may obscure the original three-dimensional angle between successive dichotomies. Phyllotactic order appears to be maintained across the forks where preservation allows this to be assessed, but the exact regularity of the branching system remains uncertain.

Variation in leaf-cushion morphology along crown axes should also be interpreted cautiously. In material described by Gensel and Pigg (2010), attributed to *Lepidodendropsis*, leaf-base morphology varied along individual crown stems and was interpreted as potentially reflecting different levels of decortication and/or regions bearing sporophylls. That material bears ligules and may require taxonomic revision, so *Lepidodendropsis* is treated here cautiously as a broad comparative form rather than as a secure architectural model. A similar range of possibilities may apply to *P. pulchra*: changes in cushion shape near dichotomies may reflect developmental change, but they could also indicate decortication, preservation at different cortical levels or, more speculatively, a change in appendage type. Because no reproductive structures are preserved in the Svalbard material, any interpretation involving sporophyll-bearing regions remains speculative.

The isotomous crown provides the key to interpreting developmental transitions across the whole plant. Equal apical bifurcation is interpreted here as a late stage in aerial growth, marking the transition from an unbranched trunk to a compact crown. However, because no reproductive structures are preserved, this bifurcation cannot be used as direct evidence for reproductive maturity. It is possible that the plant had

formed a crown but was killed before becoming reproductive, or that reproductive structures were not preserved. The compact, vertically tiered crown geometry may have minimised lateral interference among neighbouring individuals and is consistent with growth in dense stands such as those preserved in the Plantekløfta forest.

4. Developmental Model

Integrating morphological evidence from the base, trunk and crown allows a reconstruction of *P. pulchra*'s growth history, summarised in a four-phase developmental model. This framework brings together the observed changes in cushion size, spacing and phyllotaxy to describe the progressive widening, elongation and eventual bifurcation of the axis during growth. Because no fertile organs are preserved, the model reconstructs vegetative architecture and crown formation rather than reproductive maturity.

Establishment Phase – Growth began from a small apical dome that produced small, tightly packed leaf cushions at the lowermost base, marking the onset of primary tissue development.

Basal Expansion Phase – As growth continued, the apical dome widened, forming progressively larger cushions while the number of helices remained constant.

Trunk Phase – Growth became primarily axial. The stem tapered upward as cushion size decreased distally and the phyllotactic pattern remained stable except close to the first dichotomy (Text Figures 63D₂, 64). This phase represents the establishment of the photosynthetic and structural column that formed the main support of the plant. Localised expansion at the base increased the spacing between cushion rows/helices (from ~2 to 6 mm; Text Figure 57), producing the distinctive swollen cormose morphology.

Crown Differentiation Phase – The apical meristem divided isotomously to produce a compact, equal-forked erect crown of reducing-diameter axes. This marks the transition from trunk elongation to crown formation, but not necessarily the onset of reproduction. The absence of clear apical dominance and the symmetrical branching pattern suggest a determinate or near-determinate crown architecture. However, because no strobili, sporophylls or fertile zones are preserved, the timing and organisation of reproductive development remain unknown.

Together, these four phases trace the ontogenetic progression from basal expansion to reproductive termination in *P. pulchra*. The isotomous crown represents the culmination of the developmental programme initiated at the base, providing a complete whole-plant model that links morphological patterning to the emergence of determinate arborescence in early lycopsids.

In evolutionary context, *Protolepidodendropsis pulchra* occupies a position between earlier, herbaceous lycopsids such as *Asteroxylon mackiei* from the Early Devonian Rhynie Chert, and the more fully rhizomorphic arborescent lycopsids of the Late Devonian and Carboniferous, such as *Leptophloeum rhombicum* and *Guangdedendron micrum*. Its determinate, pole-like body plan and limited secondary reinforcement record an early stage in the development of the lycopsid tree habit. In this sense, *P. pulchra* shows how increased stature could be achieved through a combination of controlled apical growth, a swollen basal rooting organ and cortical support, rather than through extensive secondary thickening.

5. Evolutionary and Ecological Significance

Table 19 summarises the principal characteristics of early bipolar and arborescent lycopsids. The earliest forms, such as *Longostachys* (Givetian, China) and *Chamaedendron* (Frasnian), possess dichotomous roots arising from a non-expanded base that mirrors the apical, dichotomously branched crown. Both are small in stature and represent the most primitive expression of the tree habit.

Protolepidodendropsis pulchra (Late Givetian–Early Frasnian) exhibits a more advanced morphology, with a distinctly expanded cormose base bearing fine ribbon-like roots and an erect, strictly dichotomous crown. This configuration produced a larger mechanically stable tree. Comparable but larger forms include the “Naples Tree” (Frasnian; White, 1905) and *Leptophloeum rhombicum*, which share a similar combination of expanded base and rhombic leaf-cushion morphology, though their crowns remain unknown.

Clevelandodendron (Chitaley & Pigg, 1996), a small bisporangiate form approximately 1.25 m tall, bears few basal roots and a single terminal cone, representing a diminutive but fully organised miniature tree lycopsid. By the Late

Famennian, *Guangdedendron micrum* had evolved roots attached to a branching stigmarian rhizomorph and a sparsely branched crown, although it remained relatively small. Larger rhizomorphic lycopsids such as *Jurinadendron* and *Cyclostigma* (Schweitzer, 2006) are known from Bear Island and Ireland, but their crowns have not been fully reconstructed.

Intermediate taxa with lobed cormose rhizomorphs, such as *Otzinachsonia beerboweri* (Cressler & Pfefferkorn, 2005), further document the gradual elaboration of the rooting system between simple cormose and fully stigmarian architectures. *P. pulchra* thus represents the first known successful attainment of large size among lycopsids, depicting a structurally effective yet transitional body plan that prefigured but did not ultimately define, the dominant architectures of Carboniferous tree forms.

Ecological Implications and Conclusions

The occurrence of *Protolepidodendropsis pulchra* in closely spaced stands within the Plantekløfta Formation is supported by previous work on the AF1–AF3 forest localities (Berry & Marshall, 2015) and by new field evidence from AF22B. At AF22B, photogrammetric mapping of the forest surface recorded at least seventeen small arborescent lycopsid stems assigned to *P. pulchra*, with cormose bases touching or overlapping around an upright *Archaeopteris* trunk (Text Figure 77A). This spatial arrangement supports the interpretation that *P. pulchra* formed dense local colonies on the floodplain. Its cormose basal region and shallow, ribbon-like rootlets probably provided anchorage in soft substrates and contributed to local sediment stabilisation, in a manner comparable to later rhizomorphic lycopsids (Hetherington & Dolan, 2017). The absence of deep, vertically penetrating roots suggests that *P. pulchra* occupied periodically saturated palaeosols, forming wetland communities along basin margins where flooding and sediment influx may have created repeated opportunities for colonisation.

The determinate, pole-like growth habit suggests a relatively short life cycle characterised by rapid vertical growth followed by crown formation and probable reproduction. This growth pattern may have allowed *P. pulchra* to colonise disturbed floodplain surfaces repeatedly after flooding or sediment influx. In this respect, *P. pulchra* represents an early example of arborescent lycopsid organisation, combining a swollen basal rooting organ, shallow ribbon-like rootlets, a slender upright trunk

and a determinate crown. These features show how early lycopsids contributed to sediment stabilisation and the development of vegetated floodplain surfaces before the more fully integrated rhizomorphic trees of the later Devonian and Carboniferous.

At this evolutionary threshold, *P. pulchra* represents an early experiment in controlled arborescent growth, anticipating the fully integrated rhizomorphic trees of the Famennian and Carboniferous. It can therefore be viewed as a pioneer arborescent lycopsid whose brief, coordinated growth cycle transformed unstable floodplains into the first stable forested landscapes. The Svalbard material thus records not merely an early tree, but a crucial moment when plants first began to engineer the environments (Davies *et al.*, 2021) that would, in turn, shape their own evolutionary trajectory.

Table 19. Summary of key morphological and developmental characteristics of representative Devonian tree lycopsids arranged in approximate chronological order. The table compares principal differences in overall height, rooting systems, trunk form, leaf-cushion morphology, crown organisation, fertile structures, and developmental mode, illustrating the progressive diversification of arborescent architecture through the Middle and Late Devonian. Data compiled from published descriptions and this study.

Feature	<i>Longostachys latisporophyllus</i>	<i>Protolepidodendropsis pulchra</i>	<i>Chamaedendron multisporangiatum</i>	<i>Lepidosigillaria primaeva</i>	<i>Leptophloeum rhombicum</i>	<i>Guangdedendron micrum</i>
Age / Stage	Givetian	Late Givetian – early Frasnian	Frasnian	Frasnian	Frasnian– Famennian	Famennian
Overall height (approx.)	~1–1.5 m	~2–3 m	< 0.5 m	≥ 5 m	> 10 m	up to ~7 m
Rooting system	Rhizomatous base with short dichotomous roots	Cormose, leaf-bearing base with fine ribbon-like roots	Short, dichotomous roots	Cormose base with broad ribbon roots and umbilicoid scars	True stigmarian rhizomorph with helically arranged rootlets	Four-armed stigmarian rhizomorph with rootlets
Trunk	Thin (2–3.5 cm); little taper	Straight, slender (5–8 cm); slight taper	Very slender (~7 mm); little taper	Thick (12–38 cm); tapered base	Tall, cylindrical; robust	Tall, narrow, strongly differentiated cortex
Leaf cushions	Rhombic, becoming broader distally	Rhombic on trunk; fusiform in crown	Very small, rhombic, closely spaced	Sigillarioid ribs becoming lepidodendroid upward	Rhombic, spirally arranged, decreasing distally	Narrow fusiform with ligular pit and parichnos grooves
Crown organisation	Dichotomous; few examples preserved	Compact, strictly isotomous; 6–8 dichotomies	Highly branched isotomous crown (≥ 4 bifurcations)	Probably isotomous; crown incomplete	Pseudomonopodial (dominant central axis)	Hierarchical dichotomy with terminal strobili
Fertile structures	Heterosporous strobili present	Not preserved (vegetative only)	Fertile branches bearing 4–6 megasporangia or ≤12 microsporangia per sporophyll	Not preserved	Cones terminal on branches	Monosporangiate strobili singly or in pairs
Developmental mode	Primary apical growth; no secondary thickening	Determinate, single-phase growth; stable apical control	Primary apical growth; determinate, herbaceous- to-tree intermediate	Determinate; early cortical differentiation	Determinate, pseudomonopodial; integrated growth	Determinate; modular with integrated reproductive phase
Evolutionary significance	First small tree-form lycopsid	Earliest simple tree; developmental canalisation	Miniaturised arborescence; isotomous complexity	Transitional; larger, more complex base	Intermediate cormose stage in rhizomorphic evolution.	Near-Carboniferous isoetalean plan

Devonian Forest Assemblages: New Evidence on Devonian Forest Ecology

The Middle to Late Devonian marks one of the most pivotal intervals in Earth's history, the time when forests first appeared. Plants developed increasingly complex body plans that transformed the land surface and began to influence the atmosphere and water cycle. Although rare in the fossil record, these early forests offer a glimpse into a stage of Earth's evolution when vegetation began to shape its own environment (Davies *et al.*, 2021). Their rooting systems bound and stabilised floodplains, enhanced chemical weathering and promoted carbon burial, driving large-scale changes in climate and surface processes.

Early forested landscapes were far from uniform. The oldest known forest, at Porlock England, of Eifelian age, contains only the bases of small cladoxylopsid plants (Davies *et al.*, 2024). The Mid Givetian forest of Gilboa, New York, preserves an assemblage dominated by large cladoxylopsid trees (*Eospermatopteris* with *Wattieza*-type fronds) with an understorey of aneurophyte progymnosperms and rare arborescent lycopsids (Stein *et al.* 2012). These trees formed a low, closed canopy with shallow radiating root systems that spread laterally just beneath the surface of the grey, organic-rich sandstone, showing growth in periodically flooded deltaic environments subject to short-lived colonisation events.

At the slightly younger Cairo quarry in New York, *in-situ* rooting systems of woody *Archaeopteris* occur together with cladoxylopsid and perhaps a lycopsid (Stein *et al.*, 2020). The *Archaeopteris* roots extend radially up to about 11 m and penetrate more than a metre into red palaeosols, showing the earliest known deeply rooted forest ecosystems. This site represents a better-drained floodplain where tree spacing was open and the vegetation structure was tiered, with *Archaeopteris* forming the dominant canopy element.

In contrast, the late Famennian Xinhang forest of South China represents a monospecific lycopsid stand of *Guangdedendron micrum* (Wang *et al.* 2019; Gao *et al.*

2022). Trees exceeded 7 m in height, with four-branched stigmarian rhizomorphs that penetrated waterlogged fine-grained substrates. The stand developed in a coastal floodplain or delta-front wetland, its uniform spacing and low diversity reflecting rapid recolonisation following flooding events.

The mid–Late Devonian forests of Svalbard reveal another ecological configuration. In the early Frasnian Plantekløfta Formation, dense low-canopy stands of the arborescent lycopsid *Protolopododendropsis pulchra* grew on saturated floodplain muds (as described by Berry and Marshall, 2015), while at nearby localities in Munindalen moderate-sized *Archaeopteris* trunks, roots and branches occur *in situ*, showing that lycopsid and archaeopterid trees coexisted on the same equatorial floodplain (Davies *et al.* 2021). Together these sites show that by the mid–Late Devonian forest ecosystems had already diversified into distinct ecological and structural types across the globe. Against this global background, the Svalbard forests provide new evidence of how equatorial Devonian floodplains were structured and how early tree groups coexisted within them.

In the previous sections the architecture and anatomy of the two principal tree types, *Protolopododendropsis pulchra* and *Archaeopteris*, were described in detail. The following section briefly summarises the field evidence for their ecological associations and the structure of the forests in which they occur. All forest horizons are preserved within the dark sandstones and shales of the Plantekløfta Formation (early Frasnian) and together show that both groups formed extensive tree-dominated communities in equatorial Svalbard.

Description of Forest Localities

AF22A (*Archaeopteris* forests)

Horizons containing small upright *Archaeopteris* trees show that this genus formed distinct forest stands in Svalbard. Vertical surfaces with scattered trunks were illustrated and described from the NARCH locality by Davies *et al.* (2021, fig. 13), where trees

stood 1-2 m apart and were identified by their coalified stems and attached roots, including *Callixylon* wood described in this report.

A comparable site was discovered in 2022 at AF22A. The horizon preserves at least three (Text Figure 77B - white arrows) and probably up to five **archaeopterid trees** in life position above a soft dark grey palaeosol. The trunks are small, up to 9 cm in diameter and about 48 cm in preserved height, with short sections of upright wood and basal roots that penetrate the underlying palaeosol. The trees are positioned several metres apart, but because there is no plan view the true spacing cannot be established. By comparison with the nearby lycopsid forests, the trees represent a low-density stand rather than a dense colony.

Between and around the *Archaeopteris* trees are small lycopsid fragments, including thin stems of a previously unstudied non-arborescent lycopsid (Text Figure 77B - *black* arrow; Text Figure 77C). These occur only sparsely in the assemblage.

The exposure lies along a faulted surface within a coarse conglomeratic layer, which has displaced some of the trunks and made the outcrop difficult to photograph as a whole. The relative positions of the trees have therefore been reconstructed from field sketches and notes recorded at the time of mapping. Despite this distortion, the pattern is clear: AF22A represents an *Archaeopteris*-dominated forest stand, similar in composition and spacing to the NARCH site described by Davies et al. (2021), but with additional small lycopsids preserved around the trees. Large lycopsids are absent.

AF22B (*Protolepidodendropsis pulchra* and *Archaeopteris* forests)

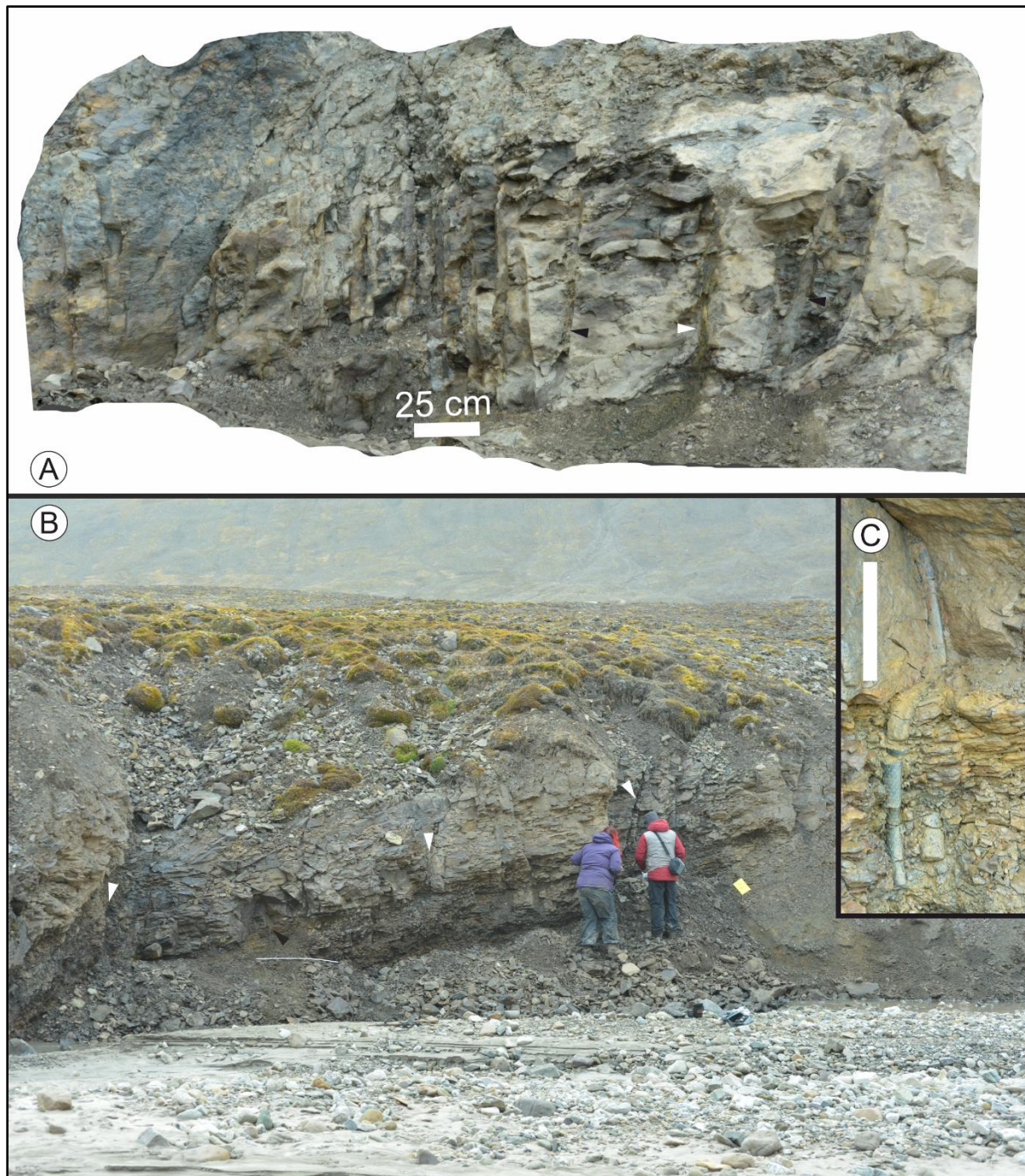
A second forest site, AF22B, slightly down the floodplain from AF22A, preserves a contrasting community. The forest surface occurs within grey mudstone underlain by a compact dark palaeosol, forming a well-consolidated fine-grained substrate with a sharp upper boundary. The site was mapped in detail using photogrammetry to record the position of individual trees (Text Figure 77A).

At the centre of the exposure stands a single upright archaeopterid trunk, described in detail in Section 5 of the *Archaeopteris* chapter. The tree is coalified and rooted in place, with lateral roots extending across the palaeosol surface. Around 40–60 cm from its base, the surrounding outcrop is densely occupied by small arborescent lycopsids assigned to *Protolapidodendropsis pulchra*. At least seventeen of these stems are preserved in situ, their cormose bases touching or overlapping within the same surface.

The arrangement shows that an archaeopterid tree grew within, or very close to, a dense *P. pulchra* colony. This association is notable because archaeopterids are often interpreted as better-drained floodplain trees, whereas arborescent lycopsids are commonly associated with wetter, fine-grained and more waterlogged substrates. The AF22B association may therefore reflect local floodplain heterogeneity rather than identical ecological preferences. Small differences in microtopography, drainage, sediment firmness, disturbance history or colonisation timing could have allowed both plant types to occur on the same surface. The archaeopterid may have occupied a slightly firmer or better-drained patch within a generally wet lycopsid-dominated palaeosol, while the surrounding *P. pulchra* stems colonised the softer, saturated substrate nearby.

The pattern contrasts with AF22A, where several archaeopterid individuals formed a more open group with only scattered probably herbaceous lycopsids. Together, the two sites record local variations in forest structure within the same floodplain, ranging from archaeopterid-dominated groves to mixed stands where the two tree types grew in close proximity. A second locality showing lycopsids and a possible archaeopterid stem was illustrated at locality A11 by Davies et al. (2021, Fig. 14c-f).

Because *Svalbardia* is not formally recombined here as *Archaeopteris*, the term archaeopterid is used in this ecological section for trunks, roots or axes that are interpreted as belonging to the *Svalbardia–Archaeopteris* plant concept, but which are not treated as a formal nomenclatural recombination.



Text Figure 77. Devonian forest localities in Svalbard. A. Three-dimensional photogrammetric model of site AF22B showing a mixed forest assemblage with *Protolpidodendropsis pulchra* (black arrows) and *Archaeopteris* (white arrow). B. Site AF22A, *Archaeopteris*-dominated forest (white arrows) with smaller, non-arborescent lycopsid stems (black arrows), also shown in C. C. Close-up view of small lycopsid stems; scale bar = 10 cm.

Discussion

The forested horizons of the Plantekløfta Formation record a diverse vegetation in which *Protolapidodendropsis pulchra* and *Archaeopteris* formed tree-dominated communities. The field evidence indicates that these plants coexisted within the same floodplain system, although their local abundance varied between nearby sites. At AF22A, the horizon preserves at least three, and probably up to five, small *Archaeopteris* trees in life position, with trunks several metres apart. Small lycopsid fragments, including thin stems of a previously unstudied non-arborescent lycopsid, occur sparsely between and around these trees, while large lycopsids are absent. This supports interpretation of AF22A as a relatively open, *Archaeopteris*-dominated stand. In contrast, AF22B preserves a single upright *Archaeopteris* trunk within a closely spaced *P. pulchra* assemblage, where at least seventeen stems are preserved in situ and their cormose bases touch or overlap within the same palaeosol surface. These contrasting spatial arrangements suggest local variation in forest structure across the floodplain, probably linked to differences in drainage, substrate stability or disturbance history.

These assemblages extend the known ecological range of *Archaeopteris* in Svalbard, showing that it formed structured stands and mixed communities as well as isolated trunks. Its association with lycopsids in clearly waterlogged sediments is unusual. Elsewhere, such as at Cairo, New York, *Archaeopteris* occupied better-drained palaeosols with roots extending more than a metre into oxidised floodplain soils (Stein *et al.*, 2020). Its presence in saturated mudstones in Svalbard implies greater ecological tolerance and the ability to persist across a wide range of moisture conditions, perhaps key to its evolutionary success.

In global context, the Svalbard forests bridge two well-known endmembers: the dense lycopsid stands of Xinhang, China (Wang *et al.*, 2019; Gao *et al.*, 2022) and the open, woody *Archaeopteris* forests of Cairo, New York. The *P. pulchra* colonies at Plantekløfta

formed low, compact canopies stabilising soft floodplain sediments, while the Cairo trees occupied drier, deeply rooted soils. Svalbard preserves both forms side by side.

Outside Svalbard, Devonian forests show clear regional contrasts. The Porlock site in southwest England (Eifelian) preserves cladoxylopsid trees, while the Gilboa forest of New York contained giant cladoxylopsids and aneurophytes in wet deltaic environments (Stein et al., 2012). These groups are absent from Svalbard, where the known forest assemblages are dominated by lycopsids and archaeopterids. This difference may reflect climatic, latitudinal and hydrological controls on vegetation composition.

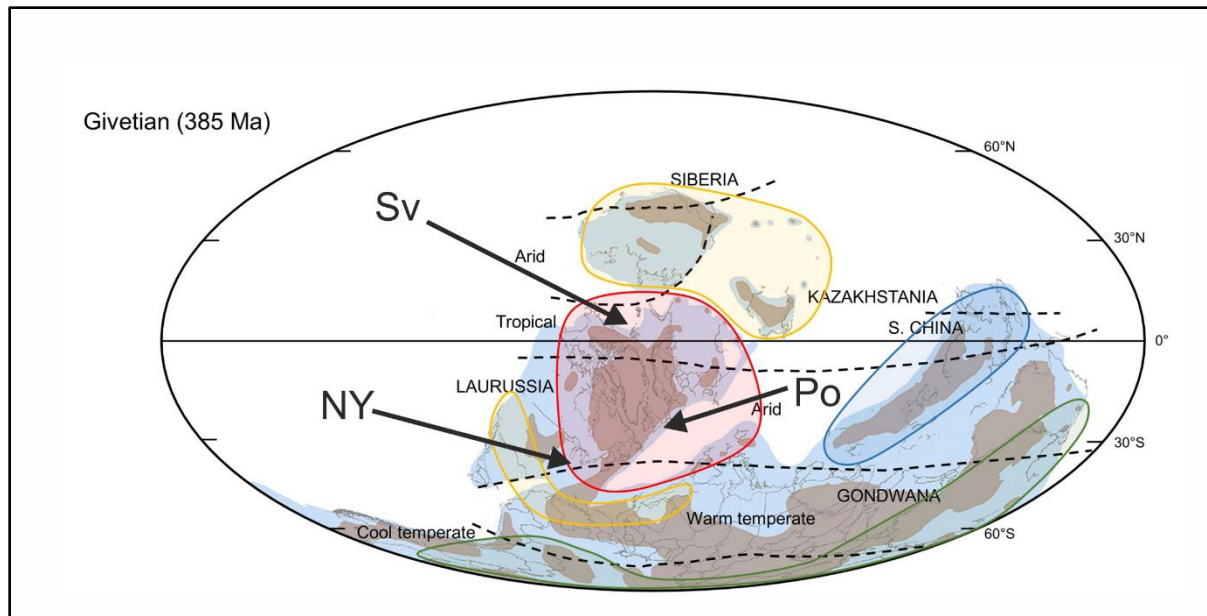
These differences can be understood in the context of Middle Devonian palaeogeography and climate (Text Figure 78). Porlock (Po) and New York (NY) lay within more seasonal belts of Laurussia, while Svalbard (Sv) occupied a near-equatorial position within the tropical zone. In South China, later Famennian forests of *Guangdedendron micrum* developed in monsoonal coastal wetlands (Wang et al., 2019; Gao et al., 2022). Together, these localities show that climate, hydrology and disturbance regime strongly influenced early forest composition.

The Svalbard forests therefore provide rare evidence for tropical forest development by the early Frasnian. Within Svalbard, *P. pulchra* formed dense stands on fine-grained, wet floodplain substrates, but at some localities it also occurred close to archaeopterid trees. This pattern suggests a heterogeneous floodplain landscape rather than a single uniform vegetation type. The relevant forest horizons are broadly comparable in representing wet, fine-grained palaeosol surfaces, but local differences in drainage, sediment firmness, microtopography or colonisation timing may explain why some surfaces were dominated by dense *P. pulchra* stands, while others preserved archaeopterid-dominated stands or mixed associations.

The close occurrence of *P. pulchra* and archaeopterids at AF22B does not necessarily mean that both taxa occupied identical microhabitats. Instead, it may record small-scale environmental patchiness within the same floodplain surface, with archaeopterid individuals occupying slightly firmer or better-drained patches and *P. pulchra* colonising wetter, softer areas nearby. This interpretation is consistent with the contrast between

AF22A, where archaeopterid individuals occur with only sparse lycopsids, and AF22B, where a single archaeopterid tree occurs close to a dense *P. pulchra* stand.

Together, the Svalbard forests show that early tropical forest ecosystems were already structurally and ecologically varied by the Mid–Late Devonian. *Protolepidodendropsis pulchra* and archaeopterid trees both contributed to substrate stabilisation, sediment retention and the development of vertical vegetation structure, although through different growth forms. *P. pulchra* formed dense stands of relatively small, closely spaced stems with shallow cormose bases and ribbon-like rooting structures, while archaeopterid individuals added woody stems, lateral roots and a more open vertical component to the vegetation. These were not tall, closed-canopy forests comparable to later Carboniferous or modern forests, but low, patchy, early forest communities that transformed wet floodplain surfaces (Berry & Marshall, 2015; Davies et al., 2021). Modern analogues are necessarily imperfect, but wetland and riparian pioneer communities provide useful functional comparisons for sediment trapping, shallow substrate binding and patchy vertical growth (Gibling & Davies, 2012). In this sense, the Svalbard assemblages capture a key stage in Earth history, when early trees began to engineer terrestrial landscapes and establish the ecological foundations of later forested ecosystems (Algeo & Scheckler, 1998; Gibling & Davies, 2012).



Text Figure 78. Middle Devonian climates and palaeophytogeography.

Global map showing Middle Devonian (Givetian, 385 Ma) climates and palaeophytogeographic regions, modified from Capel *et al.* (2023). Mid Devonian to early Frasnian forest localities are plotted: Sv = Svalbard (early Frasnian), NY = New York (mid Givetian), Po = Porlock (Eifelian). Red = Laurussia phytochorion; green = South Gondwana phytochorion; yellow = Subtropical phytochorion; blue = South China phytochorion. Map and climate data from Boucot *et al.* (2013).

Conclusions: Chapter III, Mid – early Late Devonian forest trees

This chapter set out to reconstruct and interpret two key components of the Mid–Late Devonian terrestrial ecosystems of Svalbard: two important tree taxa that formed a significant part of the palaeolandscape. The overarching aims were to (1) redescribe each taxon based on newly collected fossil material, (2) reconstruct their growth architecture and developmental organisation, and (3) situate these findings within the broader framework of Devonian forest evolution. Given the rarity of Devonian fossil forest assemblages, any new contribution provides significant insight into the structure and dynamics of early terrestrial ecosystems and yields valuable information for understanding plant evolution during this pivotal interval in Earth's history.

Bateman and Hilton (2009) highlighted the importance of viewing fossil plants as integrated organisms rather than disjointed fragments, recognising that only whole-plant perspectives can reveal their true biological and evolutionary significance. The extensive new material now makes this possible for both *Protolepidodendropsis pulchra* and the early Frasnian Svalbard form of *Archaeopteris*, transforming them from isolated fossil elements into well-contextualised components of the Spitsbergen Devonian landscape. The new understanding presented herein bridges the gap between morphology, anatomy and stratigraphy. The growth architectures and ecological roles of these plants is demonstrated and our understanding of how complex terrestrial communities developed in equatorial Laurussia is augmented.

Together, *Protolepidodendropsis pulchra* and *Archaeopteris* represent contrasting yet complementary strategies in the emergence of tree-sized vegetation. *P. pulchra* anchored itself in waterlogged floodplain substrates using a broad cormose base with fine, ribbon-like rootlets, forming dense stands with branched erect crowns that stabilised sediment and promoted soil development. In contrast, *Archaeopteris* developed a woody, architecture with stout, spreading roots and relatively long-lived lateral leafy branching systems, enabling vertical growth and canopy development. These differences reflect parallel evolutionary solutions to mechanical stability and

resource capture. Viewed together, they highlight the ecological diversity of Middle–Late Devonian vegetation and the mosaic character of the earliest wooded landscapes.

Protolapidodendropsis pulchra

All major organs are now linked for the first time, the cormose base with ribbon-like roots, the straight trunk with diamond to rhombic leaf cushions, and the attached crown. The cushion pattern is distinctive and provides a consistent marker across organs, confirming all belong to the same species. Crown material shows helically inserted leaves and determinate growth, establishing the overall tree form. These findings consolidate *P. pulchra* as one of the earliest examples of integrated arborescent organisation in lycopsids. Its small growth habit and wetland ecology illustrate an early phase in the evolution of stable, rooted vegetation, representing a key transitional stage between simple dichotomously rooted forms and the fully rhizomorphic stigmarian trees of the Carboniferous.

Archaeopteris

Linking the different organs and preservation types proved more difficult here, because the material occurs at separate stratigraphic levels within the Mimerdalen Subgroup and lacks an obvious single unifying feature. However, their overlapping ranges show that the fossils coexisted within the same depositional environments. Grouped pitting of xylem, preserved in a vertical trunk with attached roots, provides a strong link between anatomy and morphology. Anatomically preserved axes of *Actinopodium nathorstii*, with an eight-ribbed stele, broadly correspond with the branch organisation inferred for *Svalbardia polymorpha*, supporting the interpretation that *Actinopodium* and *Svalbardia* may represent different preservational states of the same plant. Casts of trunks referred to *Caulopteris* are associated by inference, based on branch-trace organisation that is consistent with the established developmental framework for *Archaeopteris*. Taken together, these varied remains form a coherent whole-plant model in which all parts are consistent with the known anatomical and morphological structure of *Archaeopteris*-type trees. However, species-level assignment remains uncertain. Leaf architecture, including the form and dissection of the laminae, may differ from described species of *Archaeopteris*, and the Svalbard material may represent a distinct local species or

archaeopteridalean form. For this reason, the material is best interpreted here as an *Archaeopteris*-type tree rather than formally assigned to a particular species.

Limitations

Although the material described here provides one of the most complete records of Devonian vegetation from Svalbard, several limitations remain. Fertile structures of *Protolopododendropsis pulchra* are still unknown, preventing full reconstruction of its reproductive biology and life cycle. Exposures in the Mimerdalen Subgroup are spatially patchy, meaning that the contemporaneity of different forest stands cannot always be demonstrated directly. No single *Archaeopteris* specimen preserves all organs in organic connection and thus aspects of the whole-plant reconstruction remain partly inferential. However, the use of multiple, independent lines of evidence, including stratigraphic continuity, morphological consistency and anatomical correspondence provides strong support for the interpretations presented here and minimises uncertainty.

Future Research

Future work palaeoecological work should focus on refining the environmental and developmental context of these forests. Integrated sedimentological and palaeopedological analyses would help constrain soil conditions and rooting depths, clarifying the substrate preferences of both *P. pulchra* and *Archaeopteris*, and explain why the vegetation is heterogenous. Quantitative studies of species associations and spatial patterns across multiple horizons, from Estheriahaugen to Planteryggen, could test ecological partitioning within the basin.

Further careful collecting, armed with current knowledge, could refine growth models by finding further key morphologies and variation. For example, targeted collecting could yield assemblages of branching crown axes from lycophytes which would allow better understanding of spacing between dichotomies and allow extrapolation beyond the single spectacular crown specimen which is unlikely to be completely representative of variation within a geologically long-lived species.

Discovery of Mid and early Late Devonian forests is limited to Laurussia. Spectacular lycopod forests in China are latest Famennian in age. Discovering contemporaneous Mid Devonian fossil forests, particularly in the South China phytochorion where plants are quite different from Laurussia, seems essential for understanding the development of forest ecosystems globally.

The Svalbard assemblages capture a stage at which Devonian terrestrial ecosystems had become both taxonomically and structurally complex. They document the coexistence of arborescent lycopsids and archaeopteridalean trees, with different developmental pathways and growth habits, within the same tropical floodplain landscape. Rather than representing simple opportunistic vegetation, these assemblages show spatial organisation, repeated forest horizons and local variation in dominance between *P. pulchra* and *Archaeopteris*. By extending the record of forests into equatorial Laurussia, this study shows that by the early Frasnian, and probably by the mid-Givetian, both taxa were contributing to organised forest communities. These findings highlight the dynamic nature of mid–Late Devonian floodplain ecosystems and their wider significance for understanding how Earth's first forests developed and diversified.

Plates

Plate 1. Poorly Preserved Carbonaceous Remains from the Siktefjellet Locality, North-West Spitsbergen.

A. Poorly preserved carbonaceous remains, likely *Prototaxites*. Undulating patterns are visible on the superior portion of the surface (white arrows) and are also present on the counterpart (C). Scale bar 1 mm.

B. Poorly preserved, unbranched carbonaceous plant axis with two horizontal breaks in the carbon (indicated by white arrows). An indeterminate spatulate structure is present on the same slab (black arrow). Scale bar 5 mm.

C. Counterpart to A. Undulating patterns (white arrows) on the superior portion correspond to those in part A. Scale bar = 1 mm.

D. Ribbon of poorly preserved plant material, possibly a sporangial stalk or an unbranched plant axis. Preservation is very poor. Part E is possibly the counterpart to this specimen. Scale bar 1 mm.

E. Possible counterpart to D. Ribbon of poorly preserved plant material. Scale bar 1 mm.

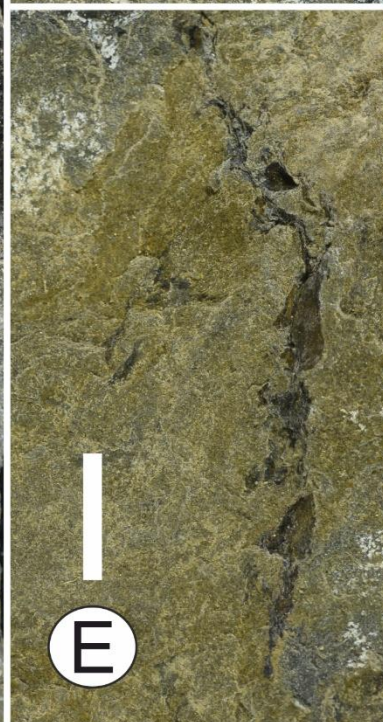
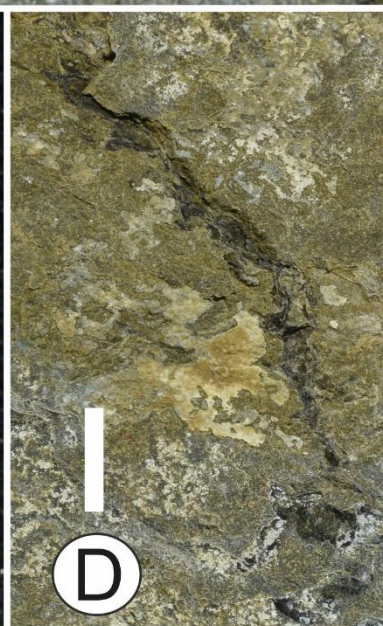


Plate 2. *Zosterophyllum fertile* axes fragments collected from Buchananhavøya, Spitsbergen.

A. Overlapping *Z. fertile* axes, minerals have leached into the sediment causing orange-brown discolouration. Scale bar 2mm. 18-Spits-25-01

B. Straight, parallel *Z. fertile* axes. White arrows show presence of Microconchida, enlarged in E-G. Scale bar 2mm. 18-Spits-25-12.

C. Isotomous bifurcation in *Z. fertile*. Scale bar 1mm. 18-Spits-25-05.

D. *Z. fertile* axis with three separate isotomous bifurcations indicated by the white arrows Scale bar 2mm. 18-Spits-25-52.

E. Poorly preserved, K type branching. Scale bar 1mm. 18-Spits-25-04.

F. Positive impressions of Microconchida on *Z. fertile* axis. Scale bar 2mm. 18-Spits-25-12.

G. Negative impressions of Microconchida on *Z. fertile* axis. Scale bar 2mm. 18-Spits-25-12.

H. *Z. fertile* axis with coalified vascular strand. Scale bar 1mm. 18-Spits-25-29.

I. Poorly preserved *Z. fertile* axis with a vascular strand impression. Scale bar 1mm.

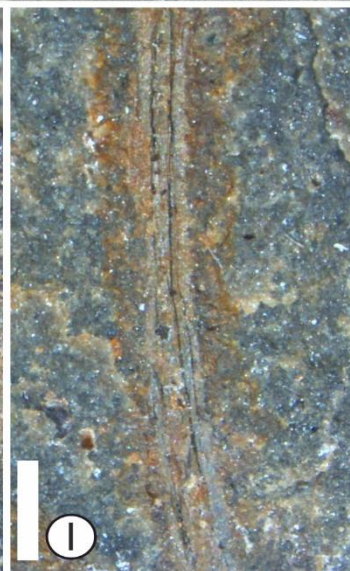
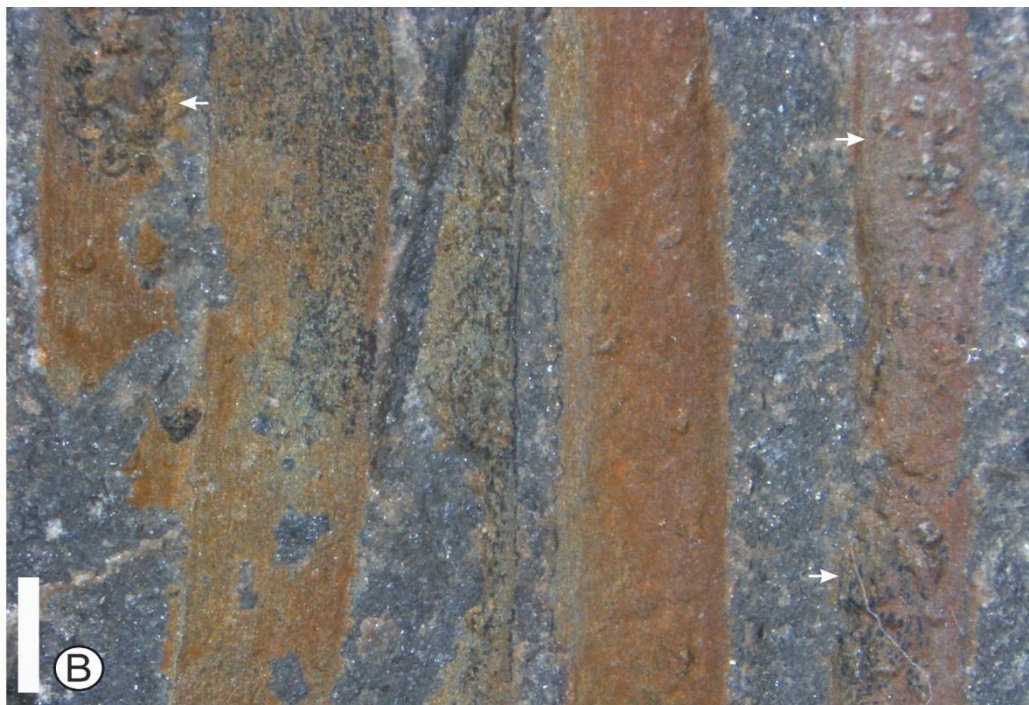


Plate 3. Fructifications of *Zosterophyllum fertile* collected from the Buchananhalvøya locality in North-West Spitsbergen.

A. Fertile spike of sporangia preserved with an axis overlaying the sporangia. Sporangial stalks can be seen in some of the sporangia in row A (left row). 18-Spits-25-39-ii.

B. Poorly preserved pairs of *Z. fertile* sporangia with overlaying axis on the left side. 18-Spits-25-12.

C. Poorly preserved sporangial spike of *Z. fertile*. 18-Spits-25-29.

D. Poorly preserved sporangial spike of *Z. fertile*. 18-Spits-25-54-L.

E. Moderately preserved spike of *Z. fertile* sporangia with visible sporangial stalks. 18-Spits-25-54-R.

F. *Z. fertile* axis with clearly visible sporangial stalks, arranged in two rows on either side of the axis. 18-Spits-25-56-B.

G. Relatively well-preserved fructification of *Z. fertile*.

Scale bar in all 1mm.

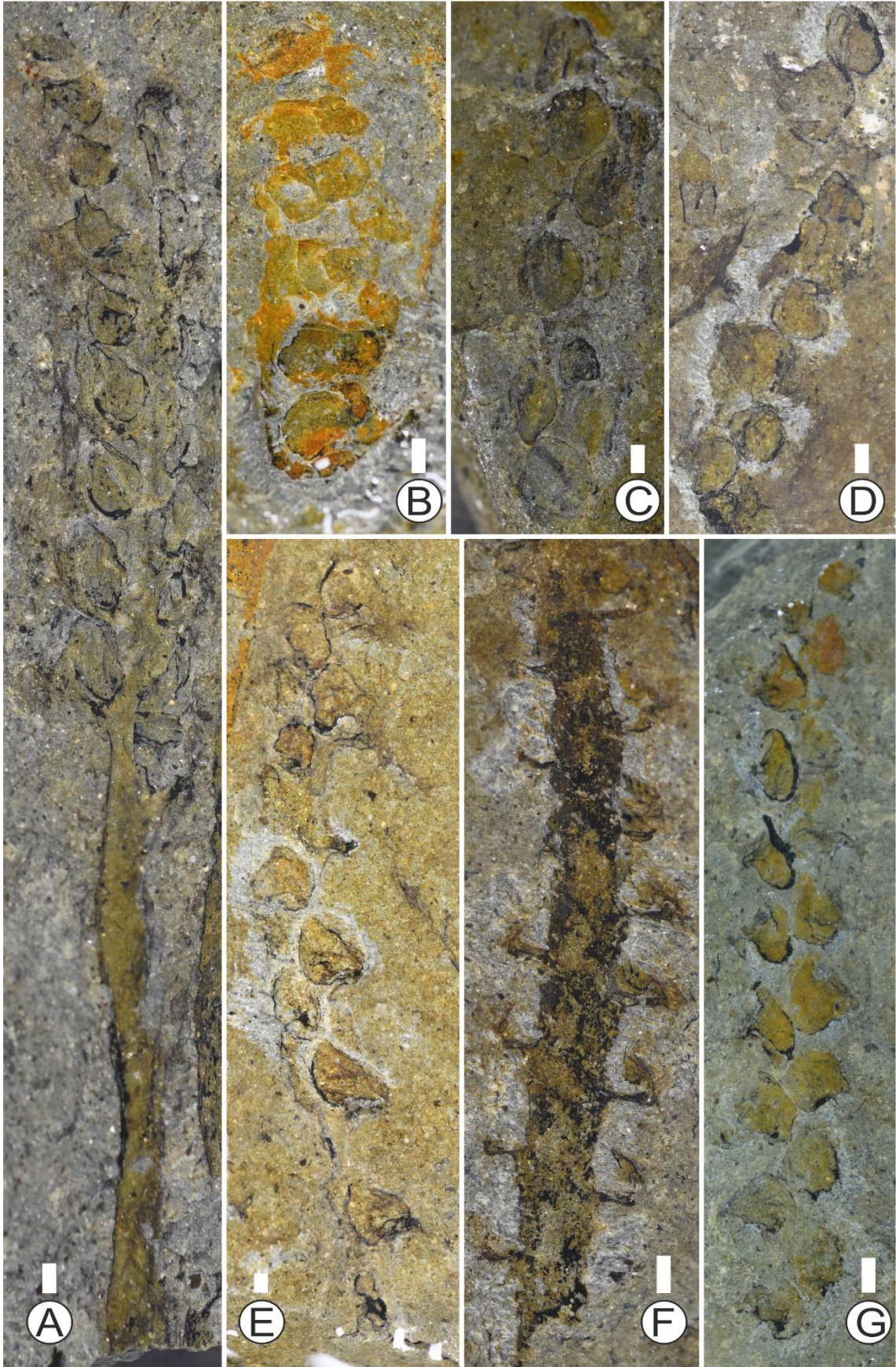


Plate 4. Individual sporangium from various fertile stalks of *Zosterophyllum fertile* collected at Buchananhalvøya.

A. Spade shaped sporangia from specimen 5-C (Text Figure 6D; S8B), a small portion of the dehiscence margin has been preserved. Near the base of the sporangium, the sporangial stalk has been folded underneath the sporangium, indicated by the black arrow.

B. Sporangium with clearly visible dehiscence margins (white arrow). The superior portion of the sporangial valve has been folded and distorted (*). Black arrow depicts where the sporangial stalk has been folded under the left side of the sporangium. Specimen 56C (Text Figure 6D; S3A).

C. Tear drop shaped sporangium with visible dehiscence margin from 39-ii (Text Figure 6C; S7A).

D. Ovate sporangium from 56C (Text Figure 6D; S6B). Black arrow shows where sporangial stalk has been folded underneath the sporangium.

E. Tear shaped sporangium with dehiscence margin from 56C (Text Figure 6D, S5B). Black arrow shows where sporangial stalk is folded under the left side of the abaxial valve. White arrow shows where a portion of the dehiscence margin is preserved.

F. Poorly preserved, tear drop shaped sporangium from 39-ii with a hint of a dehiscence margin around the lower left side of the sporangium (Text Figure 6C, S5A).

G. Ovate sporangium from 56C (Text Figure 6D, S5B).

H. Folded sporangium from 56C with very clear dehiscence margin (white arrow). Black arrow shows where sporangia stalk is folded under the left side of the sporangial valve. (Text Figure 6D, S4A).

I. Sporangium from 39-ii with small hint of a possible dehiscence margin on the lower portion of the sporangium. White arrows in all depict the presence of a thick carbonised margin, likely the dehiscence margin between the adaxial and abaxial valves. Black arrows depict where a sporangial stalk is interpreted to be present. Scale bar in all is 500 μm .

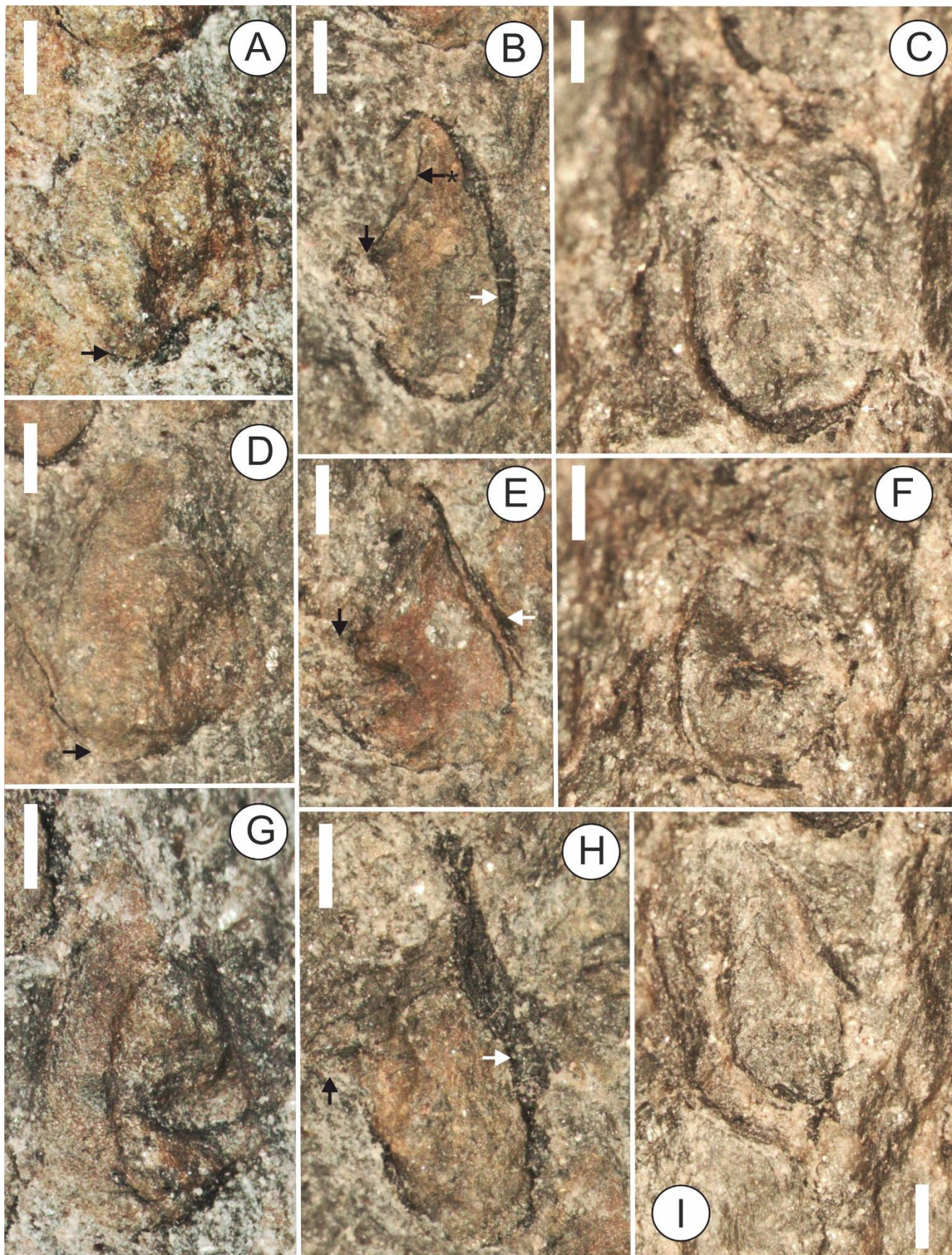


Plate 5. Assemblage of plant remains from the Frænkelryggen locality, Andr  ebreen Fm, North-West Spitsbergen.

A. Indeterminate, carbonaceous plant remains with various axes fragments. FR-A-12.

B. Thin, bare, unbranched axis. FR-A-21.

C. Bare, unbranched branched axis. FR-B-08.

D. Thin, bare, unbranched axis. FR-B-08.

E. Assemblage of mostly indeterminate plant remains, with multiple carbonaceous axis fragments. FR-B-01.

F. Long, bare, unbranched axis. FR-A-02.

G. Long, bare unbranched axis. FR-A-02.

Scale bar in all images is 1 mm.

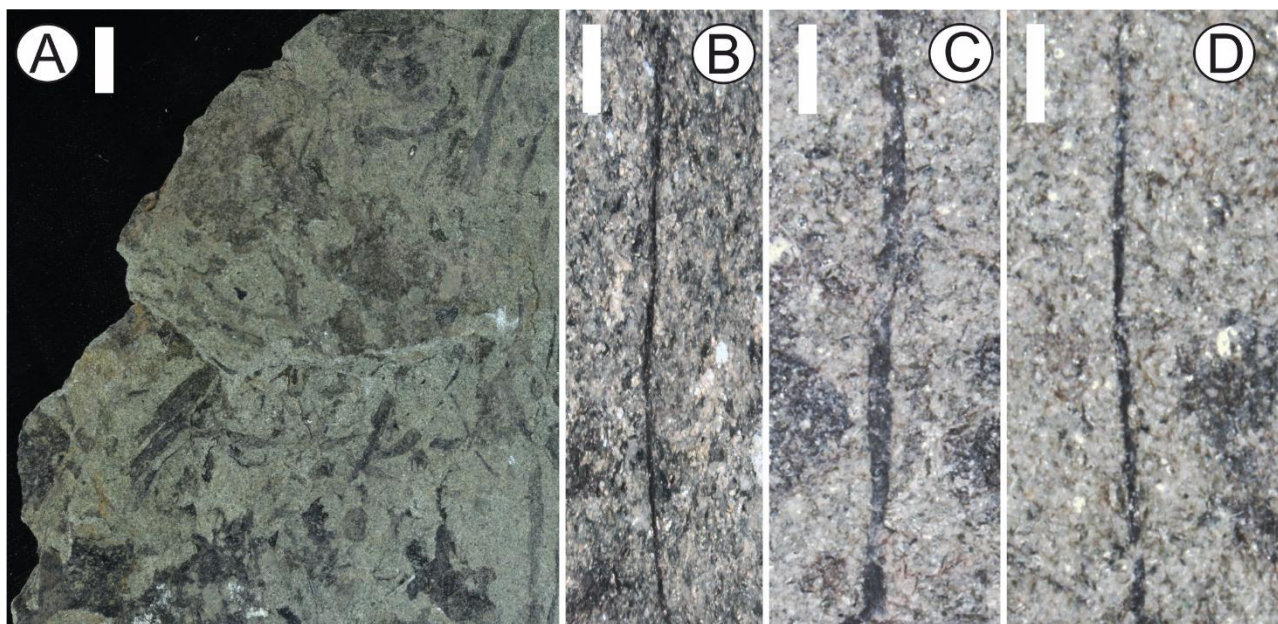


Plate 6. Assemblage of large carbonaceous remains, probably belonging to *Prototaxites*, from Frænkelryggen, Andréebreen Fm, North-West Spitsbergen.

A. Large, three-dimensional carbonaceous remains with longitudinal striations on the surface of the axis. Clearly defined margins are visible along the edge of the remains. FR-B-08.

B. Part and counterpart of a large, carbonaceous fragment with longitudinal striations. Margins of the axis are visible near the apical portion. FR-A-19.

C. Large, carbonaceous fragment with longitudinal striations. Margins of the axis visible on the right side. FR-A-13.

D. Large, carbonaceous fragment. Margins are barely visible. FR-A-10.

E. At least two carbonaceous fragments. White arrows point to the right-hand margin of each fragment. FR-A-16.

F. Carbonaceous fragment less well preserved than some of the other specimens. Margin visible on the right-hand side.

G. Large, carbonaceous fragment with both longitudinal and horizontal striations on the surface. White arrows point to the clearly defined horizontal striations. Margins are clearly visible on both sides.

Scale bar in all images is 10 mm.

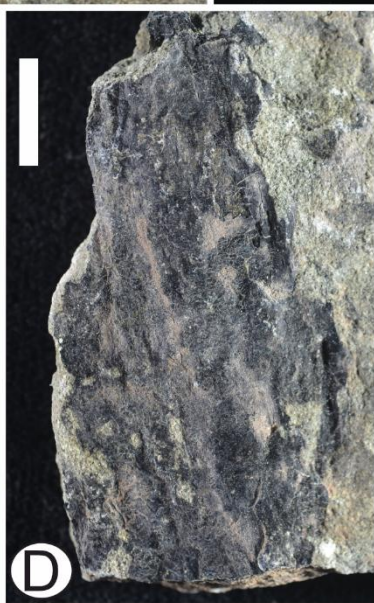
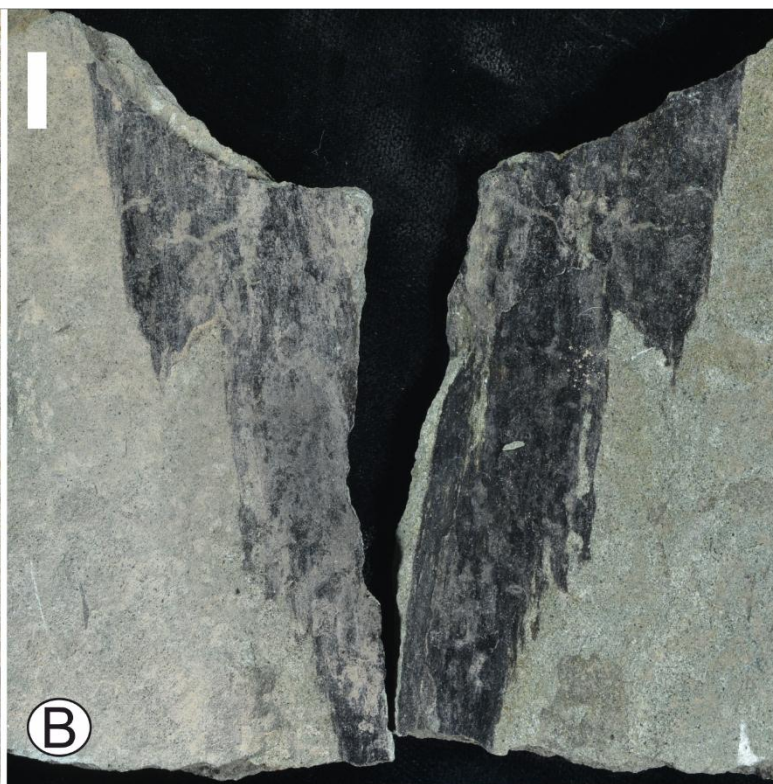


Plate 7. Black, indeterminate, carbonaceous material probably belonging to *Prototaxites*, collected from the Frænkelryggen locality, Andréebreen Fm, North-West Spitsbergen.

A. Slab with various small fragments of black, indeterminate material, highlighted by the white arrows. FR-A-01.

B. Large, indeterminate carbonaceous material across the surface of the slab, with small axis fragments mixed in. FR-C-01.

C. Poorly preserved, indeterminate, carbonaceous material scattered across the surface of the slab. FR-B-08.

D. Large, black mass of carbonaceous material. FR-B-04.

E. Black, indeterminate mass of carbonaceous material. FR-B-03.

Scale bar in all images is 5 mm.

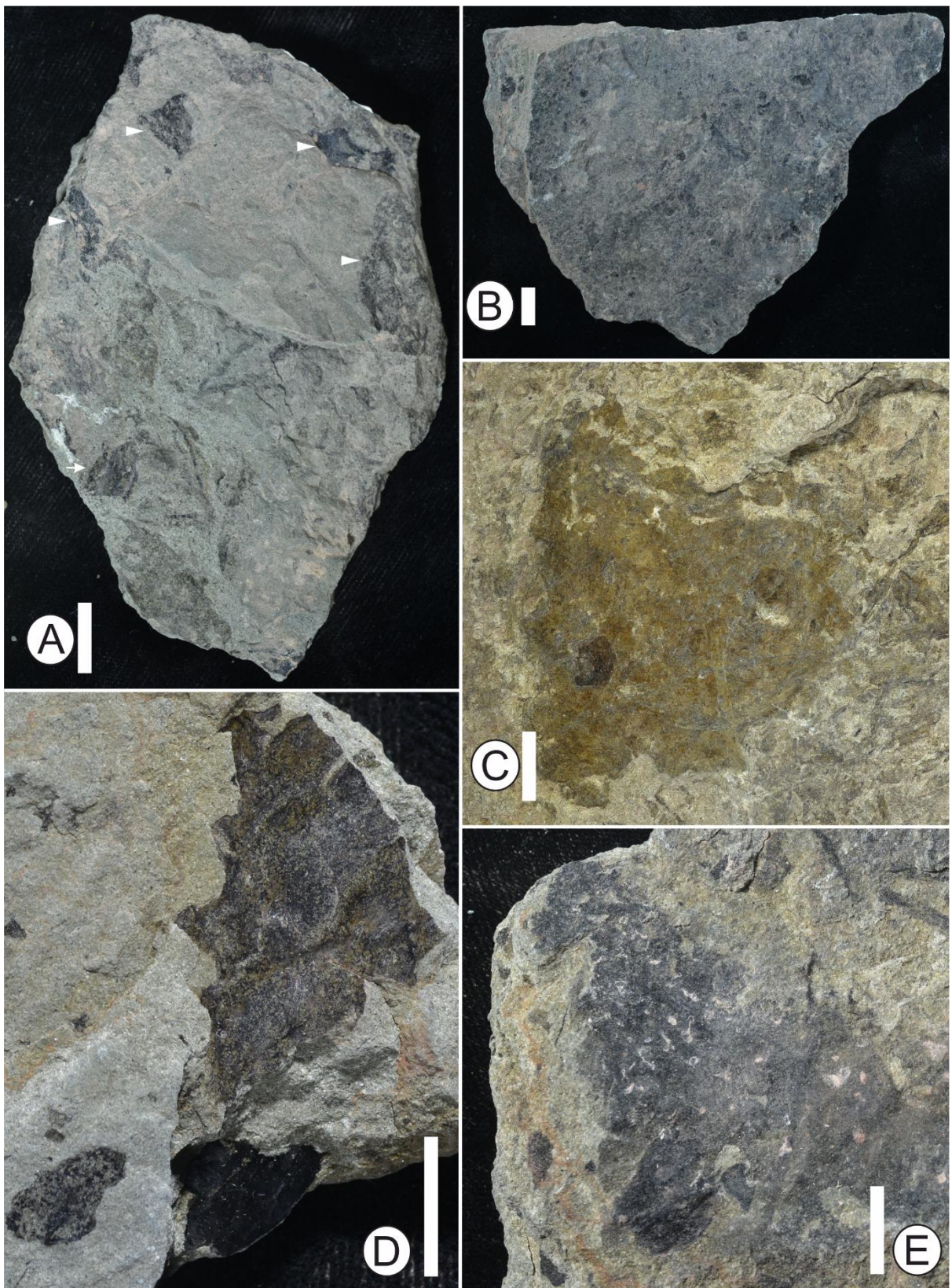


Plate 8. Various assortments of sporangia and ovate structures from the Frænkelryggen locality, Andréebreen Fm, North-West Spitsbergen.

A. Singular, ovate structure preserved as a negative impression. It could possibly be a singular sporangium. The surface of the structure is highly carbonized and cracked. FR-A-09. (S1).

B. Singular, ovate structure preserved as a positive, carbonized impression. FR-A-09. (S3).

C. A pair of partially preserved, ovate-globose structures. FR-A-11.(S4).

D. Singular, partially preserved ovate structure. FR-A-14.(S6).

E. Singular, ovate-globose, permineralized structure. FR-A-09. (S2).

F. Singular, ovate structure preserved as a highly carbonized, three-dimensional specimen. FR-B-03. (S7).

G. Poorly preserved, ovate structure with a potential axis on the right side, labelled with a white arrow. The structure shows unusual preservation, with a circular portion in the centre infilled with sediment, which could potentially be a remnant of the sporangial stalk. FR-A-12. (S5).

Scale bar in all images is 1 mm.

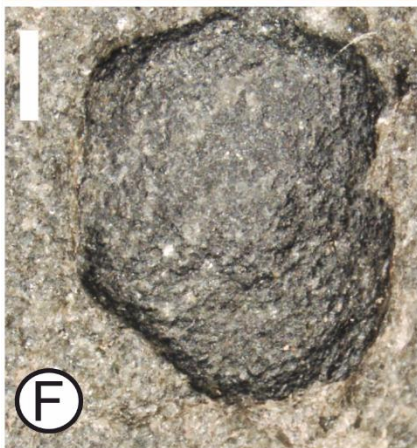
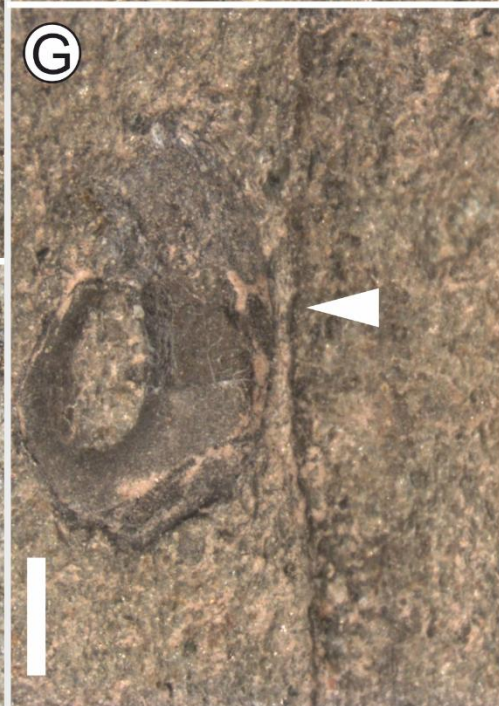
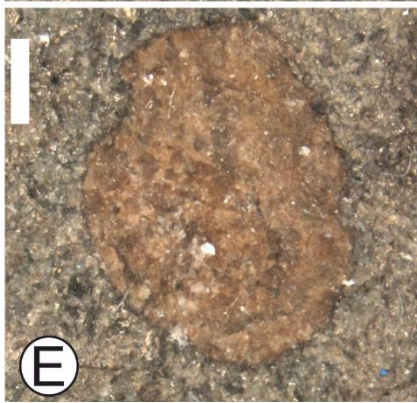
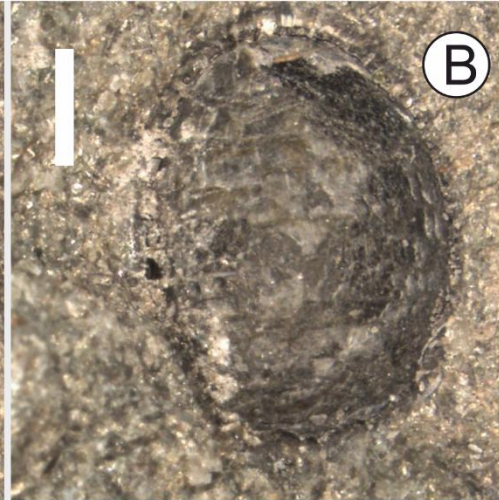
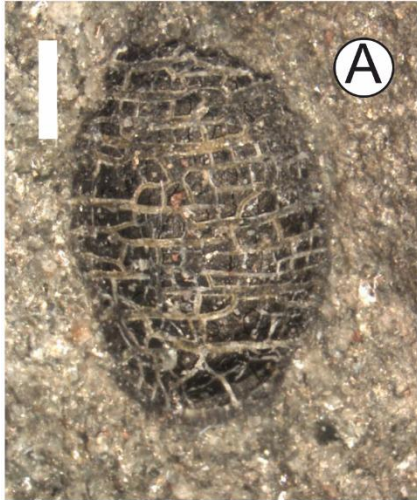


Plate 9. *Psilophytites svalbardensis* sp. nov. collected from Kapp Petermann.

A. Type specimen of *Psilophytites* showing pseudomonopodial growth form. Recurved tips present at the distal portion of the axis (black arrow). Line drawing of Text Figure 24. PMF 12. Scale bar is 5mm.

B. Part (left) and counterpart (right) of anisotomously bifurcating axis with pseudomonopodial growth form. PMF11. Scale bar is 5mm.

C. Counterpart of PMF-5. Contains the upper paired lateral axis which emerges from the primary axis. Seen in Text Figure 26J. Scale bar is 1mm.

D. Part of PMF-5 before serial *dégagement* and removal of the upper paired axis present on this part seen in 1C. The black arrow depicts lower paired axis which extends into the rock matrix below. The white arrow shows the upper paired axis which extends into the counterpart seen in 1C. *Dégagement* steps seen in Text Figure 26B. Scale bar is 1mm.

E. Primary axis of *P. svalbardensis* preserved with inclusions of limonite. PMF6. Scale bar is 1mm.

F. Impression of primary *Psilophytites* ap. axis including the bases of spines and distinctive margins along the internal portion of the axis. PMF4. Scale bar is 1mm.

G. Coalified compression of *Psilophytites* sp with tapering spines visible on the external portion of the axis. PMF12. Scale bar is 1mm.

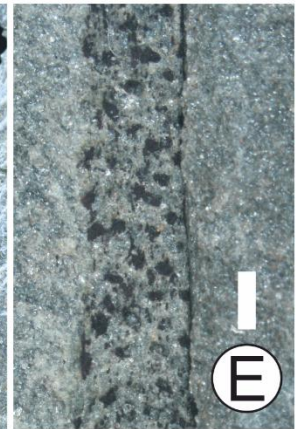
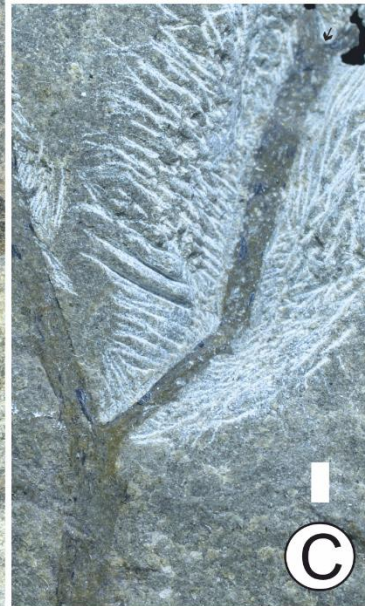


Plate 10. *Psilophytites svalbardensis* sp. nov. from Kapp Petermann, North-West Spitsbergen.

A. Close up of anisotomously bifurcating axis (PMF-4) preserved as an impression fossil. Spine bases are clearly visible in the epidermis of the axis. Scale bar is 2mm.

B. Anisotomously bifurcating axis (PMF-11) preserved as a coalified compression fossil. The white arrow shows the axillary tubercle associated with the smaller, secondary axis. Scale bar is 2mm.

C-D Part (10C) and counterpart (10D) of most distal bifurcation preserved as a coalified compression fossil with some inclusions of limonite. In both images, the white arrow depicts the axillary tubercle associated with the smaller, secondary axis. The axillary tubercle has been preserved with an inclusion of limonite. In both images, scale bar is 2mm.

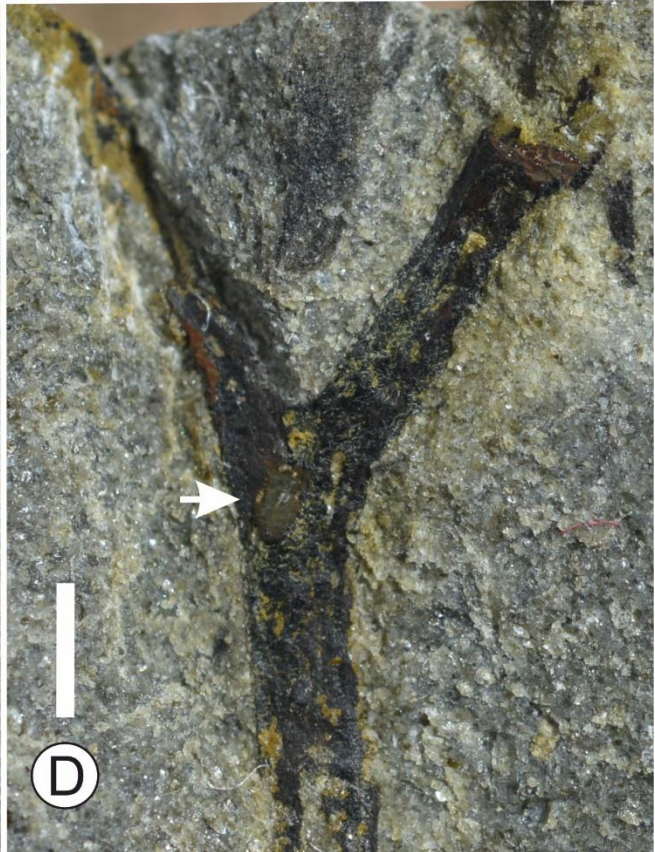
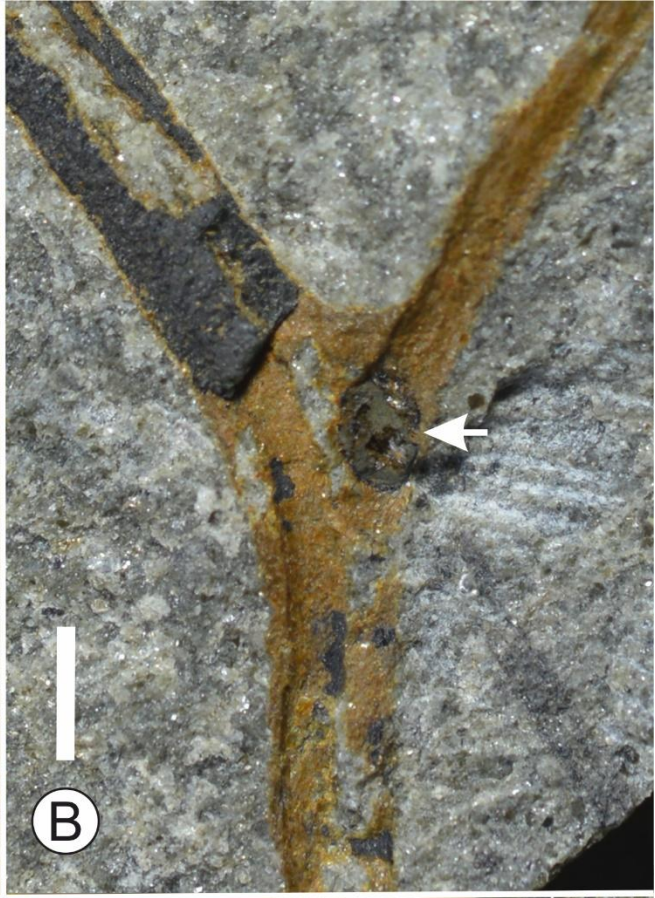


Plate 11. Spiny protrusions found in *Psilophytites svalbardensis* from Kapp Petermann, North West Spitsbergen.

A. Coalified axis (PMF-2) showing spine bases on external portion, most of which have snapped off. Scale bar is 2mm.

B. Impression (PMF-3) with spine bases organised throughout the primary axis. Scale bar is 2mm.

C. Axis of (PMF-4) with inclusions of limonite. The presence of limonite seems to correlate with the location of spine bases on the primary axis. Axillary tubercle can be seen at the distal portion of the axis between the bifurcation point. Scale bar is 2mm.

D. Impression of axis (PMF-15) where spine bases are shown clearly. Well defined margins associated with spines can be seen on either side of the axis. Scale bar is 0.5mm.

E. Coalified compression of axis (PMF-12) where spines are clearly visible from their tapered base to the fine tip of the spine. Scale bar is 0.5mm.

F. Close up of PMF-2. Spine tips have broken off, so only the spine bases remain, as indicated by the white arrows. Scale bar is 1mm.

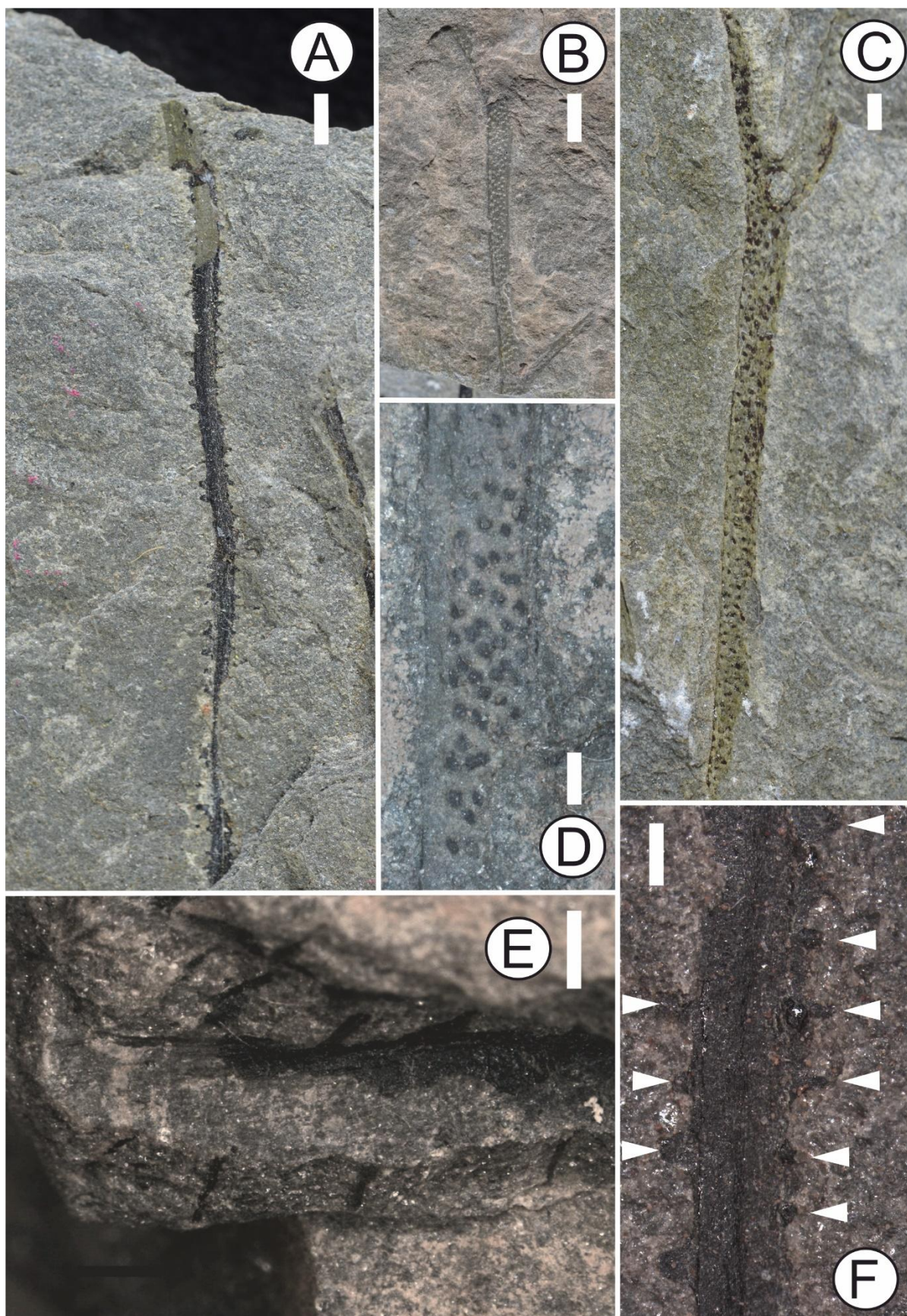


Plate 12. *Psilophyrites svalbardensis* sp. nov. from Jakobsenbukta (A, C) and Kapp Petermann (B, D).

A. Axis collected in 1939 by the E.N.S expedition to Spitsbergen, identified by Amy Wyatt, housed at the Natural History Museum in Stockholm, Sweden. Specimen number S017435. There is an apparent trifurcate arrangement on the distal portion of the axis, interpreted as a left lateral axis emerging shortly before the primary axis gives rise to a second lateral axis on the right-hand side. The white arrow points to the clearly defined margin associated with spines in this species. The black arrows point to the presence of these clearly defined margins without any spines in the left lateral axis. Scale bar is 1 mm.

B. Impression of axis (PMF-4) from Kapp Petermann. Spine bases are clearly visible. The white arrows point to the clearly defined margins on either side of the axis.

C. Axis collected in 1939 by the E.N.S expedition to Spitsbergen, identified by Amy Wyatt, housed at the Natural History Museum in Stockholm, Sweden. Specimen number S017434. Possible apparent trifurcate arrangement, although further dégagement is needed to confirm whether this represents closely spaced lateral branching. Despite poor preservation, spine bases can be just about seen on the primary axis.

D. Impression of anisotomous axis from the Kapp Petermann locality. Lateral axis is much smaller than the primary axis and bifurcates on the right hand side of the axis. The white arrow highlights this lateral axis.

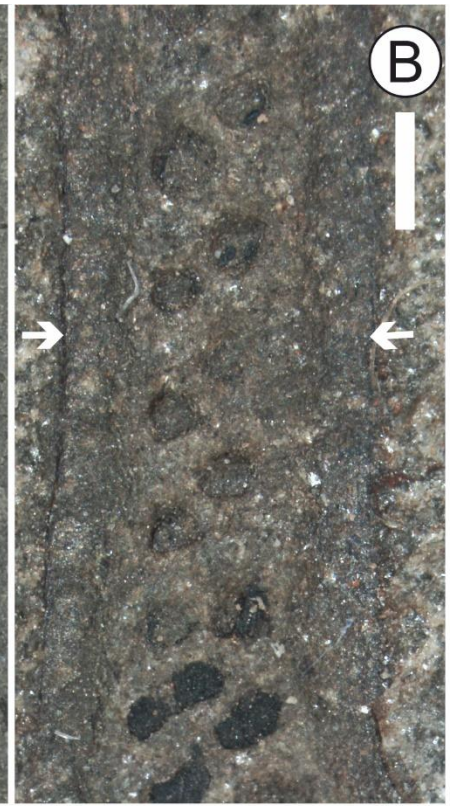
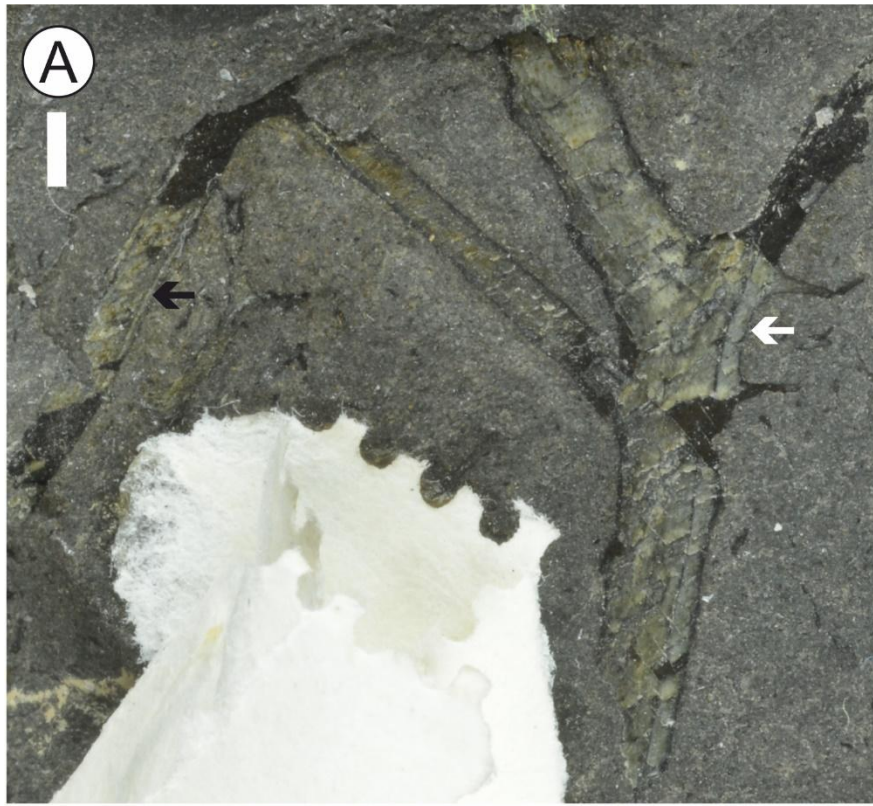


Plate 13. Various axis fragments of *Psilophytites svalbardensis* sp. nov. from the Kapp Petermann locality.

- A. Dichotomising carbonised compression (PMF-02) of a larger axis collected from this locality, seen without the tapering 'zig-zag' effect seen in smaller axis fragments.
- B. Poorly preserved axis fragment with two dichotomies down the length of the axis (PMF-03).
- C. Axis fragment preserved as an impression with iron staining (PMF-8). At the apical portion of the axis, a lateral axis diverges from the primary axis and then bifurcates again distally (white arrow). The axis terminates shortly after the lateral axis begins to bifurcate.
- D. Collection of mostly unbranched, incomplete axis fragments all orientated in the same direction (PMF-12). Spines are present on some of the axis fragments.
- E. Poorly preserved but informative coalified compression with numerous dichotomies (PMF-1), providing detail on the overall morphology of larger individuals of this taxon. The white arrows show a poorly preserved dichotomy in the lateral axis emerging from the primary axis.
- F. One of the best preserved axis fragments (PMF-14) which shows a further dichotomy in the length of the lateral axis (Black Arrow).

Scale bar in all is 5mm.

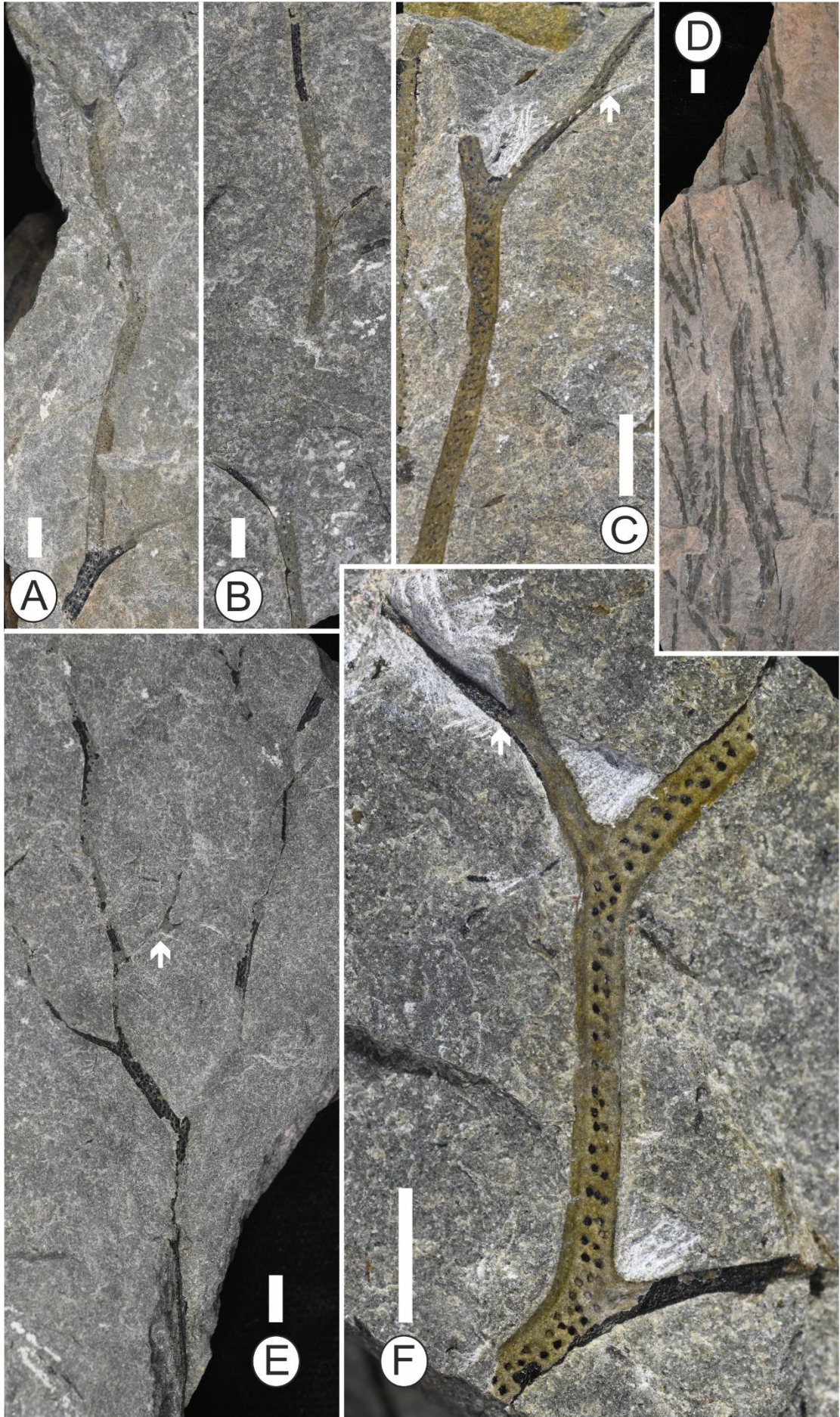


Plate 14: Part and counterpart of *S. polymorpha* from the Planteryggen type locality, photographed after leaf base dégagement.

- A.** Penultimate branch (part) with lateral ultimate branches and leaf bases after dégagement. White arrows highlight leaves on the ultimate branches. Numbers represent branching nodes. 2016-8.
- B.** Penultimate branch (counterpart) with lateral ultimate branches and leaf bases after dégagement. White arrows highlight leaves on the ultimate branches. Numbers represent branching nodes. 2016-41
- C.** Entire slab of the part, including the distal portion of the penultimate branch, which is partly buried in the matrix (white arrow). The black arrow indicates the axis shown in (A). 2016-8.

Scale bar = 10 mm.



Plate 15: Close-Up Images of the Part (A–C) and Counterpart (D–F) of *S. polymorpha* from the Plantekløfta Type Locality

- A.** Inferior portion of the counterpart of the penultimate axis, showing the first two lateral branching points. The white arrow indicates the third left lateral branch and points to that in the same structure in A–C. 2016-41.
- B.** Middle section of the counterpart of the penultimate axis. White arrow the same as A & C.
- C.** Superior portion of the counterpart, highlighting the upper two lateral branching points. The white arrow corresponds to A and B.
- D.** Inferior portion of the part of the penultimate axis, showing the first two branching points. This section corresponds to A in the counterpart. The white arrow indicates a leaf base prior to *dégagement*. All white arrows in D–F point to the same feature. 2016-8.
- E.** Middle portion of the part specimen of the penultimate axis, showing three lateral branching points. The white arrow is the same as in D and F.
- F.** Superior portion of the part specimen of the penultimate axis, illustrating the upper two lateral branching points. The white arrow matches D and E.

Scale bar 10 mm.

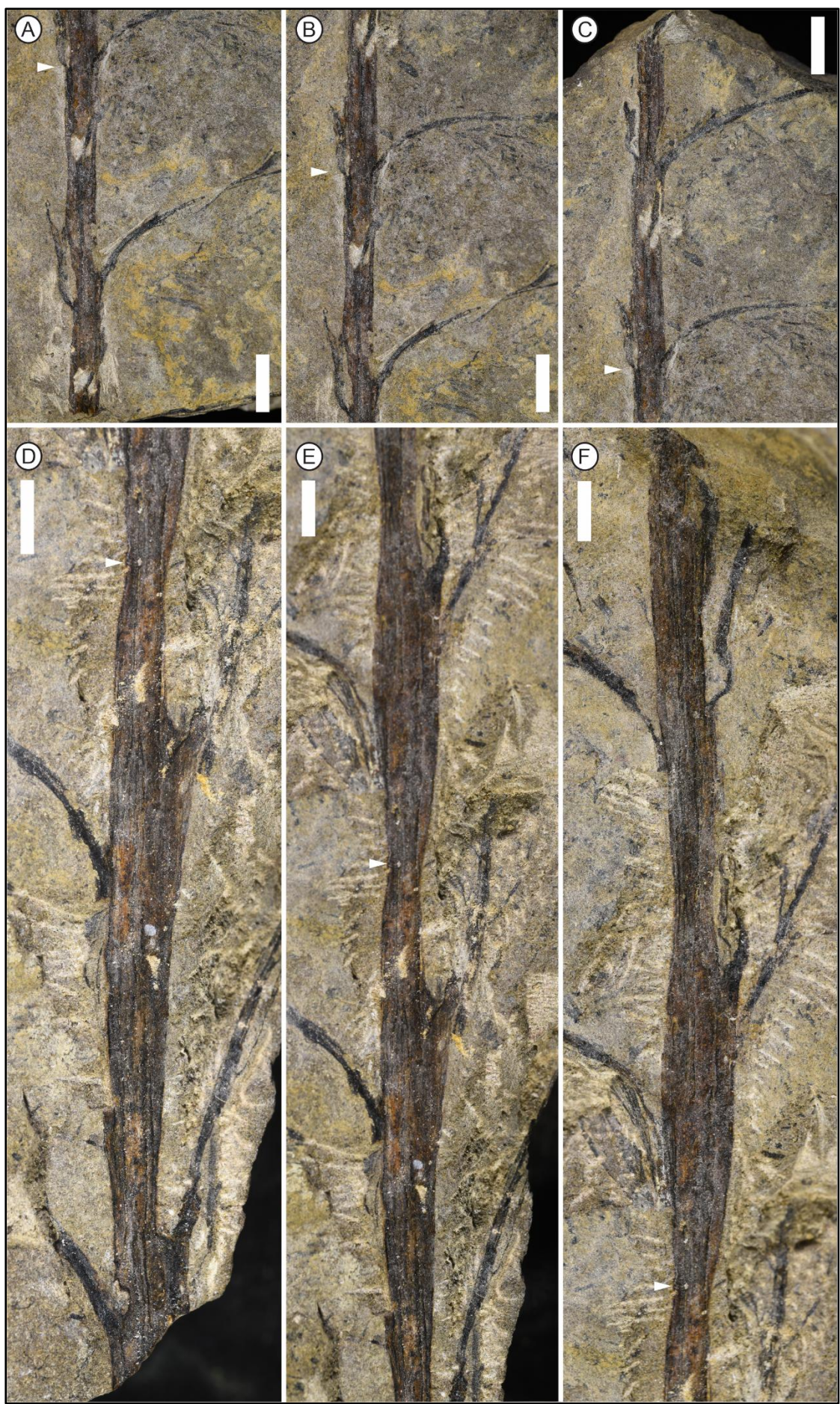


Plate 16. Leaf bases in *S. polymorpha* before (A, B, D), during (E, F), and after (C, G) dégagement.

A. Lower section of the penultimate axis (part). White arrows indicate positions of leaf bases before dégagement, visible as horseshoe-shaped carbonaceous material. Scale bar 5 mm. 2016-8.

B. Close-up of the horseshoe-shaped carbonaceous leaf base 4 on the penultimate axis, before dégagement. Upper white arrow in A above, see also Text Figure 42G. Scale bar 5 mm. 2016-8.

C. Penultimate axis (part) after dégagement, showing a bifurcating leaf base (black arrow). See Text Figure 42E, White arrow indicates the leaf blade (L1) continuing onto the counterpart shown in G. Distal part of reconstruction, Text Figure 43). Scale bar 5 mm. 2016-8.

D. Close-up of a horseshoe-shaped carbonaceous leaf base 1 on the penultimate axis, prior to dégagement. Lower arrow in A, above. See also Text Figure 42C. Scale bar 5 mm. 2016-8.

E. Penultimate axis (part) during dégagement, revealing the leaf base structure. Scale bar 5 mm. 2016-8.

F. Close-up of the partially dégaged leaf base shown in E. Scale bar 5 mm.

G. Penultimate axis (counterpart) after dégagement, showing the large leaf base (L1, white arrow) continuing onto the part shown in C. Proximal part of the leaf reconstructed in Text Figure 43. Scale bar 5 mm. 2016-41.

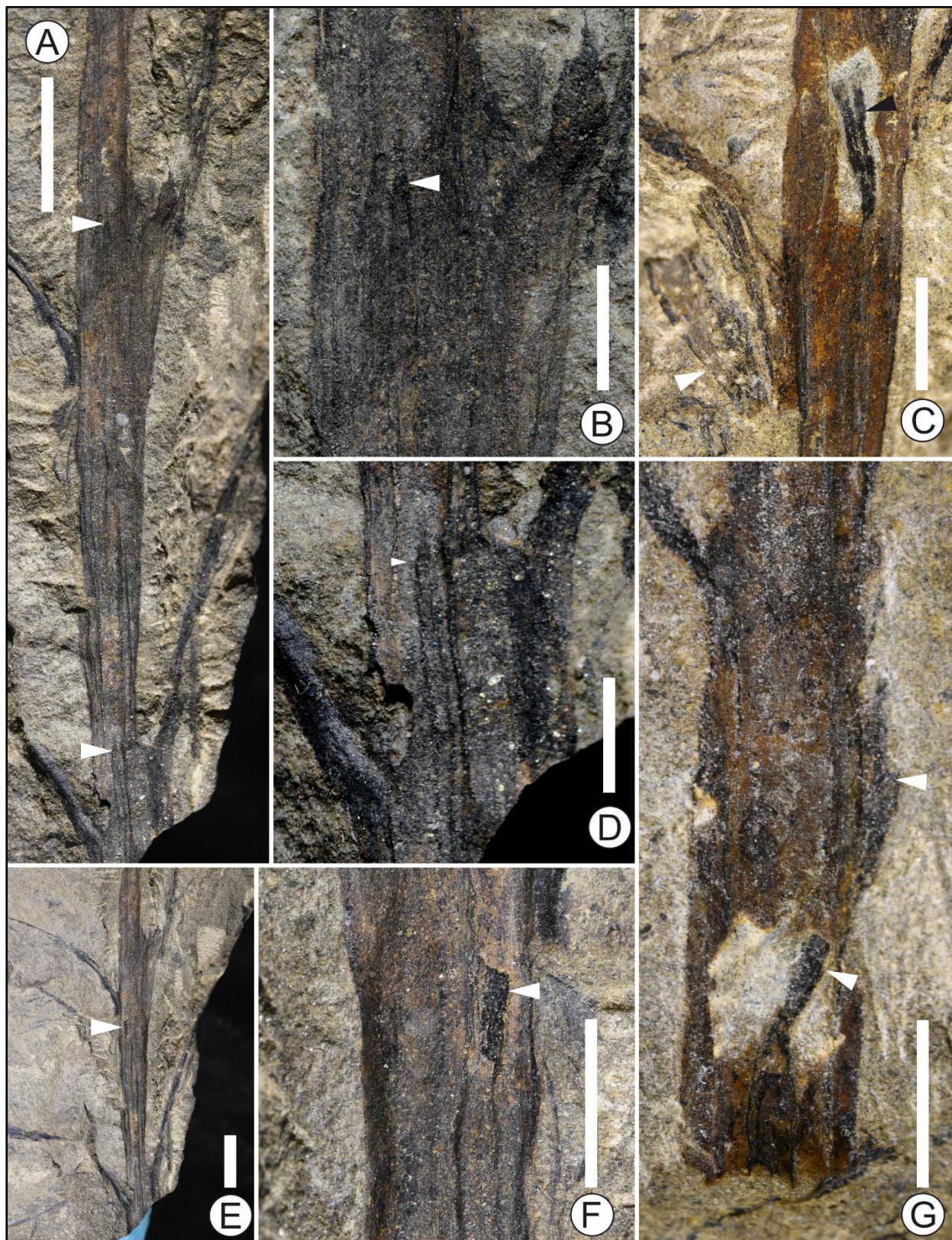


Plate 17. *S. polymorpha* penultimate branch morphology.

A. Part of the penultimate axis base. The white * indicates the probable attachment point of a lateral branch to the axis (convex). Specimen 2 (2016-2). Scale bar 10 mm.

B. Counterpart of the penultimate axis base with leaves (black *). The black arrow points to the tapered tip where surface folds are clearly visible. Specimen 2 (2016-1). Scale bar 10 mm.

C. Large intact penultimate branch with details of the lateral ultimate branching system. The white arrow indicates where the penultimate axis widens slightly after the emergence of the ultimate axis. The black arrow shows finely dissected leaves on the ultimate branch. Specimen 3 (2016-38). Scale bar 10 mm.

D. Penultimate branch with ridges and ultimate branches. Counterpart showing the 'frond-like' morphology of *S. polymorpha* preserved in mudstone, collected from the oldest stratigraphic unit in the sequence (Black Shale II, EST). White arrow indicates branching node. Scale bar = 10 mm. EST-1-CP.

E. Part specimen of D. White arrow indicates branching node, black arrow indicates leaves on ultimate branch and white * indicates folds in the penultimate branch. Scale bar 10 mm. EST-1-A-P

F. Leaves from Estheriahaugen (EST) *S. polymorpha*. Scale bar 5 mm.



Plate 18. Thin section preparations of *Actinopodium nathorstii*. (A, C–F) represent the holotype, while (B) represents *cf. A. nathorstii* both of Høeg (1942).

A. Cross-section of *A. nathorstii* axis. Slide S021014 (K).

B. *cf. A. nathorstii*, illustrated in Schweitzer (1999), Figure 49.

C. Cross-section of *A. nathorstii* axis, with a black arrow highlighting a trace emerging from a rib, seen in (D), (E), and (F) at various stages of budding. Slide S021019 (P).

D. Cross-section of *A. nathorstii* axis. Slide S021009 (F). For line drawing interpretation see Text Figure 45.

E. Cross-section of *A. nathorstii* axis. Slide S021016 (M).

F. Cross-section of *A. nathorstii* axis. Slide S021017 (N).

Rib numbers are labelled. Some images include labels for anatomical features: C = cortex, P = pith, PrX = primary xylem, SX = secondary xylem, PX = protoxylem, and T = trace.

Scale bar 2 mm.

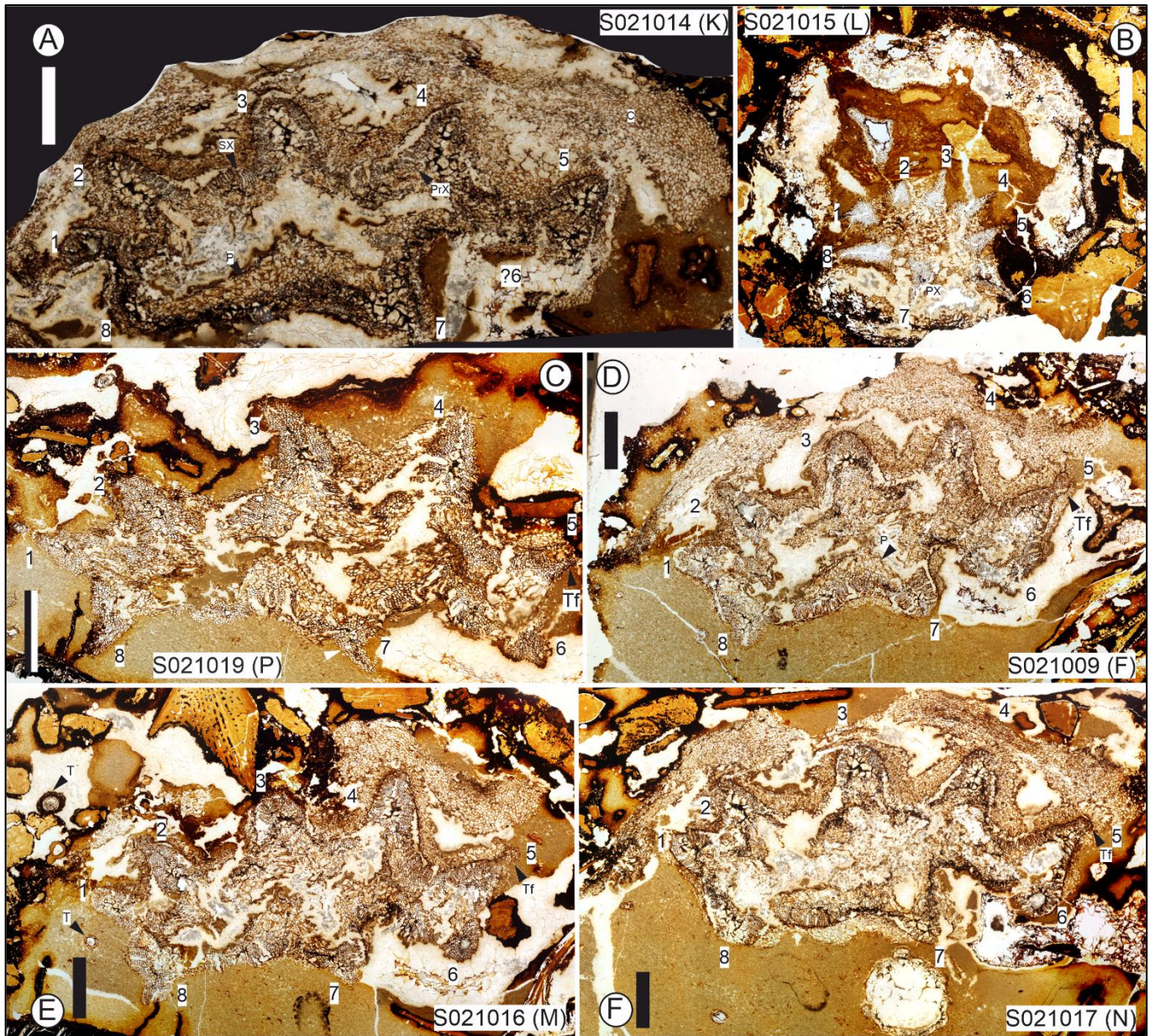


Plate 19. Thin section preparations of cf. *Actinopodium nathorstii* (Slide S021015). (L).

A. Close-up of outer cortex cells near the external portion of the axis. Black arrows = small vascular trace.

B. Close-up of rib 7 (see Plate 18B), showing details of metaxylem and protoxylem tracheids. PX = protoxylem tracheids.

C. Outer cortex cells near the axis margin. White arrow depicts small vascular trace in cortex.

D. Close-up of the stele, showing eight distinct ribs with well-preserved metaxylem tracheids. * - thin walled irregular pith cells.

Scale bar = 1 mm for all.

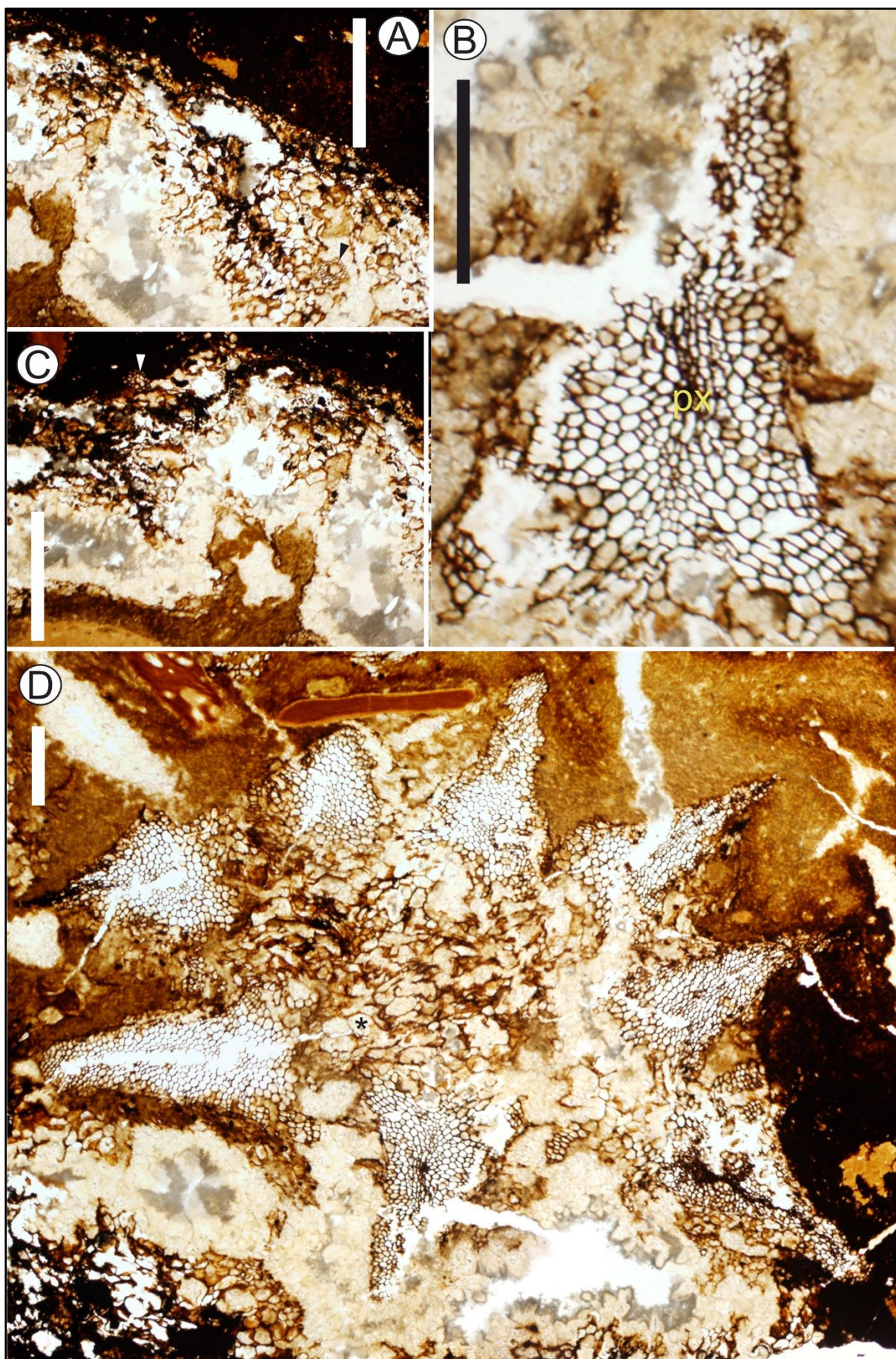


Plate 20. Details of anatomical features of *A. nathorstii*.

- A.** Secondary xylem tracheids arranged in radial files, with some metaxylem tracheids visible toward the centre of the stele. Large, thin-walled pith cells also present (black *). Black arrows highlight smaller, thicker walled pith cells. Slide S021009 (F).
- B.** Secondary xylem tracheids arranged in files, showing details of primary xylem tracheids and larger, thin-walled pith cells (*). Black arrows highlight smaller, thicker walled cells. Slide S021016 (M).
- C.** Budding trace at the end of rib 5 (see Plate 18D). Slide S021009.
- D.** Displaced rib from Slide S021015 (L). White arrows depict protoxylem tracheids. White arrow = protoxylem tracheids. Cf. *Actinopodium nathorstii*.
- E.** Poorly preserved leaf trace. Slide S021016 (M). See plate 19E.
- F.** Poorly preserved vascular trace. S021016 (M). See plate 19E.
- G.** Outer cortex containing two cell types: small, round cells with thick cell walls (black *) and larger, thin-walled cells (white*). Slide S021009.
- H.** Files of secondary xylem tracheids with suspected rays between files (black arrow). Slide S021019.
- I.** Radial files of secondary xylem tracheids with rays (black arrows). Slide S021016.
- J.** Thin-walled parenchymous cells (black *) and thick-walled parenchymous cells (white *) of the pith at the centre of the stele. S021016.

Scale bar in all 500 µm.

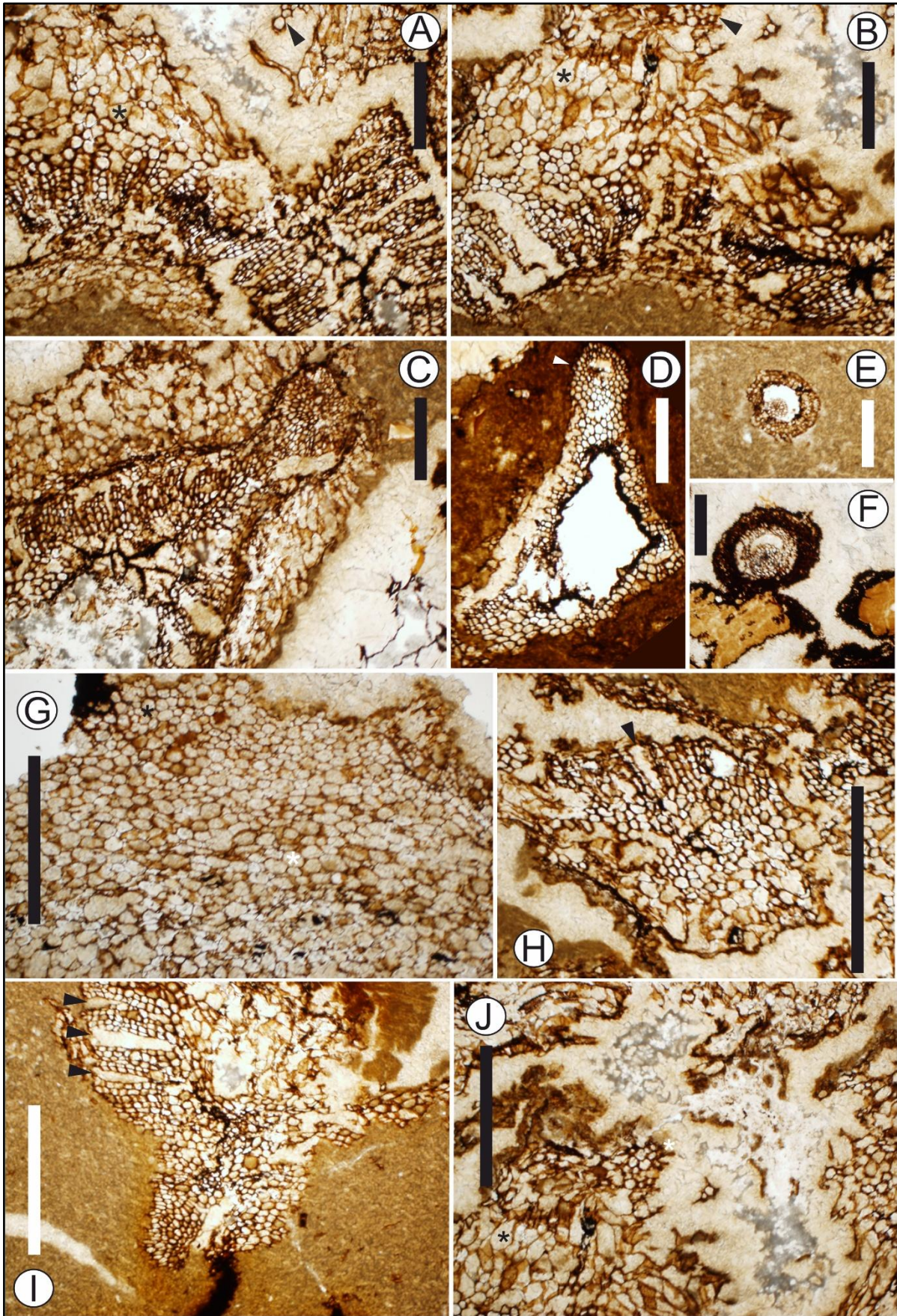


Plate 21. *Caulopteris*-1 collected from the Andréeland Group (Early Givetian - Late Frasnian).

A. Fragmented and poorly preserved compression collected from the Asterolepis Sandstone, Munindalen (CAUL). Caul-2010-A

B. Poorly preserved internal cast with some branch scars and surface details. Collected from coarse, sugary sandstone above Fiskekløfta (EC). Stem-89-91.

C. Internal cast with visible surface details of branch scars containing coalified material. Collected from coarse, sugary sandstone above Fiskekløfta (EC). No-Label-SS.

D. Fragmented and poorly preserved compression with surface ridges and branch scars, collected from the same locality and stratigraphic level as A (CAUL). Caul-2010-B.

E. Specimen from the Estheriahaugen Shale (oldest unit), preserved in an ironstone nodule. Shows branch details with some coalified material (remains of bark) and longitudinal folds in the surface texture above and below the branch scars (white arrows) (EST). EH-Nodule-Vogt.

F. Internal cast with distinct branch scars and longitudinal ridges in the trunk. White arrow shows where furrows run decurrently underneath a branch scar. Collected from coarse, sugary sandstone at Fiskekløfta (EC). Stem80-83.

G. Similar to F but more poorly preserved, (EC). Stem76-79.

H. Poorly preserved internal cast with pronounced branch scars. White arrow depicts where decurrent edge runs underneath the branch scar (EC). Stem 64-68.

Scale bar in all images = 10 mm.



Plate 22. *Caulopteris* specimen PMO.250.220A (**A–F**) and PMO.250.220B (**G–J**).

- A.** Full view of trunk cast showing branch scars and a flange-like structure interpreted as a shrinkage crack (white *) (EC).
- B.** Same specimen as A, rotated to reveal additional branch scars (EC).
- C.** Trunk surface displaying a rounded structure interpreted as a sediment-infilled pith cavity (white arrows) (EC).
- D.** Side profile of the pith cavity (white arrows); * indicates longitudinal ridges within the cavity (EC).
- E.** Same specimen as D, rotated to show the pith cavity face-on (EC).
- F.** Same as E, further rotated to show the cavity in oblique side profile (white arrows) (EC).
- G.** Specimen PMO.250.220B with original label applied by Høeg in 1939 (blue ∞) (EC).
- H.** Reverse side of G, showing a prominent shrinkage crack (white *) (EC).
- I.** Same view as H, but without cross-polarised light, making branch scars more visible (EC).
- J.** Transverse view of the trunk showing a swollen structure on one side of the axis, corresponding to the displaced pith cavity (white arrow) (EC).



Plate 23. Various *Caulopteris* specimens.

- A.** Stem 84–85 (morphotype *Caulopteris*-2). Locality EC.
- B.** UL-1-1 (morphotype *Caulopteris*-2). Locality UL.
- C.** Stem 64–68 (morphotype *Caulopteris*-2). White arrow indicates a branch scar protruding 19 mm from the trunk surface. Locality EC.
- D.** EH-Nodule (morphotype *Caulopteris*-3). White arrows highlight where the axis narrows and the ornamentation between branch scars becomes crowded and difficult to distinguish. Locality EST.
- E.** Close-up of branch scar morphology in EH-Nodule (D).
- F.** Close-up of D showing the most detailed branch scar (white arrow), with an unusual feature.
- G.** Large specimen collected from the River's Meet locality. While it does not clearly fit into any of the defined morphotypes, it is included due to its significance.
- H.** Same specimen as G, rotated to show a large visible branch scar.

Scale bar = 10 mm.

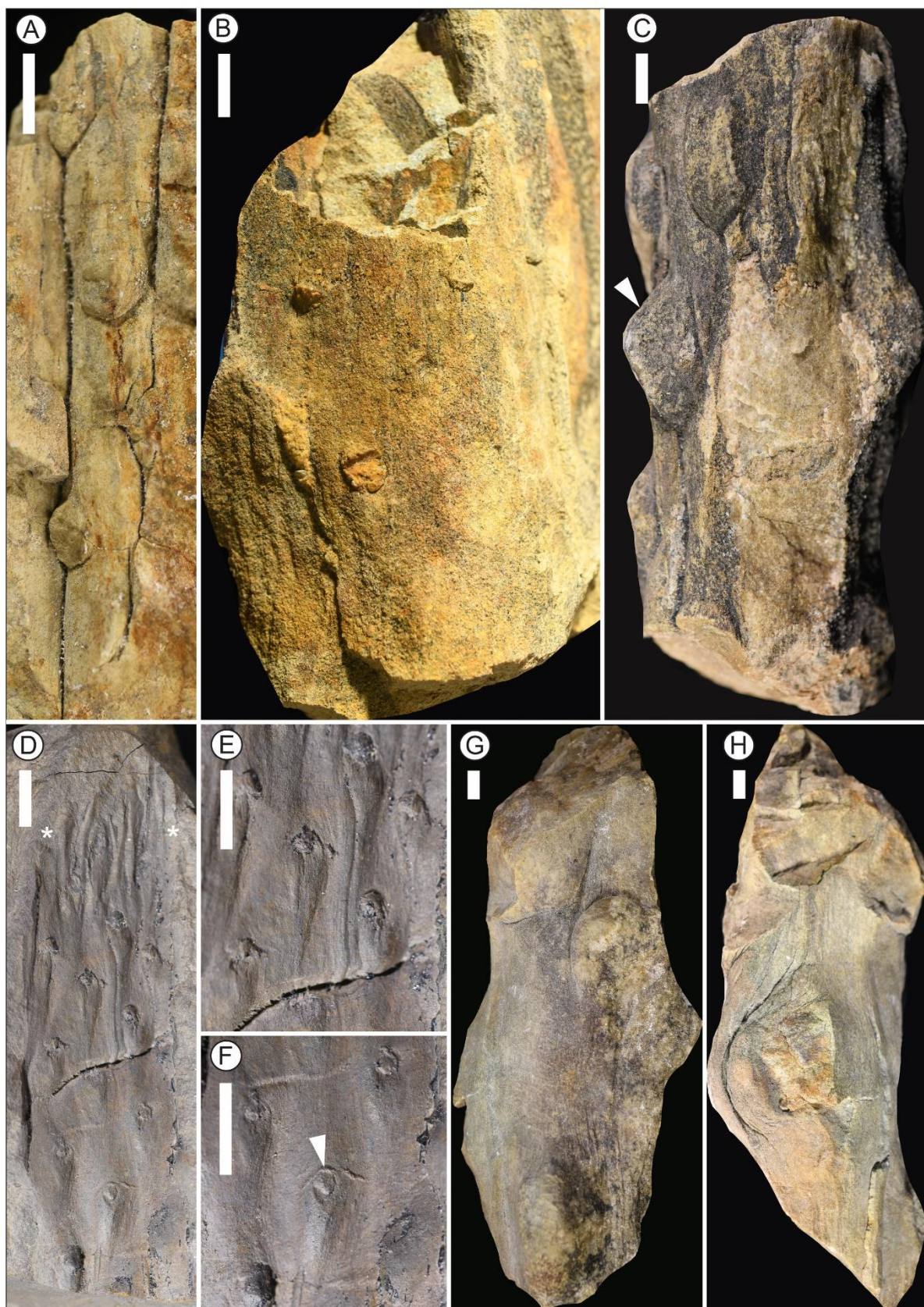


Plate 24. Medium-sized trunks with lateral branches.

A. Coalified remains of a trunk with possible lateral branches. White asterisk (*) indicates two potential branches emerging from the top of the trunk; white arrow shows a lateral branch extending beneath the surrounding matrix. Specimen ALP-1. Scale bar = 10 mm.

B. Medium-sized trunk from the Upper Lake locality (UL) with a lateral branch (black arrow). Longitudinal ridges on the trunk surface may represent taphonomic features (white *). Specimen UL-1. Scale bar = 10 mm.

C. Poorly preserved field specimen showing a lateral branch emerging from the trunk (black arrow) (RM). Scale bar = 10 mm.



Plate 25. Large trunk collected from the Estheriahaugen Sandstone Unit, above the Estheriahaugen Shale (EST).

(A) Large blocks reassembled following removal from the *in situ* position. White arrows show preserved edges of trunk. Stratigraphically lower surface is displayed.

(B) Close-up view of longitudinal striations and surface relief within the central pith cavity cast in uppermost block of A.

(C) Close up of middle portion of pith cavity cast, as seen in A.

(D) Detail of shrinkage cracks, a feature commonly observed in *Archaeopteris* and *Callixylon* trunks, associated with post-depositional drying and compression. Lower part of pith cavity cast (black arrow) as seen in A.

(E) lateral view of the compression showing arch of pith cavity when viewed in transverse profile (white arrows).

Scale bar in all 5 cm.

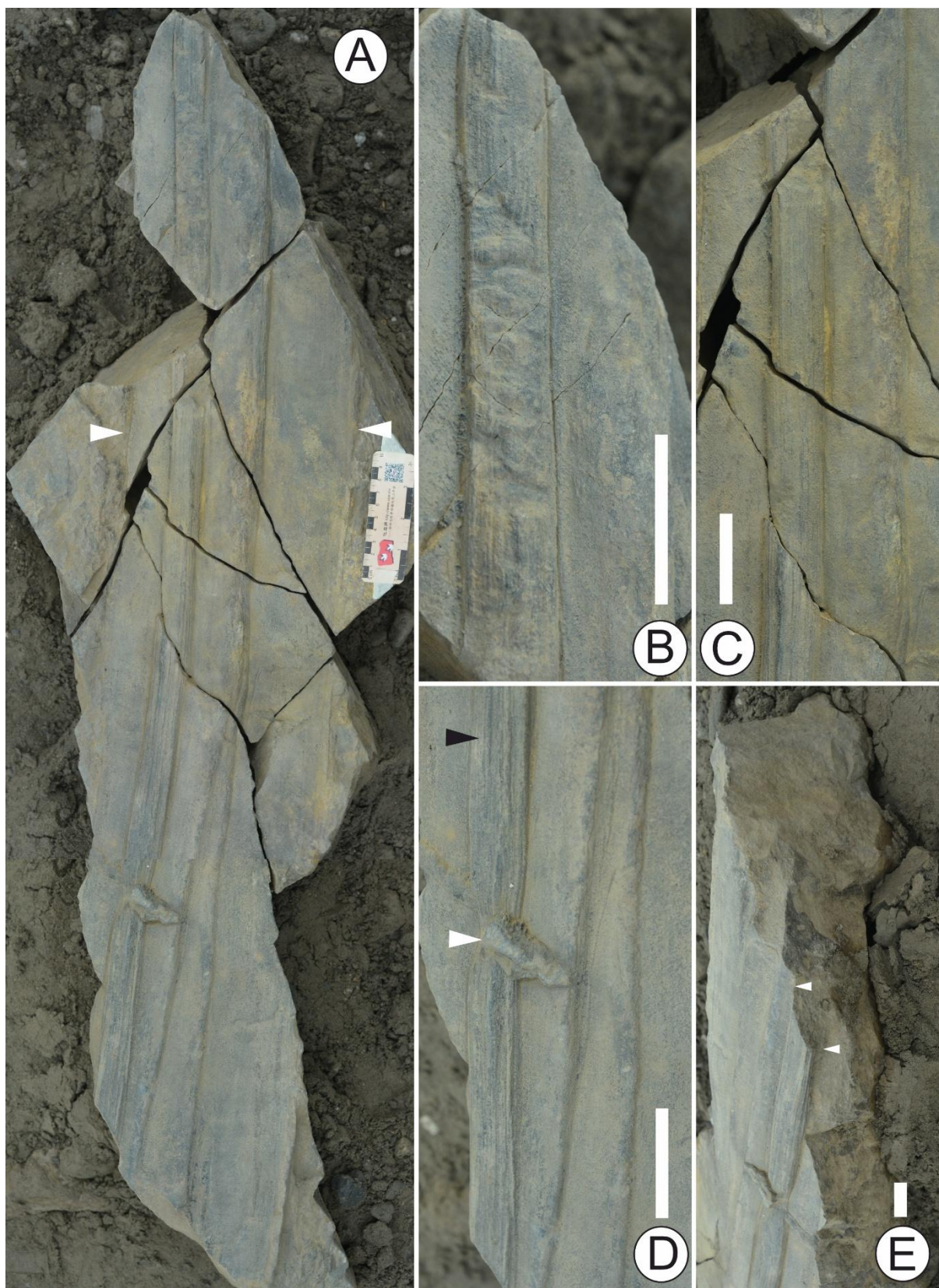


Plate 26. Scanning electron micrographs of coalified *Callixylon* wood from the Plantekløfta Formation.

A. Transverse section of coalified wood showing radially aligned tracheids (black arrow) and perpendicular parenchymatous rays (white arrow). Scale bar = 600 μm .

B. Radial longitudinal section showing groups of cohortoid pitting in tracheids of the secondary xylem. White * depicts unpitted areas between groups of pits. Scale bar = 100 μm .

C. Close-up of two tracheids in radial view, showing multiple groups of cohortoid pits and smooth cell walls between pit clusters. Scale bar = 30 μm .

D. Detail of bordered pits seen in C, bottom left. Scale bar = 10 μm .

E. Two tracheids with a poorly preserved possible parenchymatous ray (centre). Scale bar = 20 μm .

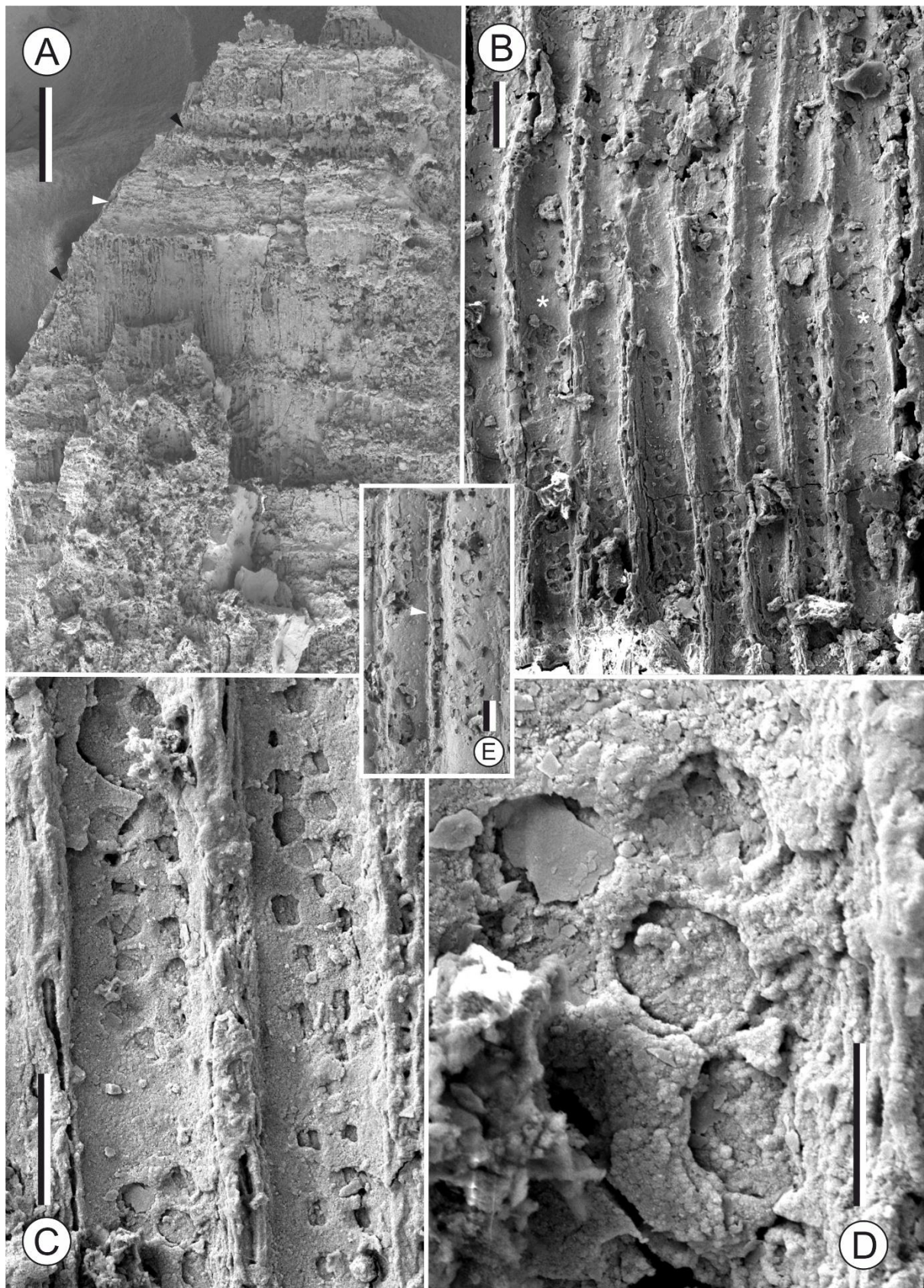


Plate 27. Scanning electron micrographs of *Callixylon* wood collected from the Plantekløfta Formation.

A. Section of secondary xylem showing radially oriented tracheids with distinct cohortoid pitting. Scale bar = 200 μm .

B. Close-up of radially oriented tracheids with cohortoid pitting arranged in discrete groups. Scale bar = 60 μm .

C. Four radially aligned tracheids displaying multiple groups of cohortoid pits along their length; tracheid walls between pit groups appear smooth. Scale bar = 30 μm .

D. Pairs of bordered pits arranged in cohortoid groups along the length of a single tracheid. Scale bar = 20 μm .

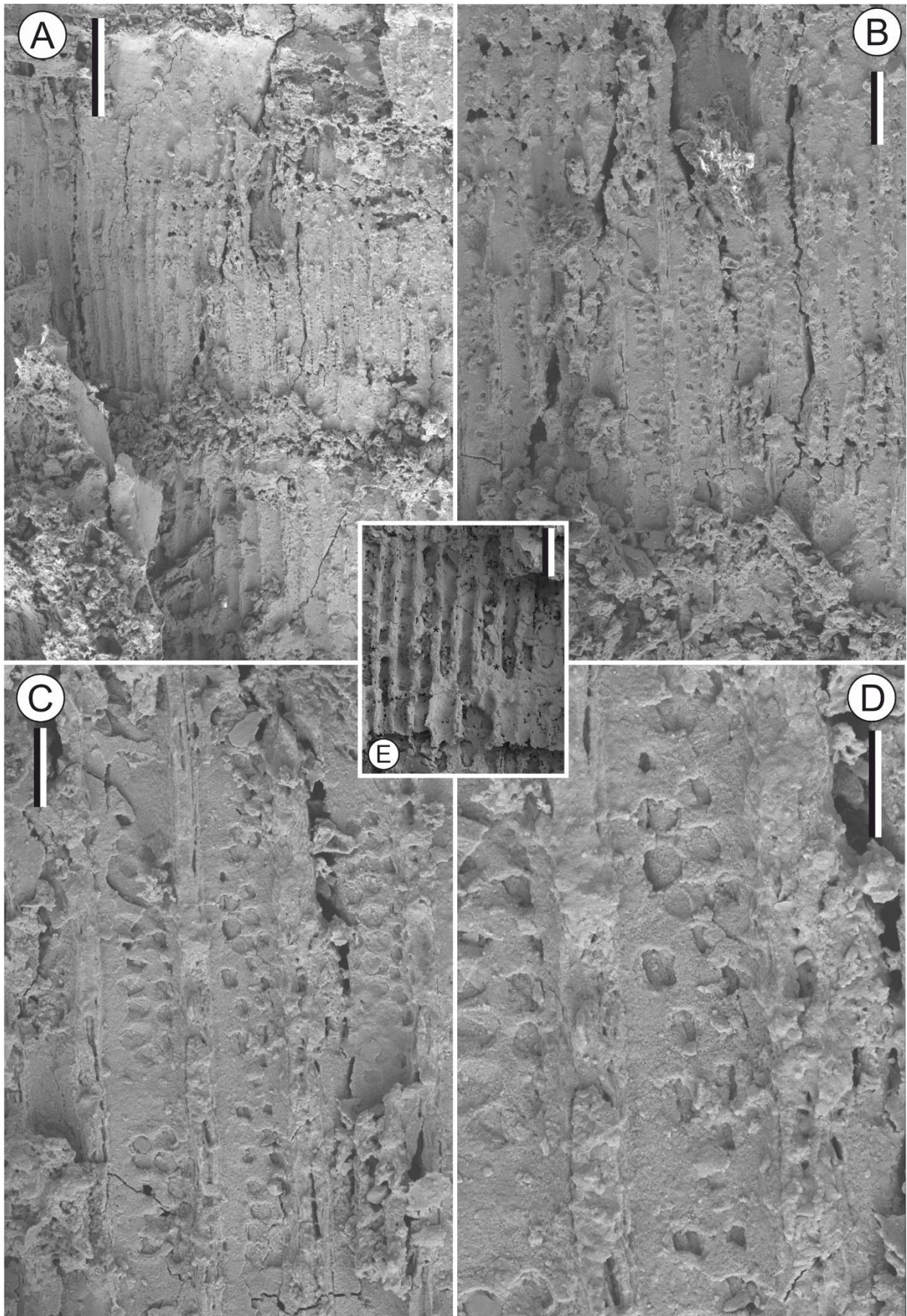


Plate 28. *In situ* rooting structures attributable to *Archaeopteris* from the Plantekløfta Formation.

(A–B) Vertical root systems preserved at NARCHF, showing a central axis with associated laterals. **A.** Entire upright tree including trunk. **B.** Close-up of trunk base with lateral roots penetrating grey palaeosol; white arrow indicates a smaller lateral root emerging from a larger one.

(C–F) Rooting systems from locality AF22B, with upright axes penetrating the palaeosol and associated lateral roots extending horizontally. **C.** Entire upright trunk with lateral root system extending horizontally in the palaeosol. **D.** Horizontal perspective showing full lateral system. White arrow shows lateral root on right side of rooting system and black arrow shows vertical orientation of roots. **E.** Close-up of left lateral root penetrating downwards into the palaeosol. **F.** Close-up of the lateral root system in its entirety.

Scale bar in all = 10 cm

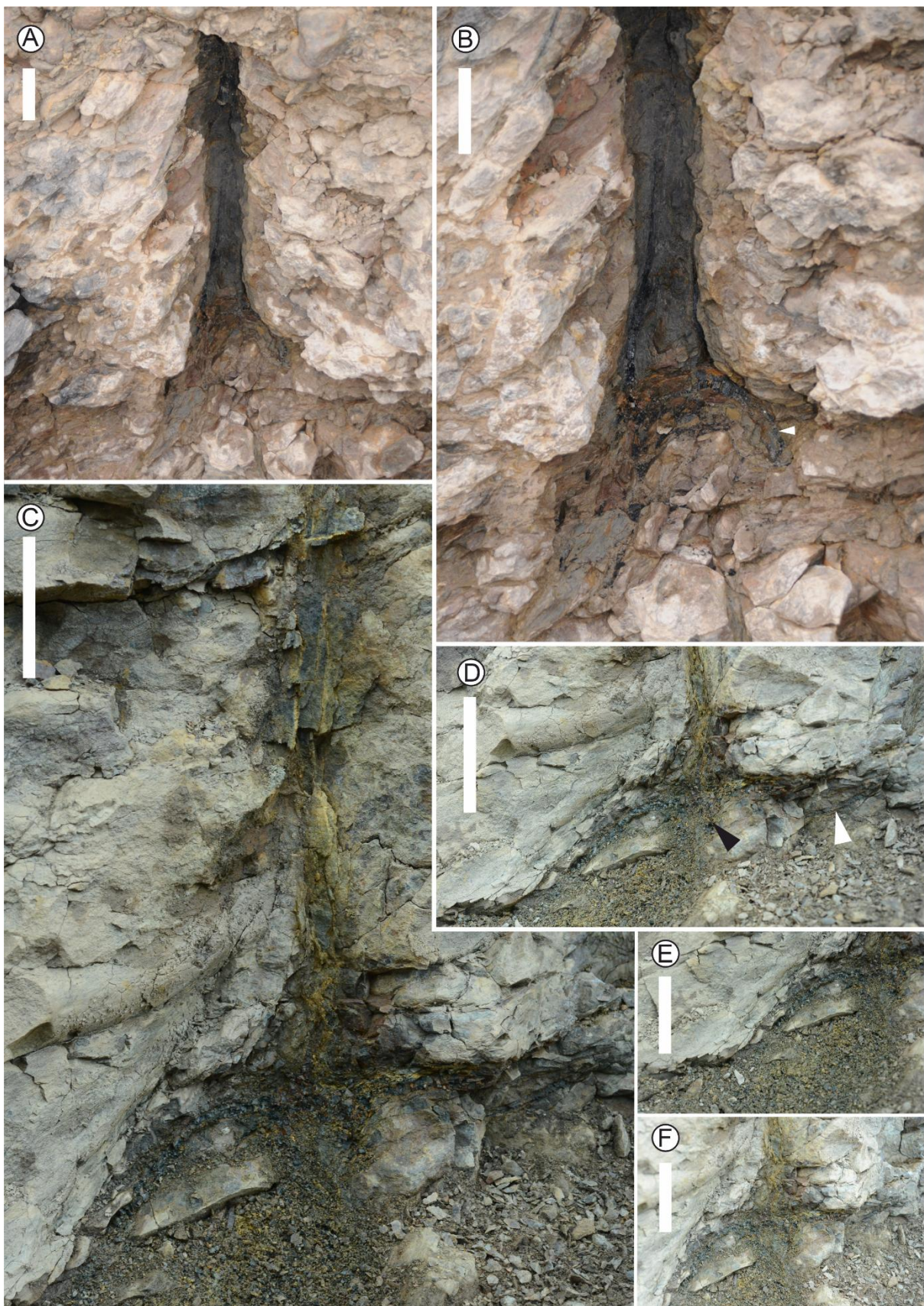


Plate 29. *Protolepidodendropsis pulchra* cormose tree base (AF-Base-01), preserved as an internal cast, with details of leaf cushions and phyllotactic patterns.

A. One side of tree base showing details of leaf cushions. The same position is marked with a red arrow in A, C, and D. White arrows indicate where the curvature of the base becomes concave. An asterisk (*) marks larger leaf bases towards the top of the base. Scale bar 50 mm.

B. Reverse side of the base, where no leaf cushions are preserved. A missing portion of the base is indicated by black arrows. Scale bar 50 mm.

C. Upper portion of the base showing the phyllotactic pattern of leaf cushions. An asterisk (*) indicates larger leaf bases towards the top, while a double asterisk (**) highlights smaller, more numerous leaf bases towards the bottom. Scale bar 25 mm.

D. Middle-lower portion of the base showing smaller, more numerous leaf cushions arranged in clockwise rows. An asterisk (*) marks larger leaf bases towards the top, and a double asterisk (**) denotes smaller, denser leaf bases at the bottom. Scale bar 50 mm.

E. Very bottom portion of AF-Base-01, oriented parallel to the palaeosol layer. Scale bar 25 mm.

F. Very top portion tree base, the entire circumference of the base is incomplete, with sections of the cast not preserved (white arrow). Scale bar 25 mm.

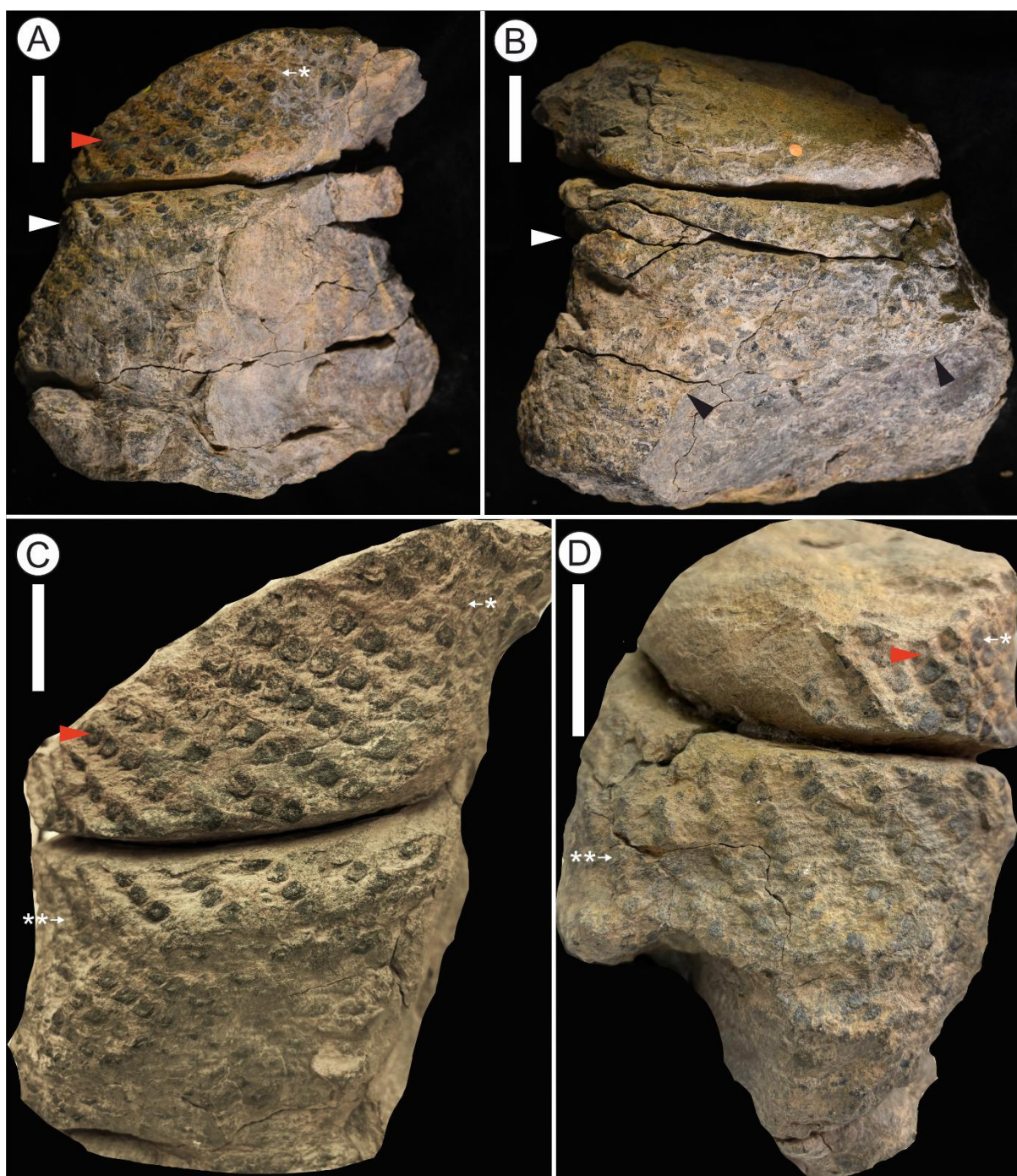


Plate 30. *Protolapidodendropsis pulchra* cormose tree base (AF-Base-02), preserved as an internal cast with vertical striations on the surface.

A. One side of the tree base showing vertical striations on the surface (black arrow). Two grooves running around the circumference of the base are indicated by white arrows. Photographed under cross-polarized lighting. Asterisk (*) depicts where angle of tapering increases. Scale bar: 25 mm.

B. Reverse side of the base. Photographed under cross-polarized lighting. Asterisk (*) depicts where angle of tapering increases. Scale bar: 25 mm.

C. Same view as A but photographed under different lighting conditions. Scale bar: 25 mm.

D. Same view as B but photographed under different lighting conditions. Scale bar: 25 mm.

E. Very top portion of AF-Base-02. The black arrow indicates a distinctive margin, which likely represents the external surface of the base. Above this margin, the cast has broken off, exposing the internal portion of the cast rather than the original external surface. Scale bar 25 mm.

F. Very bottom portion of the base preserved incompletely. White arrows indicate areas where the outer circumference of the base is missing. The black arrow marks a distinctive margin where the cast has broken off. Above this margin, the exposed section represents the internal portion of the cast rather than the original external surface of the base. Scale bar: 25 mm.

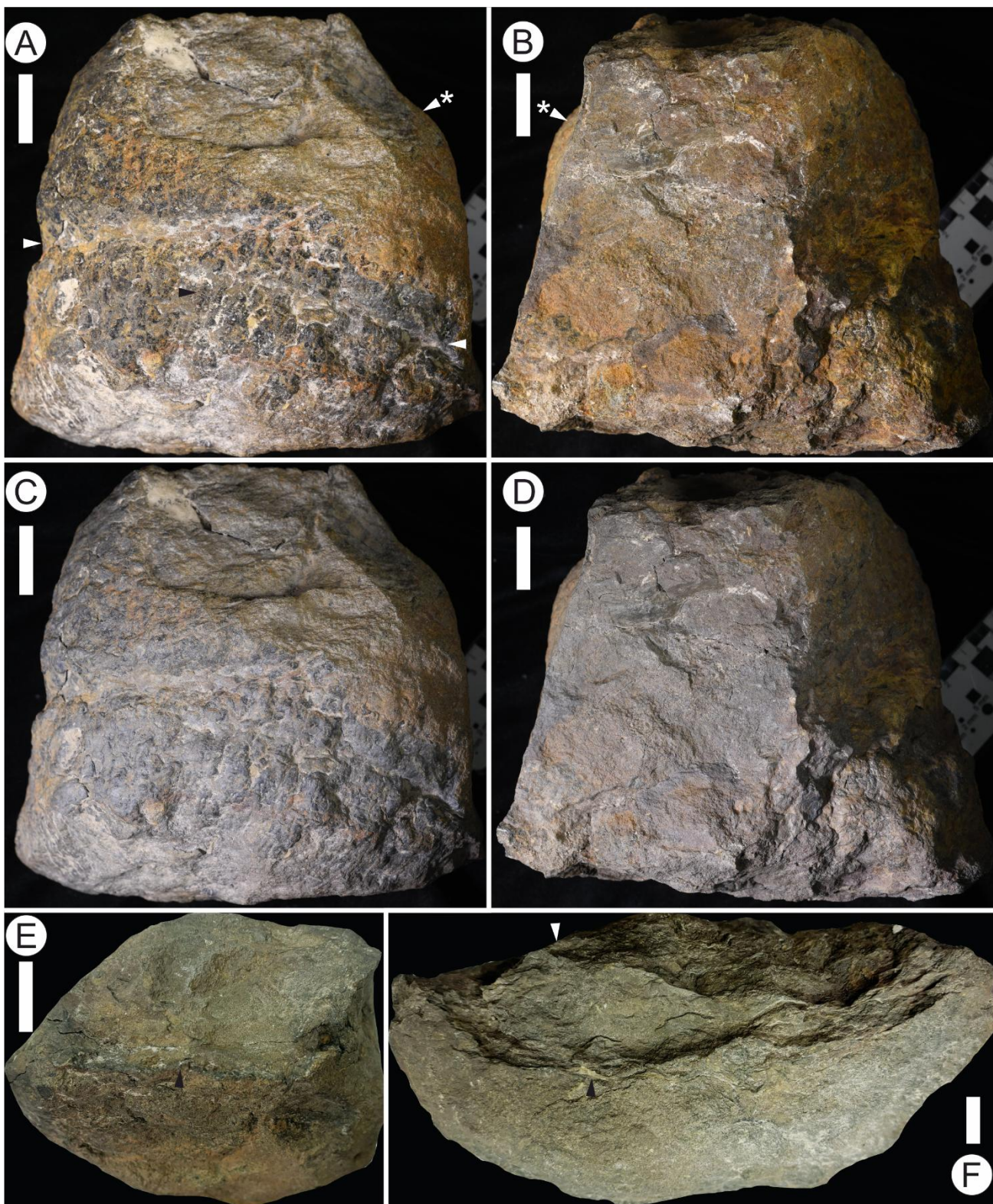


Plate 31. Ribbon-like rootlets associated with *P. pulchra*.

A. External cast of AF-Base-02 showing carbonised vertical indentations on the surface that could be interpreted as roots. White arrows outline the areas where indentations are present.

B. AF2-roots extracted from the palaeosol layer at the AF2 forest locality. This image shows the top side of the specimen.

C. AF22B-roots taken from the palaeosol layer beneath tree bases at the AF22B forest locality, also shown in Text Figure 59. This image shows the top side of the specimen.

D. Carbonised ribbon-like rootlets (from AF22B-roots; Plate 31C). Image taken under normal lighting conditions.

E. Reverse side of B (AF2-roots), showing the underside.

F. Reverse side of C (AF22B-roots), showing the underside.

G. Same as D but captured under cross-polarised light to enhance contrast.

Scale bar: 10 mm.

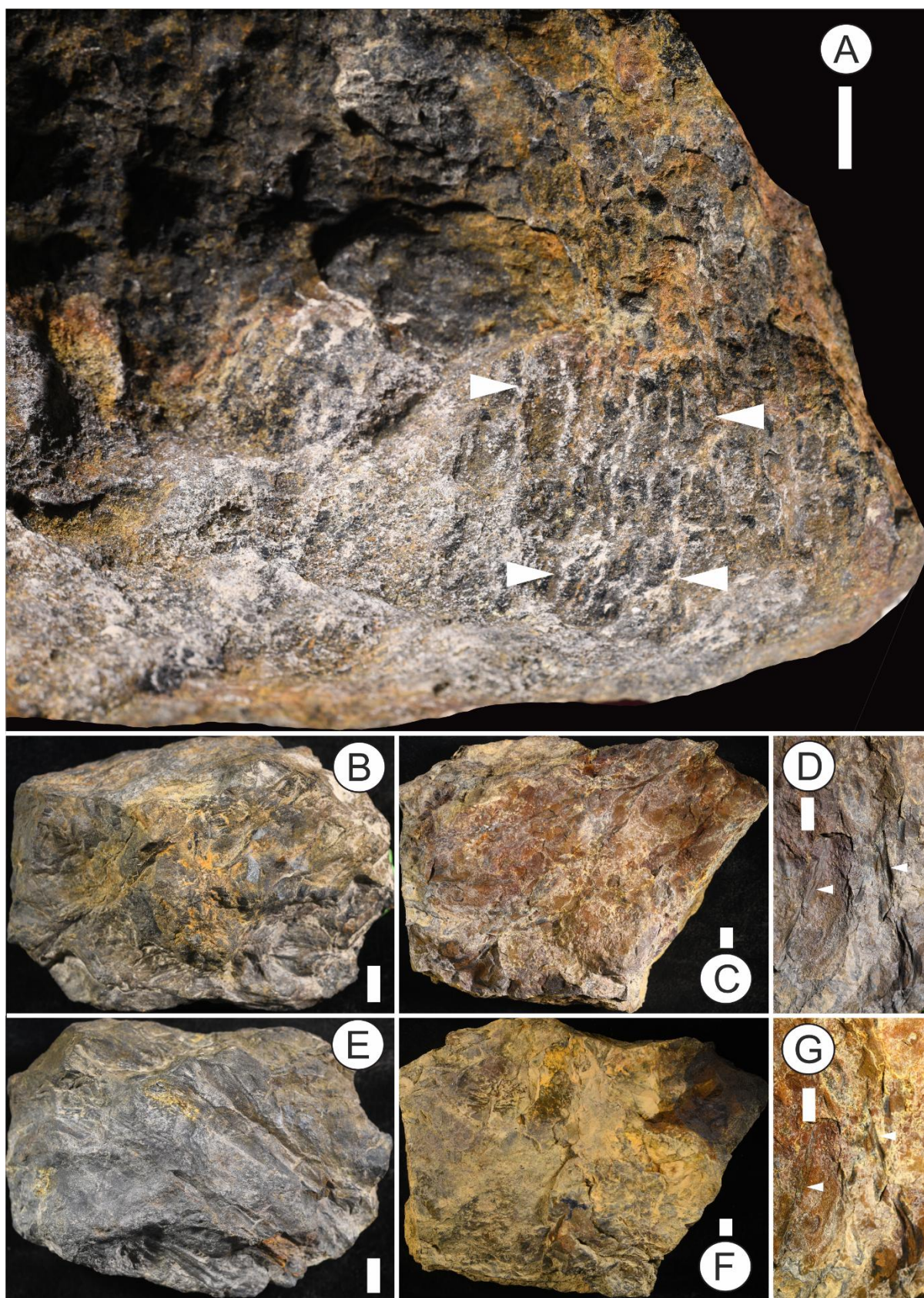


Plate 32. Microphotographs of ribbon-like rootlets found in *Protolepidodendropsis pulchra*.

A. Undulating, carbonised impression of a ribbon-like rootlet (*AF2-roots*). Scale bar: 5 mm.

B. Carbonised compression of a single rootlet (*AF2-roots*). Scale bar: 5 mm.

C. Carbonised compression of a ribbon-like rootlet with a central undulation (*AF2-roots*). Scale bar: 5 mm.

D. Impression of a ribbon-like rootlet with a distinctive negative undulation in the centre (*AF22B-root*). Scale bar: 5 mm.

E. Carbonised compression of a poorly preserved, bifurcating rootlet. The white arrow indicates where the right rootlet emerges post-bifurcation (*AF2-roots*). Scale bar: 100 µm.

F. Carbonised compression of a single ribbon-like rootlet (*AF2-roots*). Scale bar: 100 µm.

G. Impression of a ribbon-like rootlet with a very distinctive negative undulation in the central portion (*AF22B*). Scale bar: 100 µm.

H. Macrophotograph of a hook-like rootlet (I), viewed in cross-polarised light to enhance contrast. The white arrow indicates the location of the root (*AF22B-roots*). Scale bar: 1 mm.

I. Microphotograph of the hook-like rootlet from panel H, viewed without polarised light. The white arrow shows where the rootlet terminates (*AF22B-roots*). Scale bar: 100 µm.

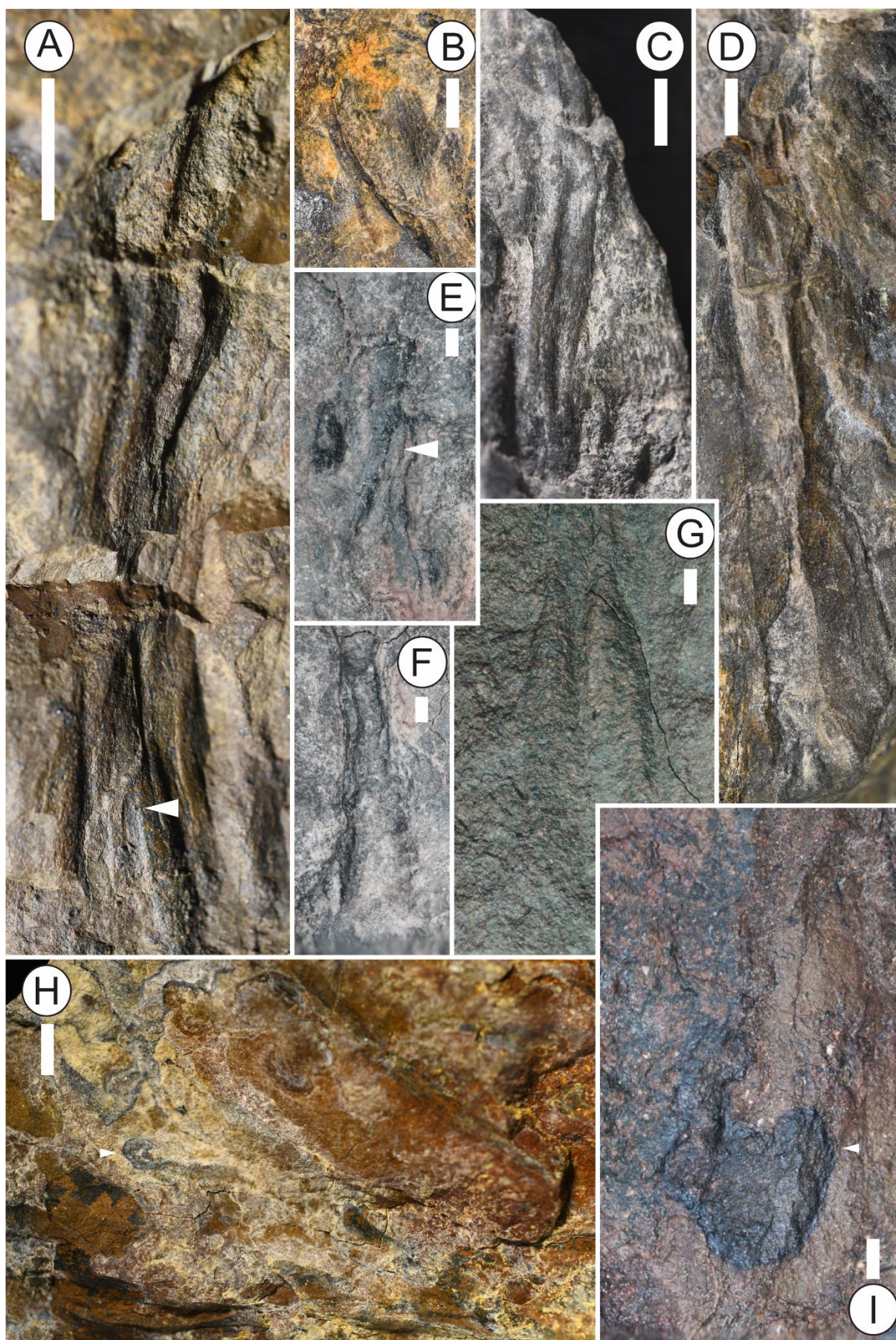


Plate 33. Macrophotographs showing variation in the preservation of leaf bases in *Protolapidodendropsis pulchra*. Although the specimens are fragmentary, the size and preservation of the leaf cushions and bases are attributed to the robust middle portion of the trunk.

A. Internal cast of trunk with preserved leaf base parenchyma (AF-2-01). Scale bar: 10 mm.

B. Fragment of carbonised external cast, including leaf base parenchyma (RM-01-01). Scale bar: 10 mm.

C. Portion of stem, preserved as an external cast of outer cortical tissues (PK-Stem-52-54). Scale bar: 10 mm.

D. Reverse side of specimen C. Scale bar: 10 mm.

E. Cross-section of *P. pulchra* trunk, preserved as an internal cast of outer cortical tissues (same specimen as A). Scale bar: 10 mm.

F. Fragment of external impression of *P. pulchra* (PMO.250.239). Scale bar: 10 mm.

G. Fragment of external impression of *P. pulchra*, with distinctive leaf cushion markings (AF-2-07). Scale bar: 10 mm.

H. Cross-section of a slightly compressed *P. pulchra* trunk, preserved as an external cast of outer cortical tissues (AF-2-05). Scale bar: 10 mm.

I. Large fragment of *P. pulchra* external impression, showing details of leaf base parenchyma (PA1262). Scale bar: 10 mm.

J. Poorly preserved fragment of middle trunk of *P. pulchra*, with leaf cushions, preserved as an external cast of cortical tissue (AF-2-08). Scale bar: 10 mm.

K. Rhomboidal leaf cushions and teardrop-shaped leaf scars, preserved as an external cast in coarse sandstone (PK-0058). Scale bar: 10 mm.

L. Coalified impressions of overlapping *P. pulchra* leaf cushions (PMO.250.178). Scale bar: 10 mm.

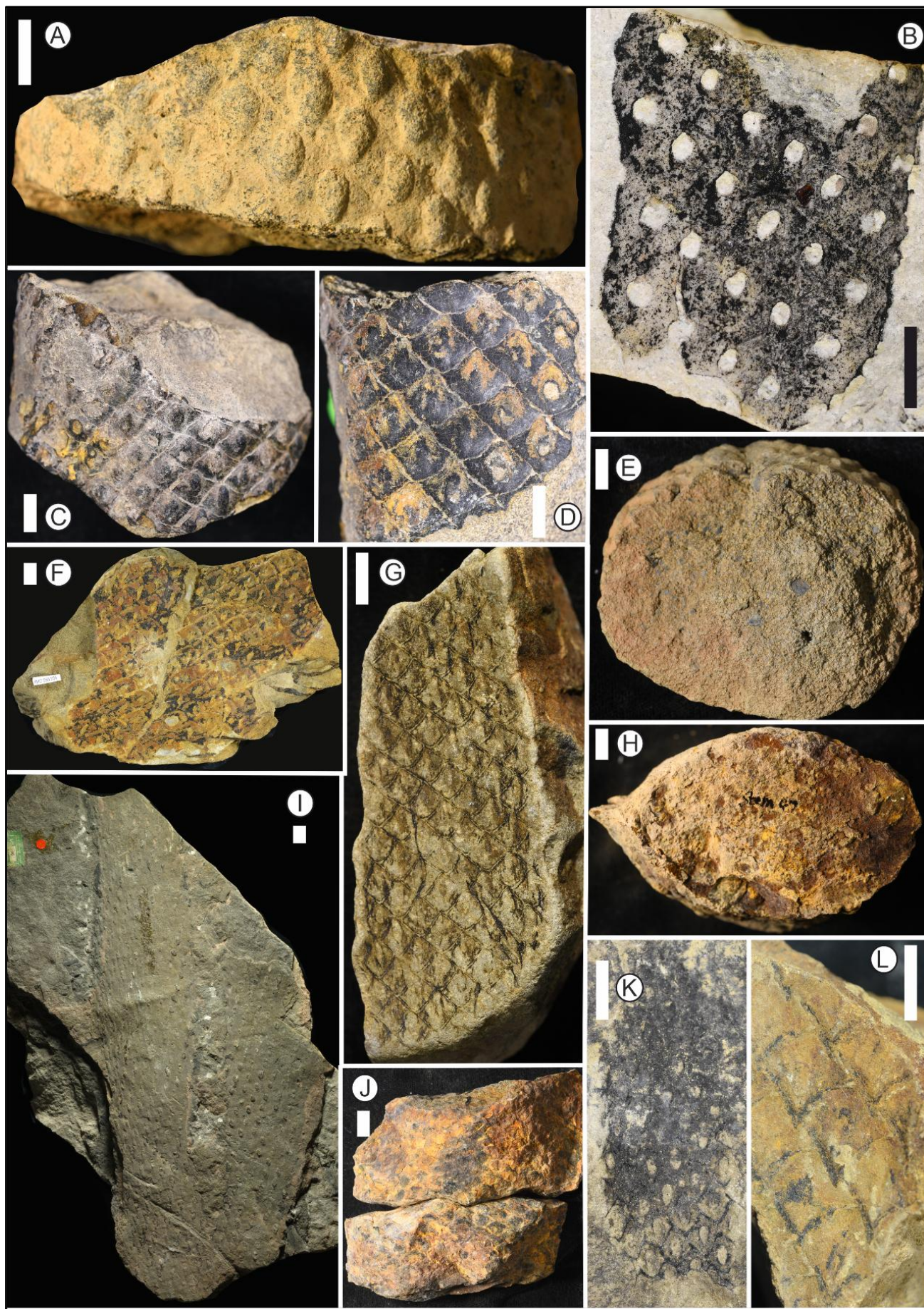


Plate 34: Macrophotographs of large trunks of *Protolepidodendropsis pulchra* from various localities across Spitsbergen.

A. Large internal cast of *P. pulchra* trunk with weakly defined rhomboid leaf cushions and details of leaf base parenchyma. From Schweitzer 1965 (Taf 35, Figure 2). Scale bar: 20 mm.

B. Reverse side of the trunk shown in A. Scale bar: 20 mm.

C. Large, poorly preserved internal cast of *P. pulchra*, showing details of leaf base parenchyma. From Schweitzer 1965 (Taf 36, Figure 1). Scale bar: 20 mm.

D. Large internal cast of *P. pulchra* preserved in coarse sandstone, with details of leaf base parenchyma. From Schweitzer 1965 (Taf 34, Figure 2). Scale bar: 20 mm.

E. Large internal cast of *P. pulchra* stem, showing details of leaf cushions and leaf base parenchyma. From Schweitzer 1965 (Taf 35, Figure 1). Scale bar: 20 mm.

F. Large internal cast of *P. pulchra*, with leaf base parenchyma preserved. Collected from Eastern Canyon and Fiskekløfta. From Høeg 1942 (Text Figure 29). *PA1184*. Scale bar: 20 mm.

G. Large internal cast of *P. pulchra* with relatively well-preserved leaf cushions and leaf base parenchyma. The trunk widens slightly at the proximal portion, suggesting dichotomisation (indicated by the white arrow). Collected from River's Meet locality (*RM-03*). Scale bar: 20 mm.

H. Reverse side of the stem shown in G. Scale bar: 20 mm.

I. Medium-sized internal cast of *P. pulchra* preserved in coarse sandstone, with details of leaf base parenchyma. From Schweitzer 1965 (Taf 34, Figure 1). Scale bar: 20 mm.

J. Reverse side of the stem shown in I. From Schweitzer 1965 (Taf 34, Figure 1). Scale bar: 20 mm.

Note: Black arrows highlight cracks likely caused by deformation during the taphonomic process and subsequent sediment filling.

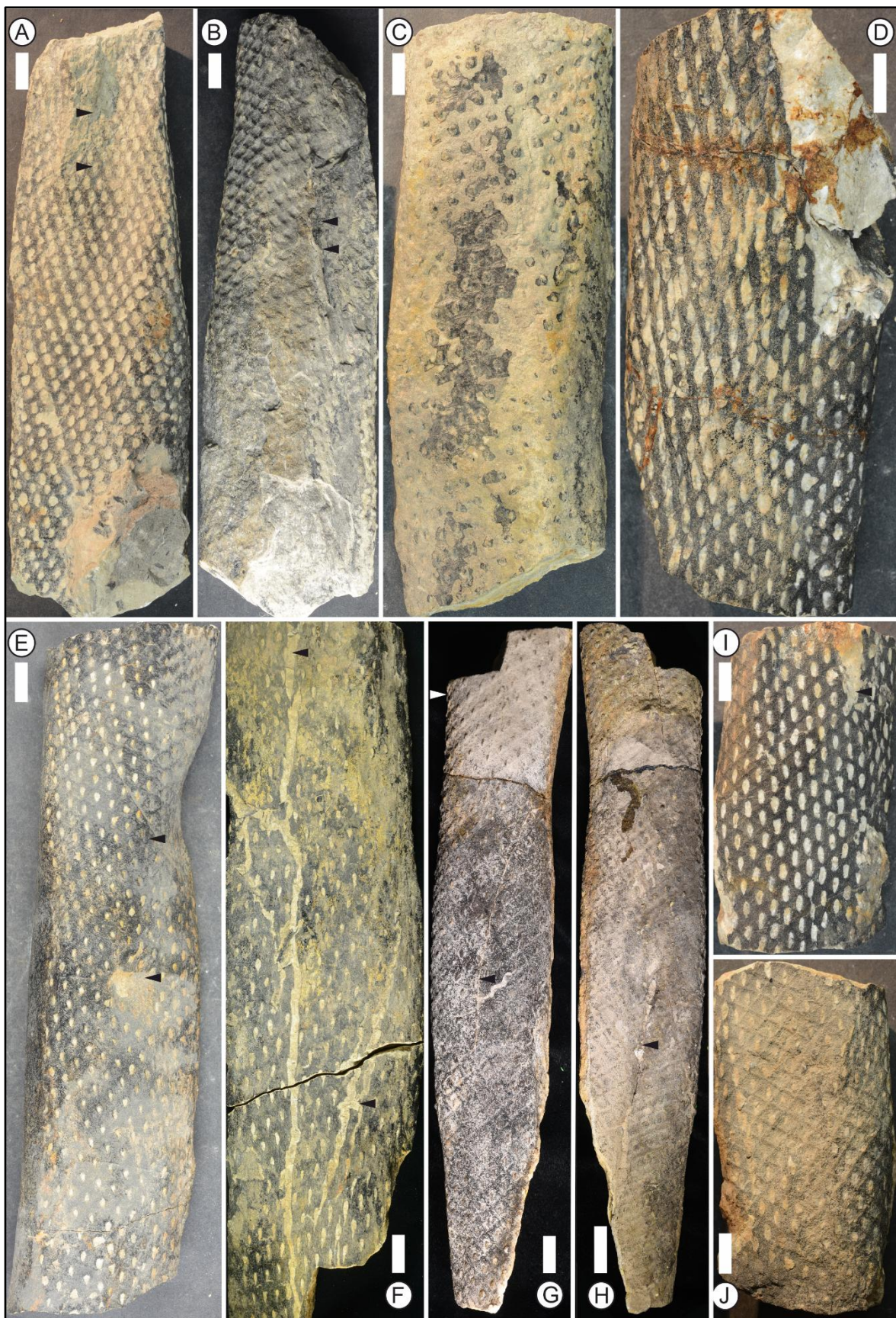


Plate 35. Macrophotographs of the trunk of *Protolapidodendropsis pulchra*.

A. Robust upper portion of the trunk, preserved as an internal cast, culminating in a first-order bifurcation at the apex. The lower portion of the trunk (below the black arrow) features flat leaf cushions consistent with typical descriptions of *Bothrodendron mimerense* from Høeg (1942). The surface texture above the white arrow corresponds to Høeg's early descriptions of *P. pulchra*. The area between the black and white arrows represents a transitional zone between the two patterns. From Schweitzer 1965 (Taf 34, Figure 4).

B. Reverse side of A, with arrows indicating the same features as in A.

C. Close-up of the bifurcation at the apex of the trunk. Cross-polarised light was used to enhance changes in surface texture.

D. External cast of the middle portion of the trunk, showing details of leaf cushions (*AF-Stem-01*). Scale bar: 10 mm



Plate 36. Various types of preservation of axes in *Protolepidodendropsis pulchra*.

- A. Slightly compressed, poorly preserved internal cast. The black arrow indicates the edge of the cast (AF22B-06). Scale bar: 10 mm.
- B. Reverse side of A, showing the external impression of the axis in the surrounding sedimentary deposit. White arrows highlight the edge of the external impression, and the black arrow indicates the edge of the internal cast. Scale bar: 10 mm.
- C. Internal cast with some details of leaf base parenchyma. The black arrow marks the edge of the cast (AF22B-10). Scale bar: 10 mm.
- D. Reverse side of C, showing the external impression of the axis in the surrounding sedimentary deposit. White arrows highlight the edge of the external impression, and the black arrow indicates the edge of the internal cast. Scale bar: 10 mm.
- E. Poorly preserved axis with unusual preservation. Portions of the leaf base parenchyma are marked with white arrows (BF-01). Scale bar: 10 mm.
- F. Axis preserved with distinctive vertical orthostichies along its entire length (BF-03). Scale bar: 10 mm.
- G. Small compression displaying the typical rhombic pattern associated with *B. mimerensis* (EST-Bergeria). Scale bar: 5 mm.
- H. Medium-sized axis displaying the typical surface texture of *P. pulchra* as described by Høeg (1942) (BF-02). Scale bar: 10 mm.
- I. External impression showing details of leaf base parenchyma. Some coalified material, likely from leaf compression, is present (white arrow) (AF22B-09). Scale bar: 5 mm.
- J. Poorly preserved internal cast and external impression (AF22A-01).
- K. Long, unbranched axis, preserved as an external impression (Mun-01). Scale bar: 10 mm.
- L. Long, unbranched internal cast (marked with a white star), with details of the external impression (black star) (PK-06). Scale bar: 10 mm.

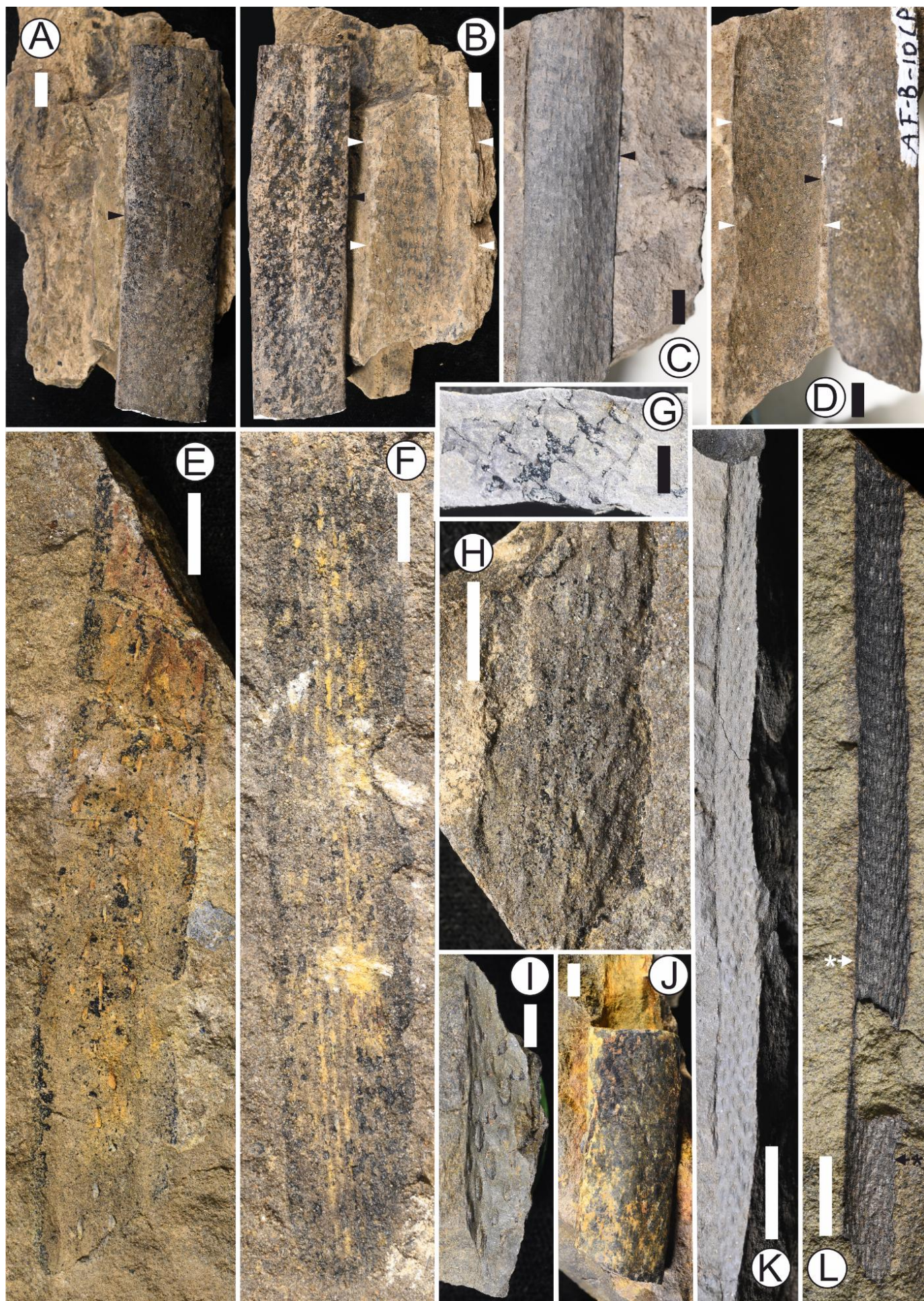


Plate 37. Bifurcating *Protolepidodendropsis pulchra* trunks.

A. Field photograph of RM-01 showing the upper trunk with a main bifurcation (white arrow) and a second incipient bifurcation in the right axis (black arrow), partly obscured by sandstone. Red arrow indicates an external cast with *Bergeria*-type leaf cushions; blue arrow indicates three-dimensional *P. pulchra* leaf cushions; green arrow marks the basal portion of the internal cast. Scale bar = 10 mm.

B. Same specimen after removal from the sandstone matrix. White arrow marks the first bifurcation and black arrow marks the second, partly obscured bifurcation. Black and white asterisks indicate positions shown in F, H and I. Red arrow indicates a fragment lost after field photography; green arrow marks the basal internal cast. Scale bar = 10 mm.

C. Bifurcating trunk collected by Schweitzer, preserved as an internal cast (black arrow) and external cast in surrounding sediment (white arrow) (Schweitzer, 1968, Plate 39, Fig. 1; Schweitzer, 1999, Plate 22, Fig. 1).

D. Reverse view of C. Scale bar = 10 mm.

E. RM-01 after preparation. The right-hand axis above the first bifurcation has been partly lost, but its morphology is recorded in field photographs and remaining material shown in F, H and I. Scale bar = 10 mm.

F. Upper portion of the right axis after the second bifurcation, corresponding to the black asterisk in B. Scale bar = 10 mm.

G. Bifurcating *P. pulchra* axis from PK, preserved as an internal cast with coalified leaf-base remains. Scale bar = 5 mm. Specimen PK-6.

H. Transverse section through the incipient dichotomy, corresponding to the white asterisk in B and I. White arrows indicate sandstone obscuring the bifurcation. Scale bar = 10 mm.

I. Alternative view of the incipient dichotomy, showing widening of the axis partly obscured by sandstone matrix. This corresponds to the same bifurcation shown in H and F. Scale bar = 10 mm.

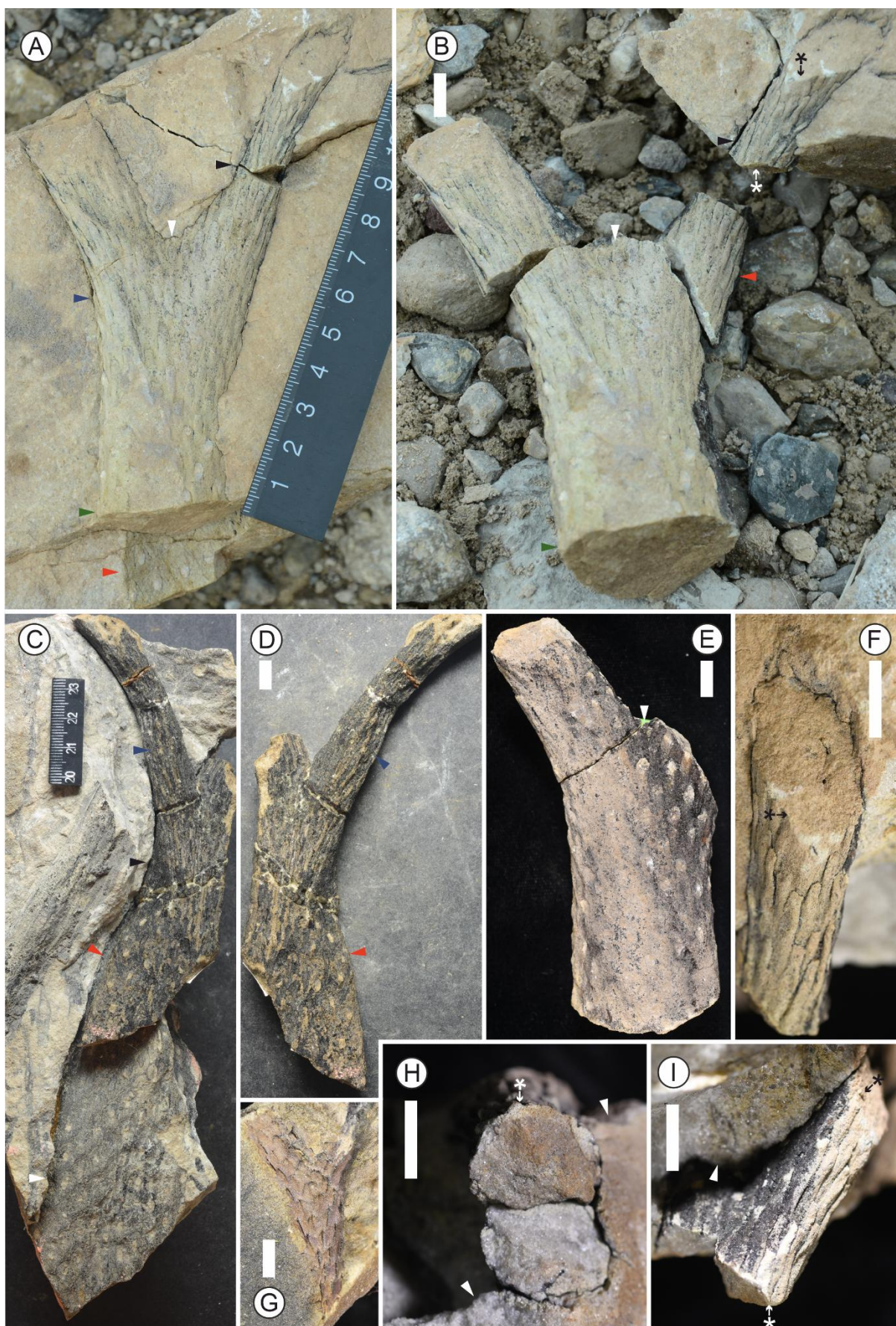


Plate 38. Ironstone nodule from EST containing a more or less intact crown of *Protolpidodendropsis pulchra*.

The nodule is composed of three large slabs, preserving the crown and the upper portion of the trunk.

- **Black arrows:** Indicate the upper portion of the trunk.
- **Green arrow:** Marks where the left portion of the crown continues underneath the surface.
- **White arrow:** Highlights the first basal dichotomy in the trunk.
- **Red arrow:** Depicts the left side of the crown.
- **Blue arrow:** Depicts the right side of the crown, assuming bilateral symmetry.
- **Black asterisk:** Indicates the overlap between the left and right branches of the crown.
- **White asterisk:** Marks the point on the right side of the crown where the splayed axes emerge.

Scale bar: 30 mm.



Plate 39. Left primary branch of *P. pulchra* crown (refer to Plate 38, red arrow).

- A. Side profile of the branch. White arrows indicate the three-dimensional structure, showing at least two layers descending beneath the sediment surface of the crown. Yellow and purple labels correspond to those described in Text Figure 67. White arrows show two descending crown layers. The black arrow marks where axis 1A disappears ~30 mm below the surface of the nodule.
- B. Alternate view of the left primary branch, with white asterisks indicating the length of axis L-L-1.
- C. Additional angle showing the distal length of L-L-1, marked by white asterisks.
- D. Top-down view of the left primary branch.
- E. Side profile view of the branch from a different orientation.
- F. Additional side profile of the left primary branch.
- G. View of the left primary branch with scale bar for reference.

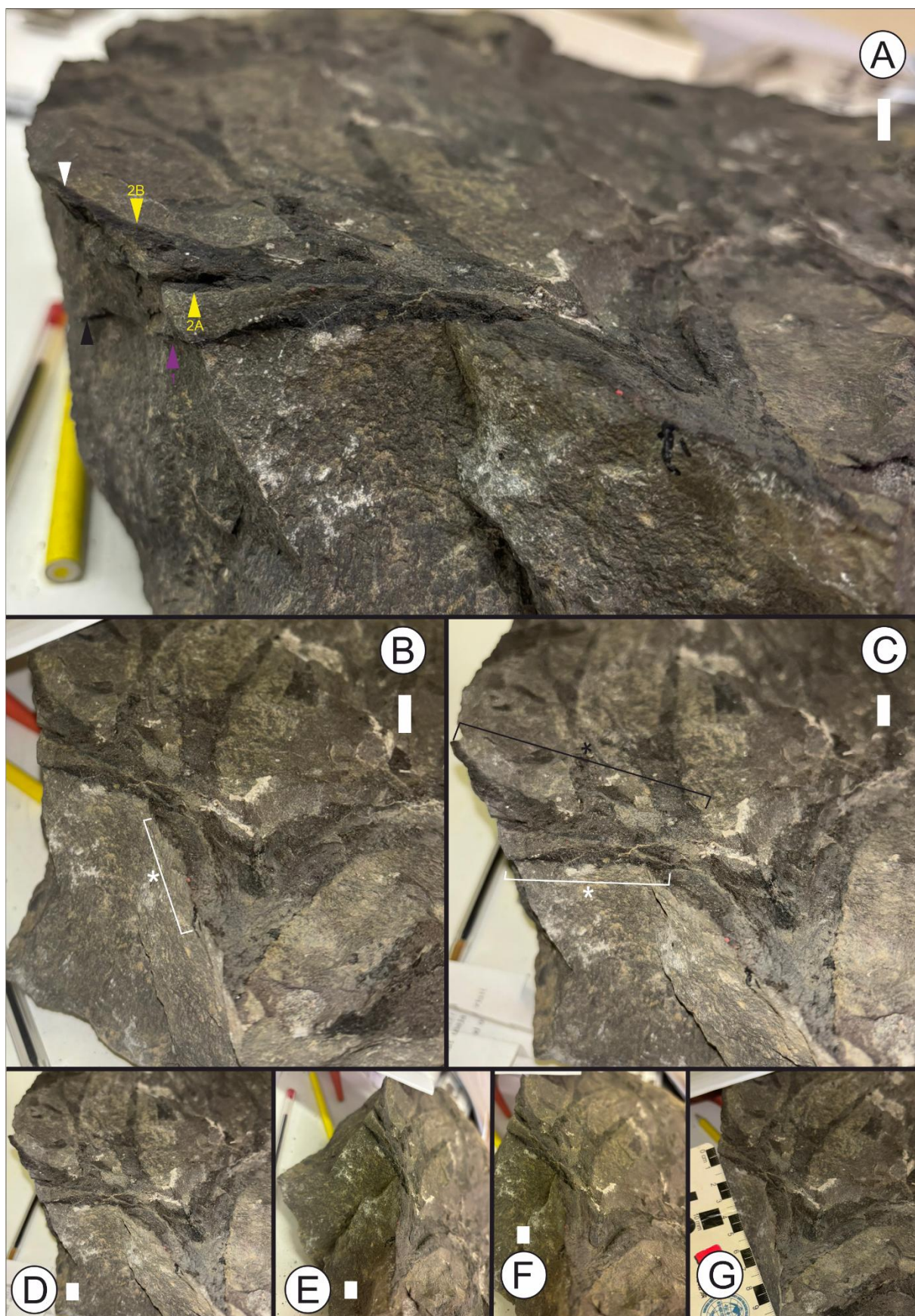


Plate 40. Fragments of ironstone concretion containing portions of *P. pulchra* crown.

A. Important counterpart containing multiple layers of bifurcating axis, likely representing the fifth dichotomy along the length of the crown (see Text Figure 69). EH-2. Scale bar 10 mm.

B. The same as in A, but with cross polarised light to enhance contrast. Scale bar 10 mm.

C. Counterpart showing thinnest axis fragment likely belonging to the most distal portion of the crown (white arrow). EH-24. Scale bar 10 mm.

D. Counterpart containing parallel upright axis fragments which likely belongs to the distal portions of the crown. EH-9. Scale bar 10 mm.

E. Close up of the left side of the crown, highlighting its three-dimensional nature. Black arrow highlights L-R-1B seen in Text Figure 12D. Scale bar 15 mm.

F. Close up of bifurcation on crown EH-6. Scale bar 10 mm.

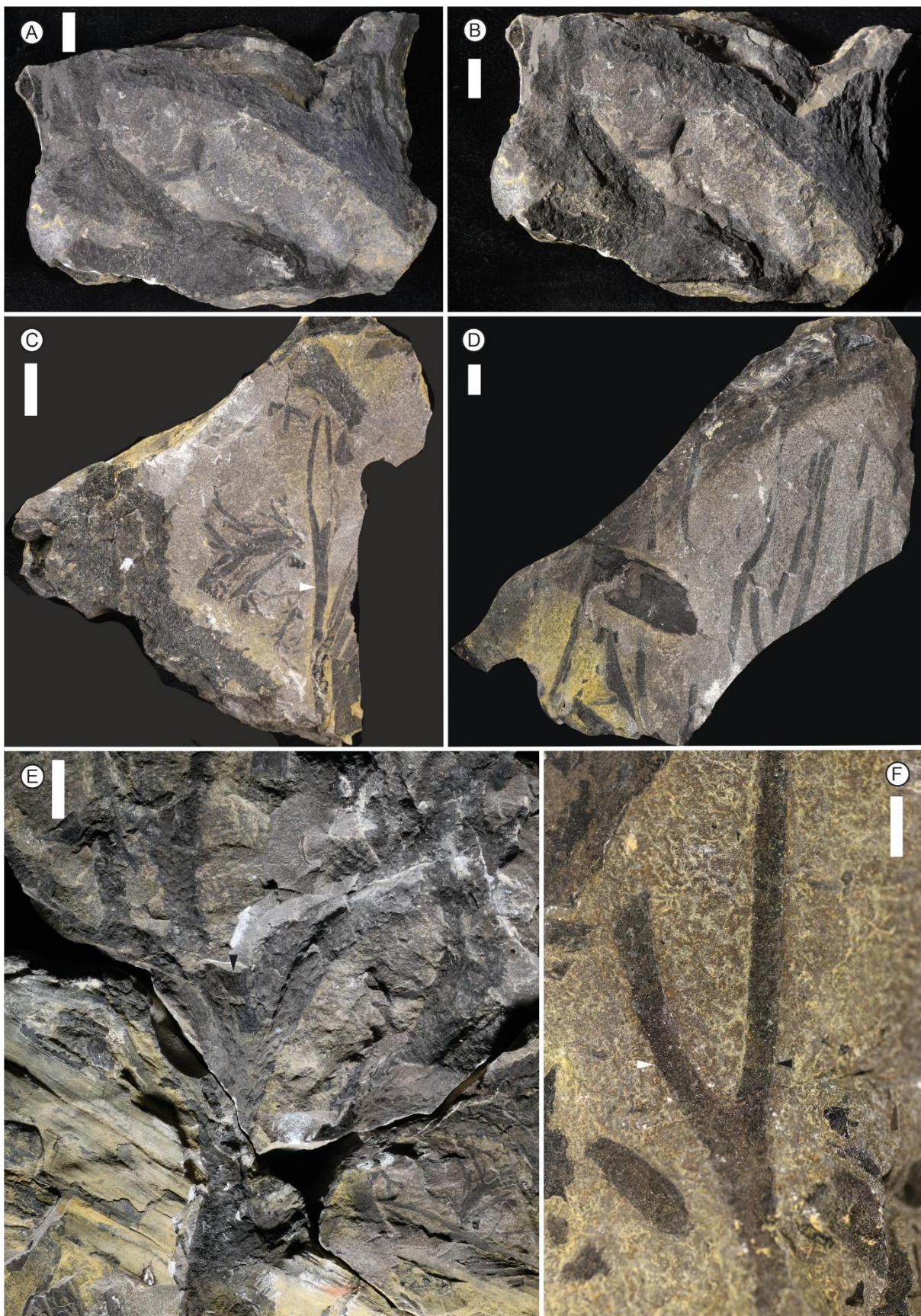


Plate 41. Right primary branch of *Protolepidodendropsis pulchra* crown contained within an ironstone nodule.

A. Right primary branch showing vertical separation of two sub-units; white arrow highlights a wedge of sediment between them. Black arrow highlights R-R-1. White * shows distal tip of R-L-2 which is overlaid by sediment. Black * shows the surface of the nodule which is above R-L-2.

B. Alternate view of the right primary sub-unit; white asterisk indicates the point of vertical separation between the two sub-units. White * depicts where slab junction between two pieces of nodule join, somewhat obscuring the margin between R-L and R-R segments.

C. Side profile of the right primary branch showing the three-dimensional spacing of axes arranged in different vertical layers within the nodule.

D. Close-up view of the R-R sub-unit.

E. Alternative angle of the right primary sub-unit showing vertical separation between components. White arrow highlights the main axis of right branch to which R-R-2B is preserved perpendicular.

F. Additional view of the right primary branch; white asterisk depicts the length of R-L-1A, and black asterisk shows the full length of R-L-1B. Black arrow depicts indistinct margin between R-R-1 and R-R-2. Bifurcation separation R-R2A and R-R-2B. Black * depicts R-L-1B. White * depicts R-L-1A.

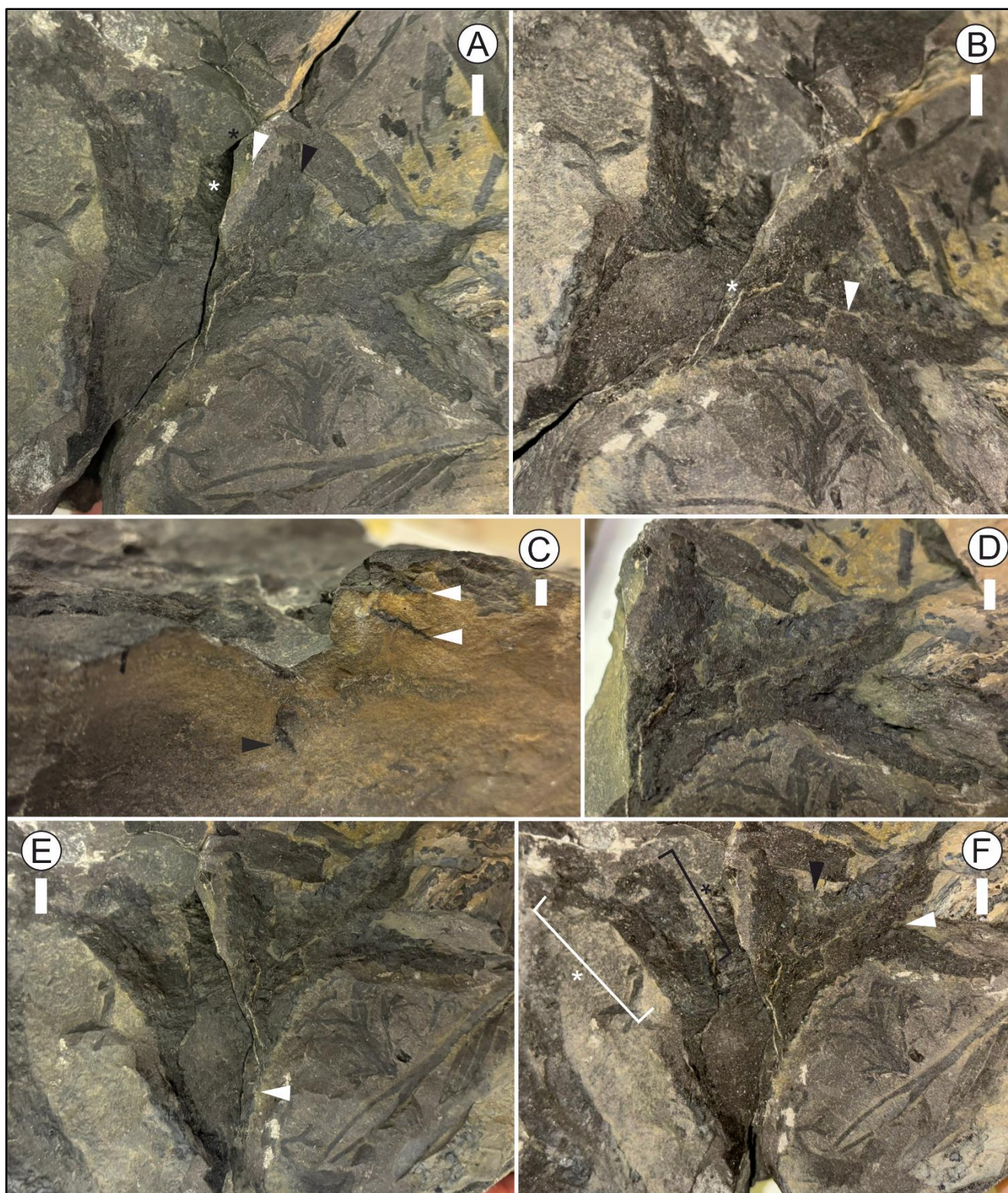


Plate 42. Leaves preserved on crown (A-C) and distal axes of *Protolepidodendropsis pulchra*.

A. Right primary branch showing leaf bases along one side, indicated by black arrows.

B. Counterpart to the specimen shown in A, with black arrows marking corresponding leaf bases.

C. Rhombic leaf bases on the upper portion of the trunk; counterpart to one of the largest slabs near the first bifurcation from trunk to crown.

D. Small bifurcating axes collected from Munindalen, showing details of leaves near the basal portion of the axes. MUNI-1 9.

E. Same specimen as in D, viewed without cross-polarised lighting.

F. Bifurcating specimen collected from River's Meet, showing details of leaf bases.

Scale bar = 10 mm in all images.

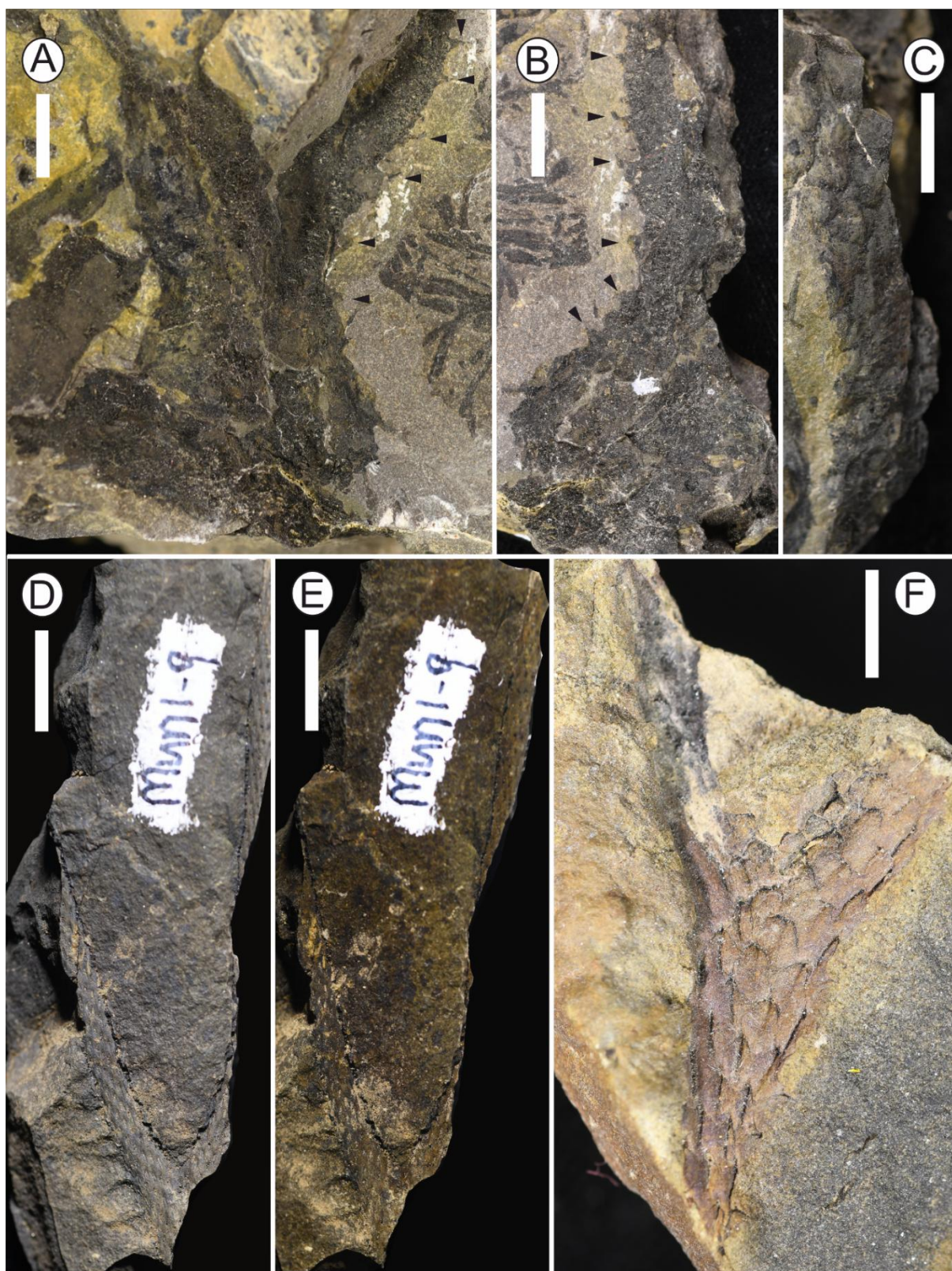
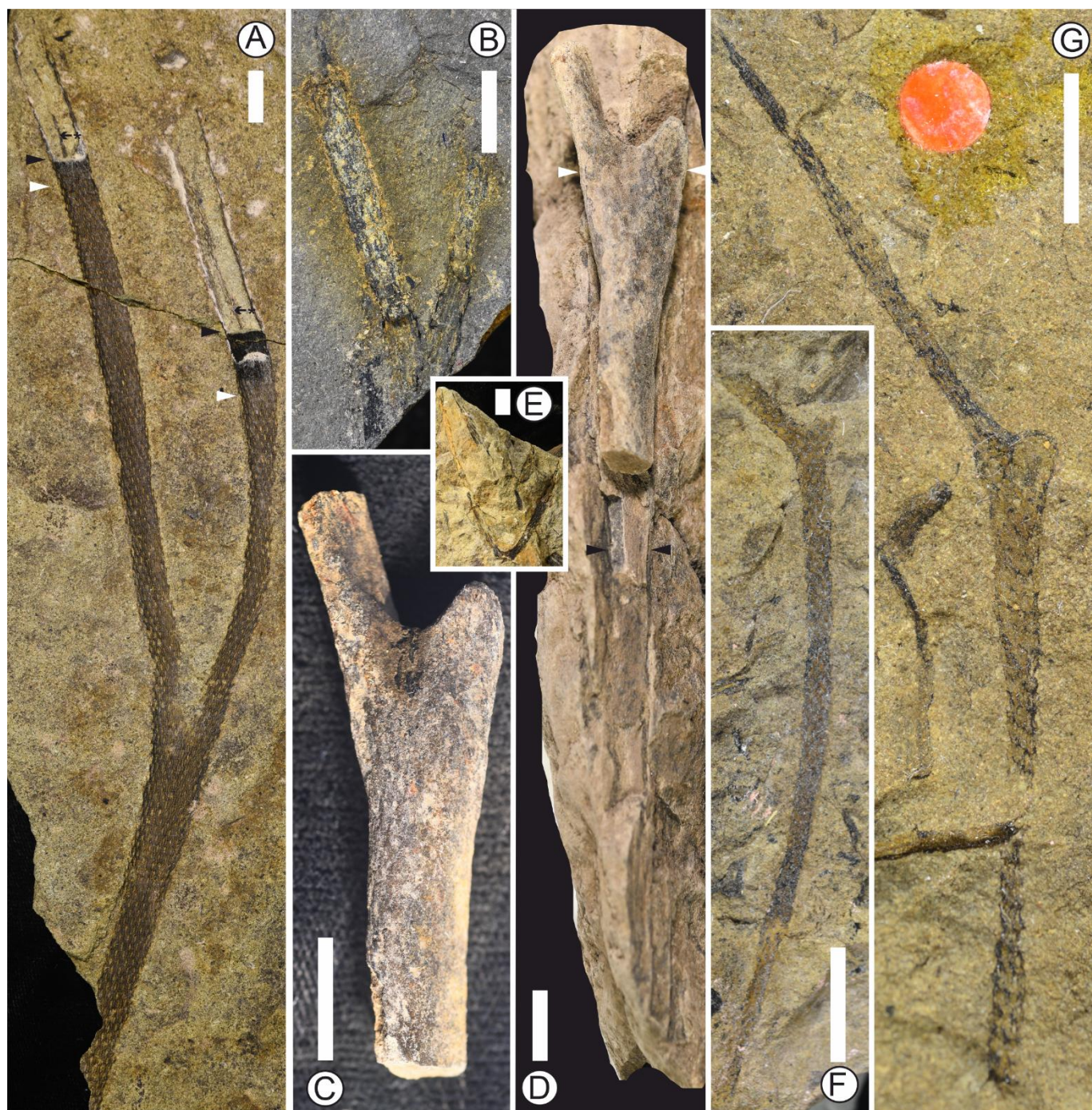


Plate 43. Distal axes from the crown of *P. pulchra*.

- A.** Larger bifurcating distal axes fragment collected from the Plantekløfta locality. Preserved as an external cast (white arrow) and internal cast (black arrow). Black asterisk indicates a central depression on the internal cast. 2016-26 (PK).
- B.** Poorly preserved bifurcating axes collected from Estheriahaugen. EST 147.
- C.** Bifurcating distal axes collected from AF22B. AF22B-2B.
- D.** External cast associated with the specimen shown in C; white arrows highlight the point where the axis is about to bifurcate.
- E.** Bifurcating axes fragment collected from Plantekløfta.
- F.** Bifurcating axes fragment from Planteryggen, illustrated in Høeg (1939), Plate XXXVII, Figure 2 (PA407).
- G.** Same slab as in F, showing a different bifurcating axes fragment.



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Appendix

Appendix A – English-Swedish-Norwegian expedition collection.

Morphotypes & the use of form genus '*Aphylopteris* & *Hostinella*'

A large proportion of the material from the historic collections consisted of fragmentary plant remains lacking reproductive organs, making it difficult to assign specimens to a specific taxon. For this reason, I have selected morphotypes that group plants with similar morphology and traits, which are listed in Table 1.

The use of form genera such as *Aphylopteris*, *Hostinella* and *Psilophytites* is essential when studying early land plant fossils from the Late Silurian to Middle Devonian periods. These taxa serve to classify plant remains based on morphological characteristics, particularly in the absence of reproductive structures. *Aphylopteris* is typically used to describe naked stems exhibiting pseudomonopodial branching and sometimes with striated surfaces, whereas *Hostinella* is applied to smooth, dichotomously branched stems. While these classifications are artificial and do not reflect natural evolutionary relationships, they provide a standardized framework for the description and comparison of fossil specimens.

Wood Bay, E.N.S Expedition, 1939

In 1939 the English, Swedish and Norwegian expedition with Professor Erik Stensio collected fossil specimens for the British Natural History Museum, the Palaeontologisk Museum (Oslo) and the Naturhistoriska Riksmuseet (Stockholm). A large amount of material was collected, 100 cases of fossils weighing around 7 tonnes. The majority of the material was fish, but a large number of plant specimens were collected. The majority of remains were indeterminate but some material of note from several well distributed localities across the lower Devonian basin will be described below. Most of the collected material is curated and stored at the Natural History Museum in Stockholm (Naturhistoriska Riksmuseet) (prefix S0...) and a

small amount of material is curated at The Natural History Museum in London (prefix V...).

Localities are shown on the geological map, Text Figure 1A in main text.

Locality: Sjettedalen (between Sjettedalen and Purpurdalen)

Stratigraphy: Andreéland Gp, Wood Bay Fm, Dicksonfjorden Mb

Morphotypes present: *Prototaxites* sp, *Aphylopteris* SJ1, *Aphylopteris* SJ2, *Aphylopteris* SJ3, Incertae sedis.

***Prototaxites* sp.**

Specimen number: S017556

(Plate ENS1F).

A highly carbonised, compressed axis fragment, 68 mm in length and 5 mm in width. Along the length of the axis fragment are very fine longitudinal striations which run parallel to one another on very close succession. Likely *Prototaxites* owing to the size, preservation and similar morphological features even if the material is poorly preserved.

***Aphylopteris* SJ1**

Specimen number: S017550

(Text Figure 1A, 2A; Plate ENS1A).

A plant fragment measuring 68mm in length and up to 5mm in width, with the widest point proximally (Plate ENS 1A). The axis is pseudomonopodial, with lateral axes bifurcating from the primary axis and curving slightly away from it. The lateral axes emerge with a gentle curve, extending decurrently from the main axis before transitioning to a perpendicular orientation relative to the primary axis.

***Aphylopteris* SJ2**

Specimen numbers: S017556, S017550

(Text Figure 1B, 2B, Plate ENS1B, G).

Plant fragments with a naked axis measuring 22 - 31 mm in length and 0.6 to 2 mm in width, axis width reduces distally. Present are both isotomous and anisotomous dichotomies (Plate ENS1B, Text Figure 1B), with a wide bifurcation angle (70 – 90°), wider in anisotomous dichotomies (80 - 90°). The main axis is deflected at nodes to give a slight zigzag, resulting in a pseudomonopodial growth form.. Lateral axes range from 0.6 – 0.9 mm in width and primary axis range from 0.9 – 2 mm in width.

In specimen S017556, two fragments (22 mm and 28 mm in length) likely represent parts of the same larger plant, though the middle section of the primary axis is not preserved (Plate ENS1G - *white dotted line*). Both axes bifurcate anisotomously, where the lateral axis is 0.8 – 0.9 mm in width and the primary axis is 1.3 – 1.4 mm in width after the bifurcation.

In S017550, the basal portion bifurcates isotomously and features a poorly preserved axillary tubercle (Plate ENS1B - *white arrow*). A 12 mm internode separates the isotomous bifurcation from a subsequent anisotomous bifurcation (Plate ENS1B - *black arrow*), where the lateral axis is 0.6 mm wide, and the primary axis is 0.9 mm wide.

Aphylopteris SJ3

Specimen number: S017549B

(Text Figure 1C, 2C; Plate ENS1E)

Naked main axis which regularly gives off single, smaller lateral branches alternatively at a broad angle 70 - 90°. The main axis 28 mm in length and is deflected at the nodes where the axis bifurcates, giving a slight zigzag appearance and overall pseudomonopodial growth form. Axis width is 0.7 – 0.9 mm, widening before each bifurcation. Length between internodes increases distally (4.2 – 5.4 mm).

Incertae sedis

Specimen number: S017549A.

(Plate ENS1C-D)

Two small axis fragments measuring 3.8–5 mm in length and 0.3–0.7 mm in width are present. Both fragments are likely portions of recurved tips or protrusions from

larger plants, possibly corresponding to morphotypes described from this locality. One fragment exhibits two isotomous bifurcations, with the distal tips recurving backwards (Plate ENS1C). The other fragment has a single isotomous bifurcation (Plate ENS 1D) but the tips curve forward against the direction of growth.

Locality: North of Mount Skansen (Coast profile)

Stratigraphy: Andreéland Gp, Wood Bay Fm, Dicksonfjorden Mb

Morphotypes present: *Aphylopteris* M1, *Psilophytites* M2, *Hostinella* M3

Aphylopteris M1

Specimen numbers: S017560, S017562, S017518, S017569, S017503(A&B)

(Text Figures 1E, 2D; Plates ENS2A, C, D, G, I, ENS3D, C)

Naked main axis that dichotomises anisotomously into smaller lateral axes at a wide angle (60-70°), displaying pseudomonopodial branching. Main axes are wider (range 3.6 - 6.3 mm) than lateral axes (2.1 mm average) and increase in width distally.

Primary axes are 43 – 80 mm in length and sometimes have a defined epidermal margin (Plate ENS2C-D). There are long internodes between dichotomies (39 mm) and in bigger specimens there is a large length of primary axis without lateral axes.

Hostinella M3

Specimen number: S017562

Text Figure 1F, 2F, Plate ENS2H.

Two isotomously bifurcating axes fragments 26 – 29 mm in length and 1.7 – 1.9 mm in width. Isotomous bifurcation occur at a wide angle (96 - 116°). One specimen has a second isotomous bifurcation 88 mm after the first (Plate ENS2H, *white arrow*). Axes after the first isotomous bifurcation are similar in width (1.5 – 2 mm).

Psilophytites M2

Specimen numbers: S017569, S017518)

(Text Figure 1D, 2E; Plates ENS2E)

Single specimen 64 mm in length and 2.2 mm in width. A spiny primary axis bifurcates at a wide angle of 74° to produce a smaller lateral branch, although the exact width of the lateral branch is unclear because of poor preservation. Spines are preserved as short, narrow, pointed projections along the axis margin. They are irregularly spaced and appear to arise from the epidermal surface rather than representing broken lateral branches. Preservation is poor, so spine length and arrangement cannot be measured reliably.

Locality: Sigurdfjellet (Mt. Sigurd, slope towards the Hoffnungsglacier)

Stratigraphy: Andreéland Gp, Wood Bay Fm, Dicksonfjorden m

Morphotypes present: *Aphylopteris* M1, *Psilophytites* M2

Aphylopteris M1

Specimen numbers: S017519, S017520

Text Figure 1E, Plate ENS3D–E

Two anisotomously dichotomising axes fragments 21.1 – 25.4 mm in length and 2.1 – 3.4 mm in width. Appear to be fragmentary portions of a bigger plant, displaying pseudomonopodial branching. Primary axis gets wider before axes bifurcates. Lateral axes are smaller (0.8 – 1.1 mm width) than primary axes and diverge at an angle of 70°.

Psilophytites M2

Specimen number: S017518

Plate ENS3B.

Single unbranched spiny axis 38 mm in length and 2.1 mm in width. Poorly preserved spines are visible mainly along the left side of the axis (Plate ENS3B - white arrow). They occur as small, pointed marginal projections or spine bases,

rather than as separate lateral axes. Their incomplete preservation means that their original length, density and full distribution around the axis cannot be determined.

Locality: Prismefjella

Stratigraphy: Andreéland Gp, Wood Bay Fm, Dicksonfjorden Member

Morphotypes present: *Aphylopteris* P1, *Hostinella* P2.

Aphylopteris P1

Text Figure 1H, 2H; Plate ENS4C

One noteworthy axis fragment 84 mm in length and up to 5.3 mm in width, with a slight decrease in width distally. The main axis branches pseudomonopodially. Along the axis length there are at least four lateral axis which emerge from the primary axis almost perpendicular to the direction of growth (Plate ENS4C - white arrows). The basal portion of the lateral axes runs decurrent with the primary axis (Plate ENS4C - white *) and the lateral axes terminate shortly after they emerge from the primary axis (length 6 – 8 mm). Near the basal portion of the axis there is a raised structure which could be a fourth axis that has broken off (Plate ENS4C - black *).

Hostinella P2

Text Figure 1G, 2G; Plate ENS4A, B

The part and counterpart feature a single axis measuring 56 mm in length and up to 2.2 mm in width. Two isotomous bifurcations are present, separated by a 33 mm internode, and occur at similar angles (65–72°). In both bifurcations, the emerging axes have comparable widths (1.4–1.8 mm), with three of them breaking off shortly after emergence.

A faintly defined epidermal margin extends along both sides of the axis. In both bifurcations, a distinct 'webbed appearance' is observed, where the epidermal layer extends from one axis to the other after the dichotomy, creating a smooth transition rather than a sharp boundary (Plate ENS4A, B - white *).

At the centre of the ‘webbed’ epidermal area between the bifurcations, an outline of an axillary tubercle is present. In the lower bifurcation, it appears as an outline in the part (Plate ENS4A, white arrow) and as a negative cavity in the counterpart, consisting of two distinct cavities connected by a central mass (Plate ENS4B, white arrow). The axillary tubercle appears to be more closely associated with one axis than the other. In the upper bifurcation, a faint outline of an axillary tubercle is visible between the axes, although the preservation is slightly poorer.

Incertae sedis

Specimen number: S07505.

Plate ENS4D, E.

A coalified, ovate structure, part and counterpart. The structure is present on a slab surrounded by indeterminate plant axes. It measures 14.7 mm in length and 9 mm at its widest point. At the base, there is a stalk measuring 3.1 mm in length and 2.1 mm in width (Plate ENS4D, E - white arrows).

Locality: Verdalen

Stratigraphy: Andreéland Gp, Wood Bay Fm, Dicksonfjorden Member

Morphotypes present: Large axis V1, *Hostinella strictissima* V2,
Hostinella V3

Hostinella strictissima V2

Specimen number: S017605.

Text Figure 1J, 2J; Plate ENS5E.

A single slender axis measuring 86.2 mm in length and 1.7 mm in width. The branching appears pseudomonopodial, but poor preservation of the lateral axis prevents definitive confirmation. The branching angles at each node are wide (50–70°) and the internode length decreases distally. This specimen is placed in *H. strictissima* due to its overall similarity to the type specimen described from Wood Bay (Høeg, 1942, Plate XX).

Hostinella V3

Specimen number: S017605

Text Figure 1K, 2K; Plate ENS5C

A single slender axis measuring 49 mm in length and up to 1.4 mm in width. Two isotomous bifurcations are present, with a 36 mm segment between internodes. The axis branches at a wide angle of 75°. It is similar in size and appearance to *H. strictissima* but has a significantly greater internode length.

Large axis 1 V1

Specimen number: S017595, S017603

Text Figure 1I, 2I; Plate ENS5A, B.

Two large axis fragments measuring 119–130 mm in length and 16.6–18.1 mm in width. One is preserved as an internal cast surrounded by an external impression in the matrix (Plate ENS5A). The internal cast is three-dimensional with parallel longitudinal striations running along its length, and the axis width remains consistent.

The other fragment is preserved as a coalified compression (Plate ENS5B). The axis appears to widen, likely due to preservation effects, as the basal portion remains embedded in the matrix. At the base, two fine structures emerge from the primary axis at a 40–50° angle, which could be interpreted as lateral axes emerging alternately from the main axis. These structures are significantly smaller than the main axis, and if connected, they would suggest pseudomonopodial branching.

Locality: Krosspyntdalen

Stratigraphy: Andreéland Gp, Wood Bay Fm, Dicksonfjorden m

Morphotypes present: cf. *Serrulacaulis* KD1

cf. *Serrulacaulis* KD1

Specimen Number S017458

Text Figure 1M, 2M; Plate ENS6D, F

A single slab contains two axes of the same species, each measuring 59 mm in length and 9.5 to 13.1 mm in width. Along both epidermal margins, two rows of tent-like emergences project perpendicularly to the axis (Plate ENS6F - white arrows). These emergences are more prominently preserved on one side.

The best-preserved emergences are associated with a ribbon-like surface depression, potentially representing the vascular strand (Plate ENS6F - black *). This depression measures up to 1.4 mm in width, excluding the height of the emergences. The emergences range from 2.1 to 2.7 mm in length (including the width of the associated vascular strand), tapering distally, with bases between 1.4 and 1.7 mm wide.

Although no reproductive structures are present to confirm identification, the size of the axes and the details, placement and size of the saw-like teeth are distinctive and closely resemble those of *Serrulacaulis*, with particular similarity in size to *Serrulacaulis furcatus* (Hueber & Banks, 1979; Berry & Edwards, 1994). However because of the lack of definitively preserved identifying features, I will place this taxa in cf. *Serrulacaulis*.

Locality: Kronprinshogda

Stratigraphy: Andreéland Gp, Wood Bay Fm, Dicksonfjorden Member

Morphotypes present: cf. *Drepanophycus* KS1

cf. *Drepanophycus* KS1

Specimen number: S017457A & S017457B

Text Figure 1L, 2L; Plate ENS6A-C, E.

Multiple large axis fragments are distributed across both the part and counterpart, with coalified remains of the same specimens also present on the reverse side of the counterpart. The axes range from 105 to 155 mm in length and 11.6 to 19.2 mm in width.

On the part and counterpart, a large axis measuring 155 mm appears to bifurcate isotomously, though only one of the bifurcated axes is preserved (Plate ENS6A).

Along this axis, emergences protrude from the margin, the longest measuring 10 mm and tapering from the base to the tip. The other emergences are significantly smaller probably because they have broken off abruptly (Plate ENS6A - white arrows). The main axis gradually widens before bifurcation, while the dichotomising axis is slightly narrower.

On the reverse side of the counterpart, another isotomously bifurcating axis dichotomises at a wide angle (75°). At its distal portion, a root-like emergence extends 37 mm and reaches a maximum width of 3.8 mm. Along its length, at least two bifurcations or forking points are present; however, poor preservation beyond these points obscures further structural details. This emergence may represent an adventitious root originating from the terminal portion of the axis.

The overall size and morphology of these remains can be compared with species of *Drepanophycus*. In particular the axes dimensions can be compared with *Drepanophycus spinaeformis*, but the lack of preserved defining features such as rhizomes, microphyll insertion and sporangia make exact species determination difficult. For this reason, I will place the taxa in cf. *Drepanophycus*.

Locality: Dickson's Bay

Stratigraphy: Andreéland Gp, Wood Bay Fm, Dicksonfjorden Member

Morphotypes present: cf. *Zosterophyllum* D1, *Hostinella* M3, cf. *Psilophytites* M2

Hostinella M3

Specimen numbers: V32370

Plate ENS7D

A single axis bifurcates isotomously at a 100° angle. It is 41 mm long and up to 2.7 mm wide, widening before the bifurcation. Both secondary axes appear to bifurcate again (Plate ENS7D - black arrows). A poorly preserved axillary tubercle is present at the first bifurcation but absent in the secondary ones.

Psilophytites M2

Specimen numbers: V32367

Plate ENS7E

A single, poorly preserved bifurcating axis, 69 mm long and up to 2.5 mm wide.

Poorly preserved spine bases are present on part of the axis. It resembles *Psilophytites* KP but lacks sufficient defining features for accurate identification, so it will be placed in cf. *Psilophytites* M2.

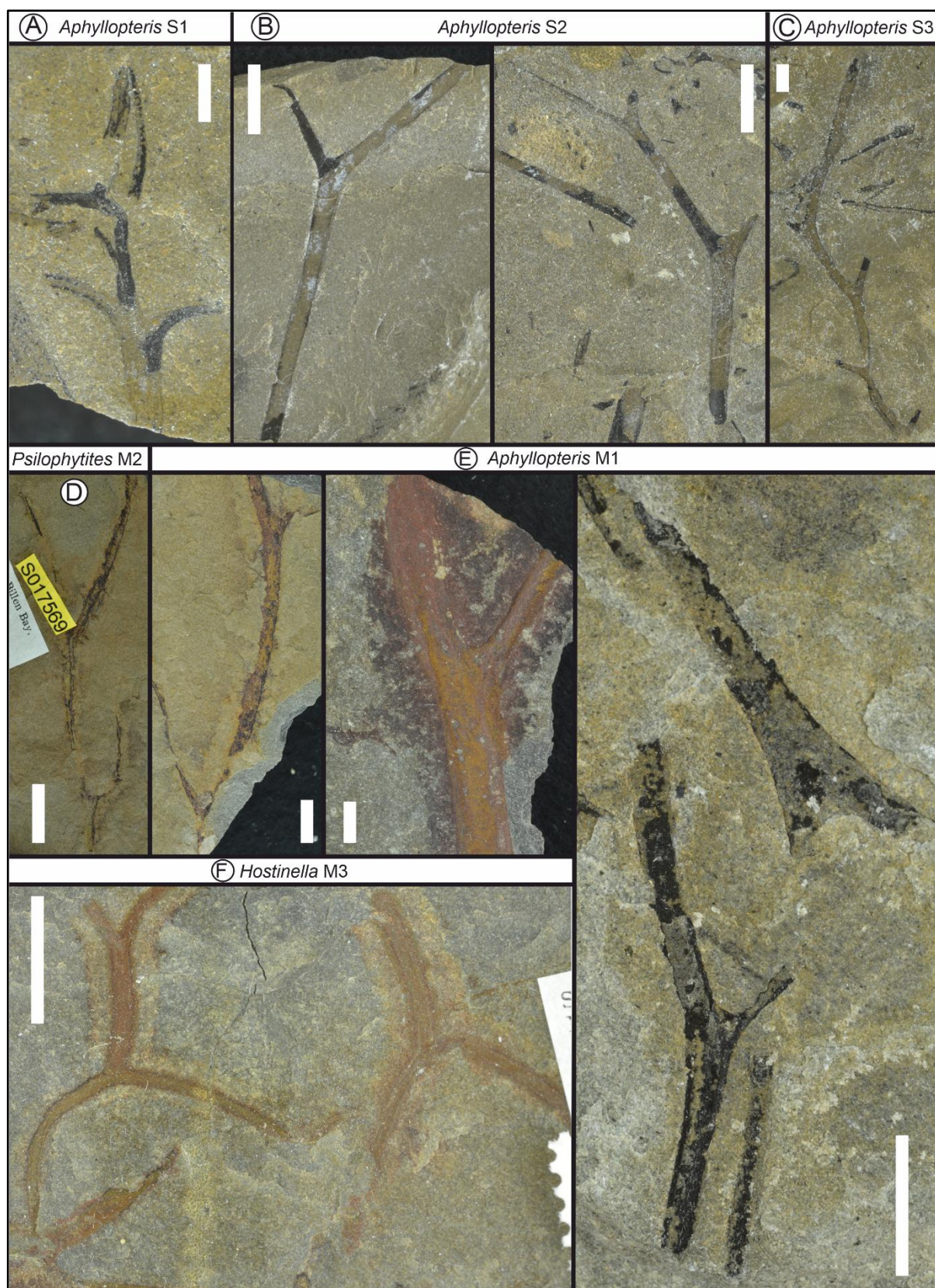
Cf. *Zosterophyllum* D1

Specimen numbers: V32358, V32360, V32361, V32366.

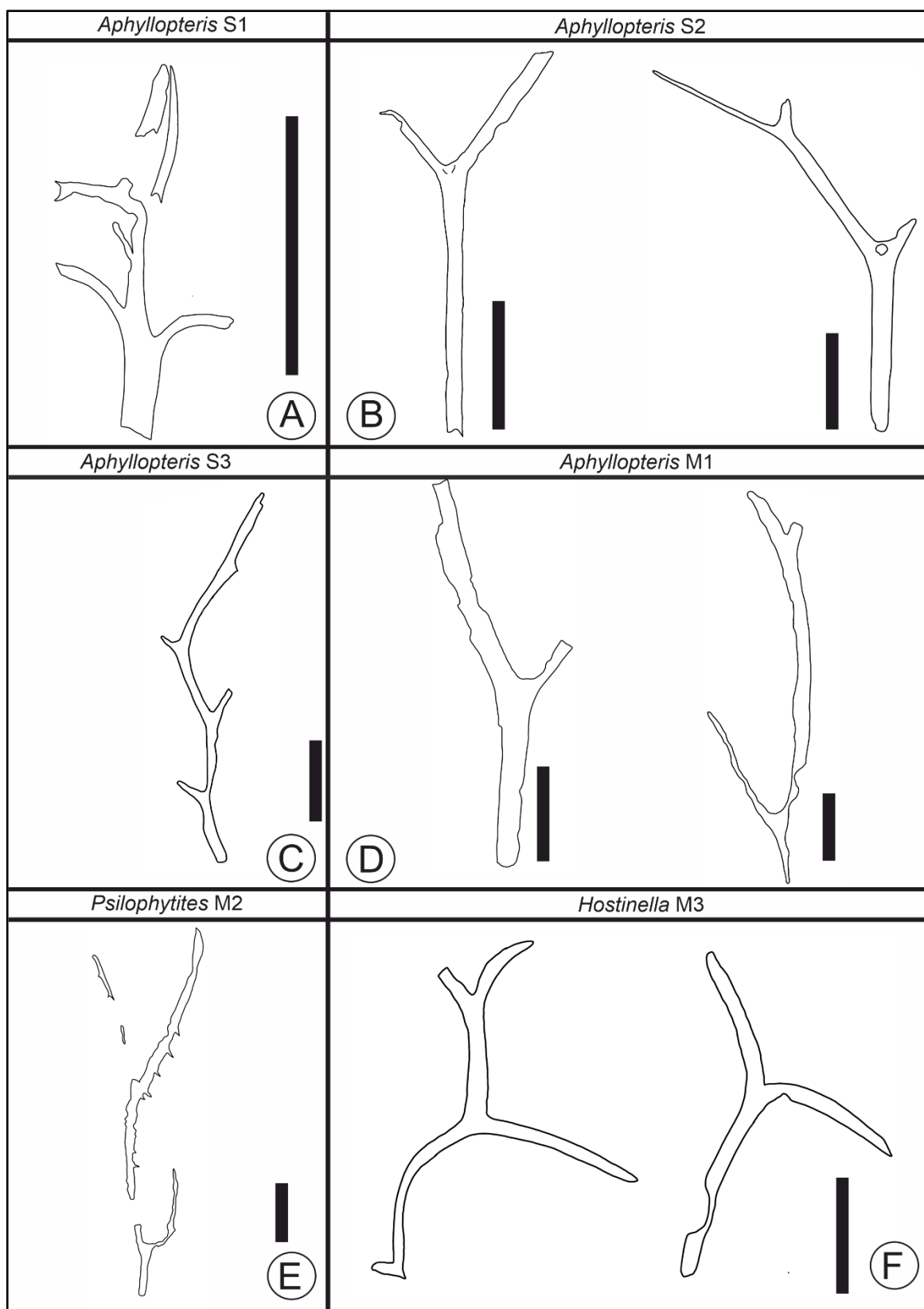
Text Figure 2N; Plate ENS7A-C, F.

Multiple specimens contain mats of parallel, unbranched axes resembling *Zosterophyllum* clumps (Plate ENS7C). All axes lie parallel to each other, with one displaying circinate venation (Plate ENS7F). Some axis fragments extend as long as the slab they were found on (120 mm), with widths of up to 2.8 mm.

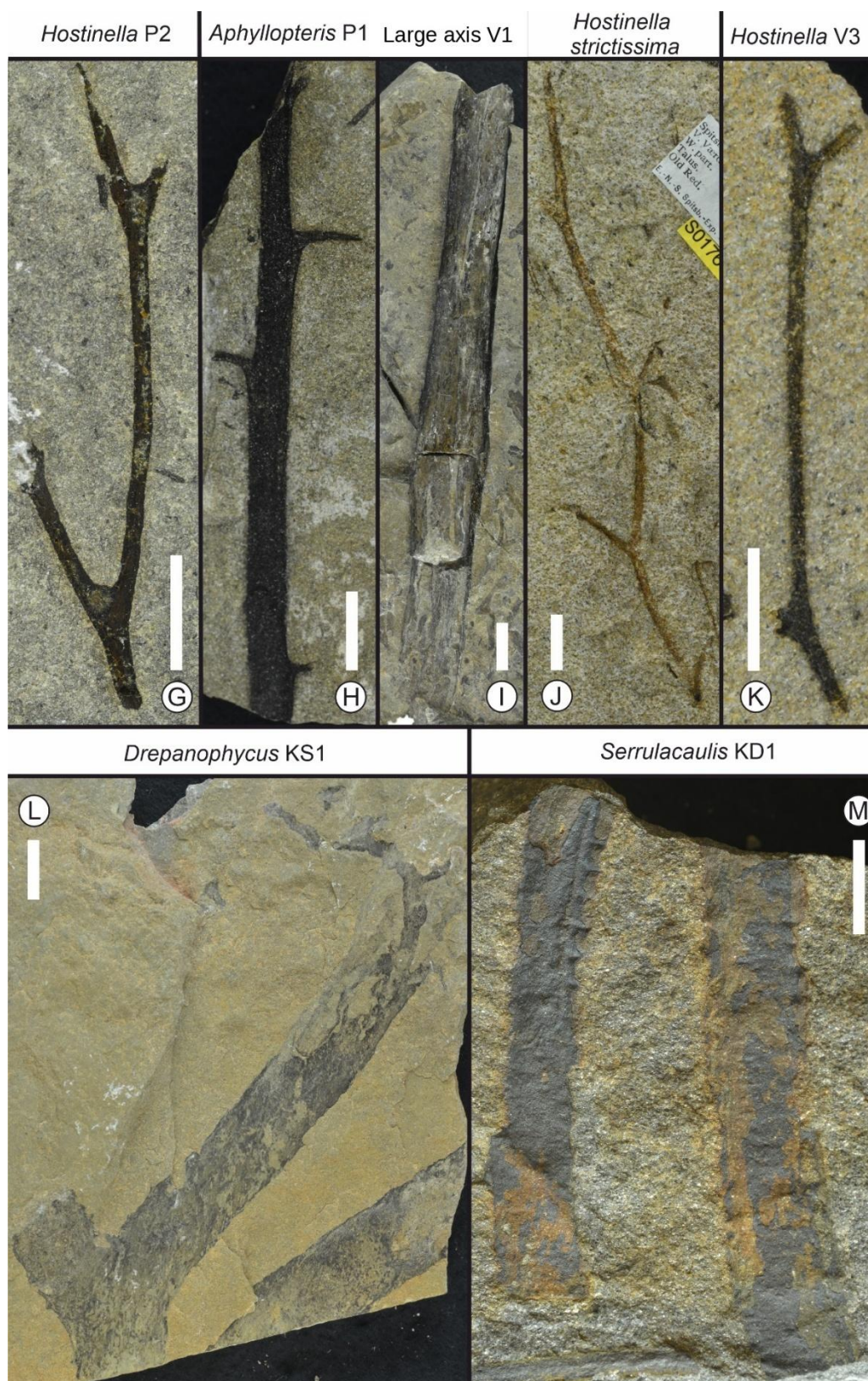
A 48 mm sporangial spike has partially preserved sporangia arranged in two distinct rows (Plate ENS7A, B), though the underlying axis is not preserved. Due to the clear arrangement of two distinctive rows of sporangia, it is placed in the subgenus *PlatyZosterophyllum*. Visible sporangia range from 2.3 to 3 mm in length and 1.3 to 1.8 mm in width. Their exact morphology cannot be established.



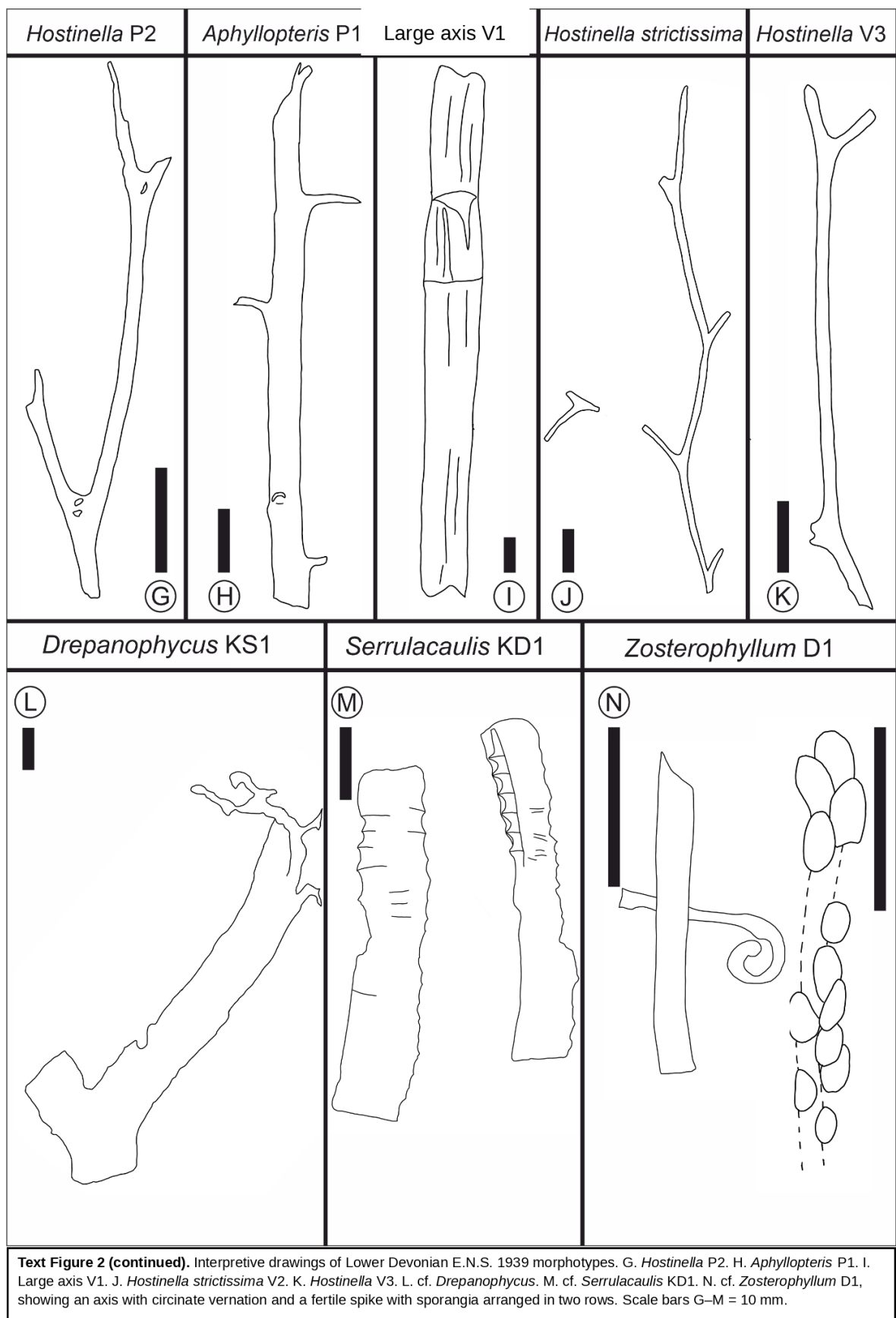
Text Figure 1. Lower Devonian E.N.S. 1939 morphotypes. A. *Aphylopteris* S1. B. *Aphylopteris* S2. C. *Aphylopteris* S3. D. *Psilophytites* M2. E. *Aphylopteris* M1. F. *Hostinella* M3. Scale bars: A = 2 mm; B = 5 mm; C = 2 mm; D–F = 10 mm.



Text Figure 2. Interpretive drawings of Lower Devonian E.N.S. 1939 morphotypes. A. *Aphylopteris* S1. B. *Aphylopteris* S2. C. *Aphylopteris* S3. D. *Aphylopteris* M1. E. *Psilophytites* M2. F. *Hostinella* M3. Scale bars: A = 2 mm; B = 5 mm; C = 2 mm; D–F = 10 mm.



Text Figure 1 (continued). Lower Devonian E.N.S. 1939 morphotypes. G. *Hostinella* P2. H. *Aphylopteris* P1. I. Large axis V1. J. *Hostinella strictissima* V2. K. *Hostinella* V3. L. cf. *Drepanophycus* KS1. M. cf. *Serrulacaulis* KD1. Scale bars = 10 mm.



Appendix B – Høeg 1939 expedition collection.

In 1939, Ove Arbo Høeg arranged an expedition to Spitsbergen, accompanied by Reidar Jörgensen and Jakob Vaage to further his study of Devonian plant fossils. The party set up their main camp at the South side of Pyramiden mountain and were actively collecting specimens from 3-30 July 1939. During this time, collections were made from Carboniferous strata in Pyramiden, with additional collections being made inland from Mimer Valley (Mimerdalen Sbgp) and extensive collections made from the Western side of Klaas Billen Bay (Wood Bay Fm), the latter of which will be discussed in this section.

Seven different localities were noted on the Western side of Klaas Billen Bay, however only vague descriptions of the localities were ever reported by Høeg and no expedition notes or field notebooks have been found. After extensive investigation of this material and associated museum labels, each locality has been assigned a title and the corresponding symbol assigned by Høeg in his handwritten specimen notes. Each of the collection localities were described as on the West side of Klaas Billen Bay, so it is safe to assume that they all come from the Dicksonfjorden Member of the Wood Bay Formation because this is the only Lower Devonian stratigraphy which has been mapped within this area. Additionally, a lot of the plant material collected at these sites is similar in overarching morphology, which supports the idea that these sites are stratigraphically similar. Some of the localities refer to the astronomical cairn erected by Nordenskiöld (position marked on Fig. 30 of Nathorst, 1910).

The majority of specimens collected were fragments, but some material of note will be described below. All material is curated and stored at the Natural History Museum in Oslo (Naturhistorisk museum) and has remained unpublished until now. These fossils were not included in Høeg's (1942) monograph of the Svalbard Devonian and were collected after he had done most of the work for his publication.

Locality: Locality 1 (III), West Side of Klaas Billen Bay

Stratigraphy: Andreéland Group, Wood Bay Formation, Dicksonfjorden Member

Morphotypes present: *Aphylopteris* M1, *Hostinella strictissima*, *Aphylopteris* L1,
Zosterophyllum L2

***Aphylopteris* M1.**

Specimen numbers: PMO.250.066, PMO.250.076

Plate: Høeg Plate 1C, 1H

Two wide axis fragments (5.8–12.9 mm) measuring 112–245 mm in length both appear to bifurcate, though the axis is broken off immediately after the bifurcation. Internode distances are relatively long, ranging from 59–72 mm. In a portion of one axis fragment a poorly preserved vascular strand is present (Høeg Plate 1C, between *white* *).

These specimens closely resemble *Aphylopteris* M1 collected from Mt. Skansen (Plate ENS 2A, C-D) and Sigurdjellet (Plate ENS 3D-E) in size, morphology, and internode spacing. While the presence of a vascular strand suggests they could belong to a new *Taeniocrada* morphotype, their similarity in size and overall morphology to previously described *Aphylopteris* supports their placement in this morphotype. Although the secondary axis is not preserved beyond the bifurcation, the branching is likely pseudomonopodial, consistent with specimens from other localities.

Hostinella strictissima

Specimen numbers: PMO.250.078

Høeg Plate 1D

A part and counterpart specimen feature a single slender axis, the part is 56 mm in length and counterpart is 45 mm. The axis tapers distally, ranging from 1.6 to 0.7 mm in width.

The axis bifurcates widely (60–80°), with internode lengths varying from 15.2 to 9.7 mm. The longest internode occurs between the third and fourth bifurcation (Høeg

Plate 1D - white arrow), while the shortest follows immediately after (Høeg Plate 1D - black arrow). This specimen is placed in *H. strictissima* due to its overall similarity in size and branching angles to the type specimen described from Wood Bay (Høeg, 1942, Plate XX).

***Aphylopteris* L1**

Specimen number: PMO.250.076

Høeg Plate 1G.

A distinctive, single, smooth axis measuring 34 mm in length and 1–1.8 mm in width which bifurcates twice in close succession. The first bifurcation is dichotomous, giving rise to what appears to be the main axis (Høeg Plate 1G - black arrow). A second bifurcation occurs 3.4 mm later, producing two slightly narrower daughter axes (Høeg Plate 1G - white arrows).

The first bifurcation likely represents the main axis, suggesting an overall pseudomonopodial branching pattern. The axis narrows just before the first bifurcation, gradually widening before branching again, with the lateral axis reducing in width as it emerges.

This specimen has been assigned to a new morphotype of *Aphylopteris* L1, as it lacks spines. It does not fit within *Hostinella* due to its more complex branching pattern.

***Zosterophyllum* L2.**

Specimen number: PMO.250.066, PMO.250.067

Høeg Plate 1A, B, E, F

A single specimen from this locality features a sporangial stalk with at least seven sporangia in relatively poor preservation (Høeg Plate 1A, B). The stalk measures 50 mm in length and has a distinctive 75° bend approximately halfway along its length (Høeg Plate 1A - black arrow). Sporangia are present both above and below this bend, with those below more poorly preserved, while those above are better preserved overall.

The sporangia are relatively large, ranging from 3.0 to 4.9 mm in length and 1.6 to 2.4 mm in width. The two most distal sporangia are the best preserved, retaining some three-dimensionality and showing their relative orientation. They appear to be inserted in two rows at perpendicular angles to one another, with a 3.3 mm spacing between their abaxial surfaces.

The shape is best observed in the most distal sporangia (Høeg Plate 1A, B - white *), where the abaxial surface is distinctly flat, while the adaxial surface is rounded and fan-shaped. In a more proximal sporangium (Høeg Plate 1B - black arrow), compression has flattened the rounded adaxial surface, distorting its shape. Sporangia become increasingly compressed and poorly preserved moving proximally down the stalk. No sporangial stalks are present on any of the preserved sporangia.

A specimen from the same locality features an axis measuring 30 mm in length and up to 2.7 mm in width, displaying circinate venation (Høeg Plate 1E, F), a characteristic commonly associated with *Zosterophyllum*. As the taxonomy of the sporangial stalk cannot be determined beyond *Zosterophyllum*, both specimens are grouped under the morphotype *Zosterophyllum* L2.

Locality: 100m from Nordenskiöld cairn (∞)

Stratigraphy: Andreéland Group, Wood Bay Formation, Dicksonfjorden Member

Morphotypes present: *H. strictissima*, *Psilophytites* M2

H. strictissima

Specimen number: PMO.250.108

Høeg Plate 2F.

A single slab contains a cluster of smooth, fragmentary axes ranging from 7 to 111 mm in length and 0.8 to 1.8 mm in width (Høeg Plate 2F). The axes occasionally bifurcate anisotomously, giving the appearance of pseudomonopodial branching. Some exhibit a distinctive raised margin, similar to *H. strictissima* from other localities (Høeg Plate 2G-H). The overall similarity in size and branching pattern supports their placement within *H. strictissima*.

Psilophytites M2

Specimen number: PMO.250.106

Høeg plate 2A

A single spiny axis, 78 mm in length and 0.8–1.6 mm in width. Poorly preserved spines, ranging from 1.2 to 1.7 mm in length, are present along part of the axis. The axis appears to bifurcate anisotomously, giving the impression of pseudomonopodial branching. Its overall appearance and branching morphology closely resemble *Psilophytites M2* collected from Mt. Skansen (Plate ENS 2E).

Locality: 200m from Nordenskiöld Cairn (≈)

Stratigraphy: Andreéland Group, Dicksonfjorden Member, Wood Bay Formation

Morphotaxa present: *Psilophytites svalbardensis* (Kapp Peterman).

Psilophytites svalbardensis

Specimen number: PMO.250.125

Høeg Plate 2B

The only species present from this locality is *Psilophytites svalbardensis*, the species described and named in the main text. The specimen is exceptionally well-preserved, featuring an axis 17.4 mm in length and up to 3.9 mm in width, with at least five anisotomous bifurcations along its length. Due to its relevance to the species description and the additional morphological details it provides, this specimen will be discussed in the relevant section.

Locality: 300m from the beach (Ø)

Stratigraphy: Andreéland Group, Wood Bay Formation, Dicksonfjorden Member

Morphotaxa present: *Aphyllopteris M1*

Aphyllopteris M1

Specimen number: PMO.250.128

Høeg Plate 2E

A single large axis, 166 mm in length and 4–6.4 mm in width which bifurcates anisotomously, producing pseudomonopodial branching in alternating directions along the main axis. Lateral axes emerge thinner (2.3–3.9 mm) than the primary axis and bifurcate at broad angles (80–90°). The specimen closely resembles *Aphyllopteris* M1 collected from various other localities.

Locality: 400m from Nordenskiöld Cairn (~)

Stratigraphy: Andreéland Group, Wood Bay Formation, Dicksonfjorden Member

Morphotaxa present: *H. strictissima*

H. strictissima

Specimen numbers: PMO.250.130, PMO.250.136

Høeg Plate 2G-H.

Two smooth, bifurcating axis fragments measuring 40–78 mm in length and 0.5–1.5 mm in width. The axes widen before bifurcating, with internode lengths varying from 9 to 15 mm and increasing distally. The overall branching pattern is pseudomonopodial, with a wider dominant axis at the centre of the plant.

The bifurcation angle ranges from 50° to 80°, depending on the insertion of the lateral axis on the main stem. Similar to the type specimen of *H. strictissima*, a central strand is visible in some sections where the vascular strand is present (Høeg Plate 2G-H).

***Psilophytites* N1**

Specimen numbers: PMO.250.137

Høeg Plate 2C-D.

The same specimen contains two axis fragments with similar preservation, likely from the same plant. Both are poorly preserved, measuring 11 and 32 mm in length and between 0.7 - 1 mm in width.

The largest axis bifurcates at least three times (Høeg Plate 2C), though only the most proximal bifurcation is preserved, with a 4 mm segment of the axis remaining. The other bifurcations break off immediately after branching. Each bifurcation happens on opposite sides of the main axis. Near the top of both fragments, curved protrusions are present (Høeg Plate 2C), which may represent recurved tips. On the smaller axis (Høeg Plate 2D), two such curved projections are visible distally.

Although preservation is too poor for precise identification, the presence of possible recurved tips suggests greater morphological complexity than the simple dichotomising axes characteristic of the form genus *Hostinella*. Consequently, these specimens will be placed in a new morphotaxon, *Psilophytites* N1.

Locality: 200m above Nordenskiöld Cairn (⊗)

Stratigraphy: Andreéland Group, Wood Bay Formation, Dicksonfjorden Member

Morphotaxa present: *Aphylopteris* N1, *Aphylopteris* M1, *H. strictissima*,
Psilophytites L1, *Psilophytites* N1

***Aphylopteris* N1.**

Specimen numbers: PMO.250.105A, PMO.250.105B

Høeg Plate 3E-F, J

Multiple wide axis fragments measuring 18.8–37.6 mm in length and 0.9–3.3 mm in width. The axes bifurcate anisotomously, producing a distinctly pseudomonopodial branching pattern. Long spines or emergences are present, ranging from 1.0 to 2.1 mm in width, occasionally exceeding the width of the axis. The width of these spines remains consistent along their length, varying between 0.6 and 1.2 mm.

Although their overall morphology resembles the morphotaxon *Aphylopteris* M1, the presence of spine-like emergences makes them highly distinctive. This feature provides sufficient justification to classify them as a new morphotaxon within *Aphylopteris*. While *Aphylopteris* typically consists of smooth axes, the distinctly pseudomonopodial branching in these specimens is a defining characteristic. As *Aphylopteris* is a form genus rather than a formally recognized taxon, these specimens are best placed within it rather than in a genus such as *Psilophytites*.

***Aphylopteris* M1**

Specimen number PMO.250.103C

Høeg Plate 3I

A single bifurcating axis measuring 59 mm in length. Before bifurcation, the axis is 5.8 mm in width. After bifurcation, the two resulting axes measure 3.2 mm and 3.7 mm in width. Although similar in width, the left axis appears to function as the main axis due to its growth direction, giving the impression of pseudomonopodial branching, with the right axis emerging as a secondary branch.

The bifurcation occurs at a wide 70° angle. An axillary tubercle, measuring 3.0 mm in length and 1.9 mm in width, is present between the two bifurcating axis fragments.

H. strictissima

Specimen number: PMO.250.100

Høeg Plate 3K

A part and counterpart of a large slab containing multiple bifurcating axis fragments. Axes range from 15 to 60 mm in length and are slender (0.9–2.1 mm in width), widening slightly before bifurcation. Bifurcation occurs at wide angles (80°–100°).

These specimens are assigned to *H. strictissima* due to their morphological similarity to other *H. strictissima* specimens collected from the same strata (see Høeg Plate 2G-H) and their resemblance to the type specimen described by Høeg (1942, Plate XX).

***Psilophytites* N1**

Specimen number PMO.250.103B

Høeg Plate 3G

A single bifurcating axis measuring 21.9 mm in length and 0.9–1.3 mm in width. The axis bifurcates widely (80°–110°), with thinner lateral branches, giving the appearance of pseudomonopodial branching.

At the distal portion of one lateral branch and the main axis (Plate 3G, white arrows), poorly preserved structures resembling recurved tips are present. These are similar to those observed in the same morphotype in Plate 2C-D. The recurved tips bifurcate distally into two isotomous recurved tips that reorient back onto themselves.

***Psilophytites* L1.**

Specimen number PMO.250.103A, PMO.250.103D

Høeg Plate 3A-D, 3H

A single slab containing both a part and counterpart, with numerous axis fragments. The axes bifurcate anisotomously from the main axis, exhibiting an overall pseudomonopodial branching pattern. Axes measure 44–48 mm in length and 0.9–2.0 mm in width, tapering distally. Lateral axes emerge from the primary axis at variable angles (50°–80°) in an alternate arrangement.

On the axis preserved in both the part (Plate 3C-D) and counterpart (Plate 3B), a distinctive branching pattern is observed at the distal end. Three axes emerge from the same point, with a wider main axis (Plate 3B-C, white arrow) branching twice in close succession, giving rise to a primary axis and two smaller daughter axes, similar to the pattern seen in Plate 2G. The main axis is 0.5 mm in width, while the two lateral axes emerging on either side measure 0.4 mm in width.

Along the main axis of the part and counterpart specimen, poorly preserved spine-like emergences are present. These structures maintain a consistent width and range from 0.7–1.1 mm in length. Notably, they are only observed on the primary axis.

They have been assigned to the morphotaxon *Psilophytites* L1 due to the distinctive double bifurcation in close succession, resulting in a main axis and two clearly defined daughter axes.

Locality: Next to the red bolts (V)

Stratigraphy: Andreéland Group, Wood Bay Formation, Dicksonfjorden Member

Morphotaxa present: *Aphylopteris* M1, *Aphylopteris* S3, *Psilophytites* B1

***Aphylopteris* M1**

Specimen number: PMO.250.099

Høeg Plate 4A

A single large axis, 129 mm in length, extends across multiple slabs and bifurcates anisotomously, producing a pseudomonopodial branching pattern. The axis measures 2.9–5.6 mm in width, gradually tapering distally.

Three anisotomous bifurcations are present (Høeg Plate 4A, white arrows). Although the full width of the lateral axes is not preserved, they are clearly narrower than the main axis. In some sections, a central strand representing vascular tissue is visible (Høeg Plate 4A, white *).

***Aphylopteris* S3**

Specimen number PMO.250.096.

Høeg Plate 4B.

Anisotomously bifurcating naked axis fragment producing smaller lateral branches in an alternating pattern at a broad angle (90° – 100°), these are deflected from the growth direction of the primary axis. The axis measures 19.6 mm in length and varies in width between 0.4–0.7 mm. Internode distances between branch points are consistent, ranging from 5.5–6.5 mm. At the distal portion of the axis is a circular stricture (Høeg Plate 4B - white arrow)

***Psilophytites* B1.**

Specimen number PMO.250.101

Høeg Plate 4C-E

A large slab contains multiple axis fragments ranging from 25 to 139 mm in length, with widths varying from 1.8 to 4.0 mm, gradually tapering distally. The axes are arranged parallel across the slab.

The branching is pseudomonopodial, with anisotomous bifurcations occurring at a narrow angle (30° – 45°) into thinner lateral axes. In most specimens, only a single anisotomous bifurcation is preserved, but in one, the internode between bifurcations measures 38 mm.

A particularly notable axis (Høeg Plate 4E - white arrow) exhibits a complex branching organization at its branching nodes. The main axis branches, producing a lateral axis on the left (Høeg Plate 4E - white *), which extends 4.5 mm before further

bifurcating into two smaller axes that terminate shortly after. Before this bifurcation, the lateral axis is 2.5 mm in width.

At the same branching node, another axis branches off to the right (Høeg Plate 4E - black *). This axis measures 1.7 mm in width and extends 44.8 mm before disappearing into the matrix. Around this point, the main axis bifurcates again, producing two additional axes. Due to poor preservation, it is unclear whether this bifurcation is equal or gives rise to lateral branches. 26 mm after the second bifurcation, another branching node is observed (Høeg Plate 4E - red arrow). Although preservation limits visibility, it appears to give rise to at least two, possibly three, branches.

Adjacent to this axis, another distinctive feature is preserved (Høeg Plate 4D - black arrow). This axis appears to emerge from a larger primary axis although the connection is not definitive (Høeg Plate 4C - white arrow). After it emerges, it bifurcates isotomously at a broad angle (115°), producing two equal branches. One branch terminates shortly after, while the other extends 7.6 mm before recurving back on itself, forming an involute axis that recurves back on itself and continues for an additional 10 mm.

All of these axis fragments are parallel to one another, and their relative orientation, along with their similar size and proportions, suggests that they belong to the same species, likely part of the same plant, though its basal portion has not been preserved. The branching patterns are significantly more complex than any previously described from the Lower Devonian collections of Høeg 1939 and E.N.S. 1939.

Due to their distinct morphology, these specimens have been placed in the new morphotaxon *Psilophytites* B1. They are clearly separate from any other *Psilophytites* morphotype; however, the absence of reproductive structures prevents their assignment to *Psilophyton* or another genus. This highlights the complexity of their branching patterns and, by extension, the anatomy of the plant.

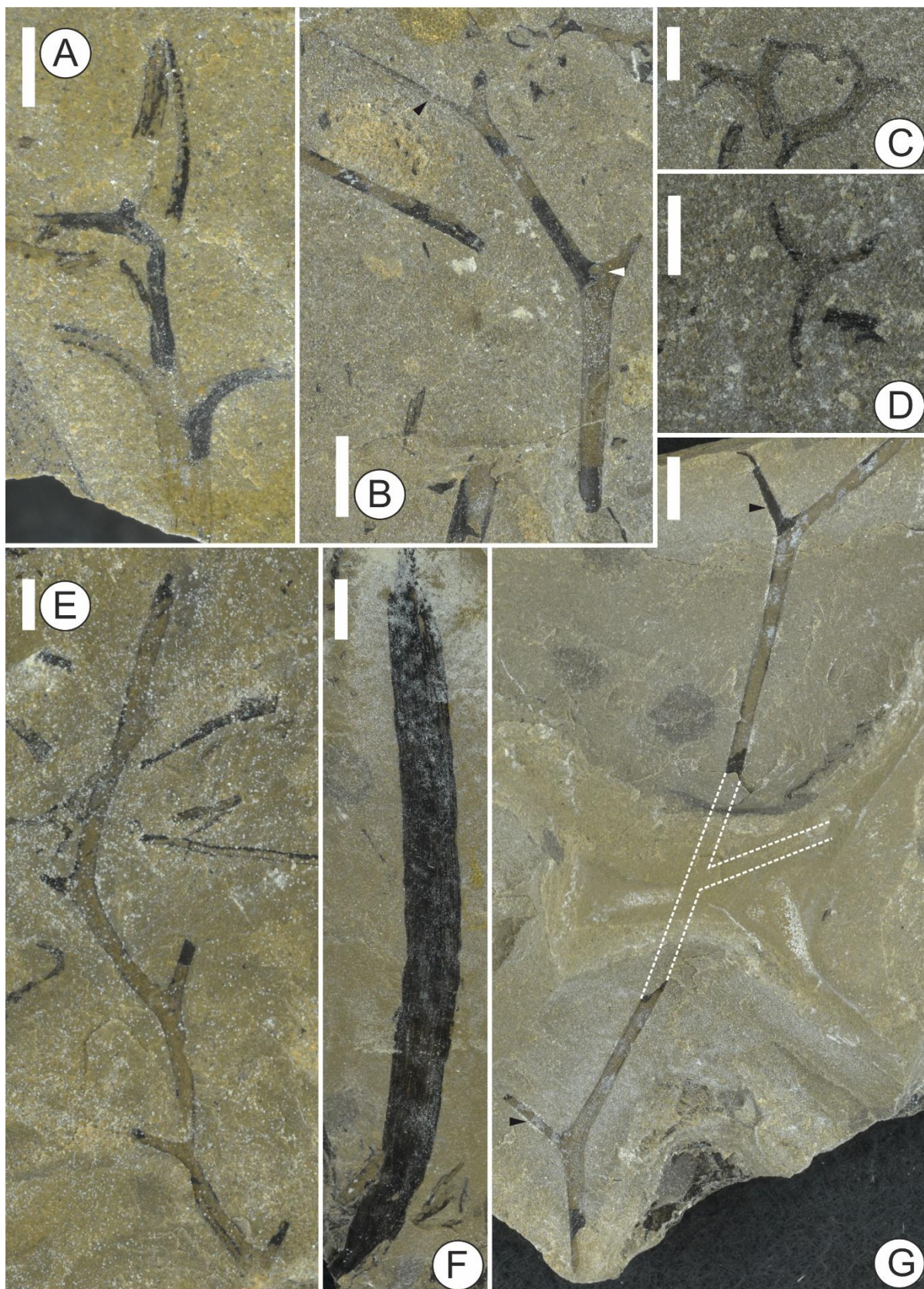


Plate ENS1. Plant remains from the Sjettedalen locality, Spitsbergen, collected during the E.N.S. expedition of 1939.

A. *Aphyllopteris* S1. Pseudomonopodially branching axis with lateral axes. Specimen number: S017550. Scale bar = 2 mm.

B. *Aphyllopteris* S2. Axis showing an isotomous bifurcation and a subsequent anisotomous bifurcation (black arrow); a poorly preserved axillary tubercle is present at the proximal bifurcation (white arrow). Specimen number: S017550. Scale bar = 5 mm.

C. Pair of poorly preserved recurved axis tips. Incertae sedis. Specimen number: S017549A. Scale bar = 2 mm.

D. Single recurved axis tip. Incertae sedis. Specimen number: S017549A. Scale bar = 2 mm.

E. *Aphyllopteris* S3. Pseudomonopodially branching axis with alternate lateral branches. Specimen number: S017549B. Scale bar = 2 mm.

F. Probable *Prototaxites* sp. Highly coalified compression with fine longitudinal striations. Specimen number: S017556. Scale bar = 10 mm.

G. *Aphyllopteris* S2. Two fragments probably belonging to the same plant; the intervening section is not preserved (white dotted line). Both fragments bifurcate anisotomously. Specimen number: S017556. Scale bar = 5 mm.

All specimens are housed at the Swedish Museum of Natural History (Naturhistoriska riksmuseet), Stockholm.



Plate ENS2. Plant remains from the Mt Skansen locality, Spitsbergen, collected during the E.N.S. expedition of 1939.

A. *Aphylopteris* M1. Anisotomously bifurcating axis fragment. Specimen number: S017560.

B. Overlapping, unbranched axis fragments on the reverse side of specimen S017560. Incertae sedis.

C. *Aphylopteris* M1. Anisotomously bifurcating axis with clearly defined epidermal margins. Specimen number: S017562.

D. *Aphylopteris* M1. Two axis fragments probably belonging to the same individual; the intervening section is not preserved. The lower fragment bifurcates anisotomously. Specimen number: S017562.

E. *Psilophytites* M2. Spiny, anisotomously bifurcating axis with poorly preserved spine-like emergences (white arrows). Specimen number: S017569.

F. *Aphylopteris* M1. Anisotomously bifurcating axis with two bifurcations along its length. Specimen number: S017569.

G. *Aphylopteris* M1. Fragmentary axis with two probable bifurcations (white arrows); the lateral axes are incompletely preserved. Specimen number: S017562.

H. *Hostinella* M3. Two isotomously bifurcating axis fragments; the left-hand fragment shows a second isotomous bifurcation (white arrow). Specimen number: S017562.

I. *Aphylopteris* M1. Axis with at least one anisotomous dichotomy and a possible second dichotomy (white arrow). Specimen number: S017562.

Scale bar = 10 mm in all panels.

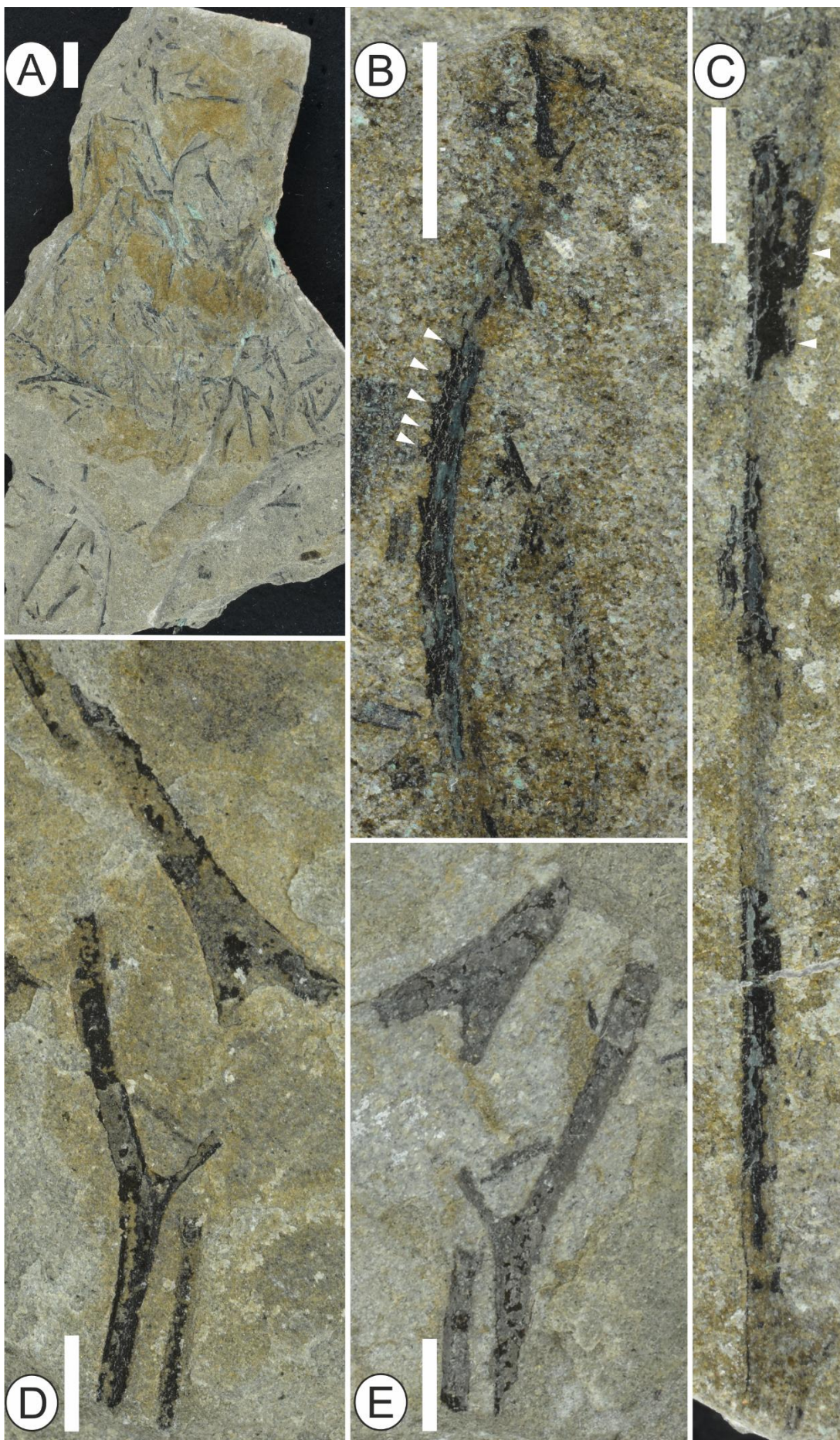


Plate ENS3. Plant remains from the Sigurdfjellet locality, Spitsbergen, collected during the E.N.S. expedition of 1939.

A. Overlapping coalified axis fragments of *Hostinella* sp. showing isotomous and anisotomous bifurcations. Specimen number: S017517. Scale bar = 10 mm.

B. *Psilophytites* M2. Coalified, compressed axis fragment with poorly preserved spine bases visible along the axis margin (white arrow). Specimen number: S017518. Scale bar = 5 mm.

C. Long, unbranched axis fragment with a clearly defined epidermal margin. Identification indeterminate. Specimen number: S017518. Scale bar = 5 mm.

D. *Aphyllopteris* M1. Anisotomously bifurcating axis fragment, part. Specimen number: S017520; counterpart: S017519. Scale bar = 5 mm.

E. *Aphyllopteris* M1. Counterpart of the anisotomously bifurcating axis shown in D. Specimen number: S017519; part: S017520. Scale bar = 5 mm.

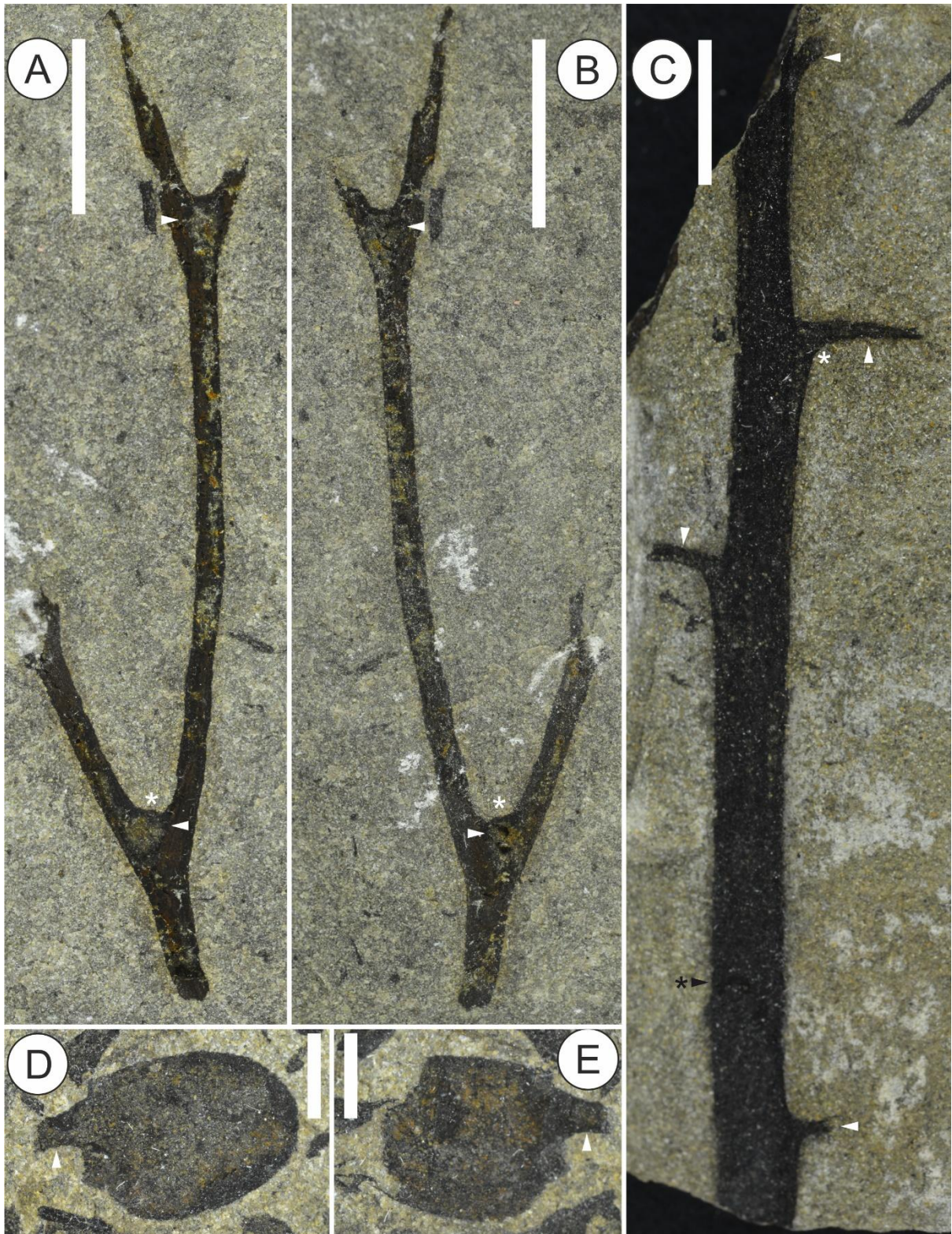


Plate ENS4. Plant remains from the Prismefjella locality, Spitsbergen, collected during the E.N.S. expedition of 1939.

A. *Hostinella* P2. Isotomously bifurcating axis with poorly preserved axillary tubercles at the bifurcations (white arrows) and a webbed epidermal appearance between the axes. Specimen number: S017503. Scale bar = 10 mm.

B. *Hostinella* P2. Counterpart of A, showing two isotomous bifurcations, epidermal webbing and axillary tubercles (white arrows). Specimen number: S017503. Scale bar = 10 mm.

C. *Aphylopteris* P1. Pseudomonopodially branching primary axis with lateral axes emerging at approximately right angles (white arrows). White asterisk indicates the decurrent base of a lateral axis; black asterisk indicates a possible broken lateral axis. Specimen number: S017503. Scale bar = 10 mm.

D. Ovate, stalked structure of uncertain affinity. Incertae sedis. White arrow indicates the stalk. Specimen number: S07505. Scale bar = 5 mm.

E. Counterpart of D. Ovate, stalked structure of uncertain affinity. Incertae sedis. White arrow indicates the stalk. Specimen number: S07505. Scale bar = 5 mm.



Plate ENS5. Plant remains from the Verdalen locality, Spitsbergen, collected during the E.N.S. expedition of 1939.

A. Large axis V1. Three-dimensionally preserved axis with parallel longitudinal striations. Specimen number: S017595.

B. Large axis V1. Coalified compression with two fine structures emerging near the base; the white arrow indicates the visible attachment of the left-hand structure. Specimen number: S017603.

C. *Hostinella* V3. Slender axis with two isotomous bifurcations. Specimen number: S017605.

D. Unbranched axis from the same slab as C. Identification indeterminate. Specimen number: S017605.

E. *Hostinella strictissima* V2. Slender branching axis with broad branching angles. Specimen number: S017605.

Scale bar = 10 mm in all panels.

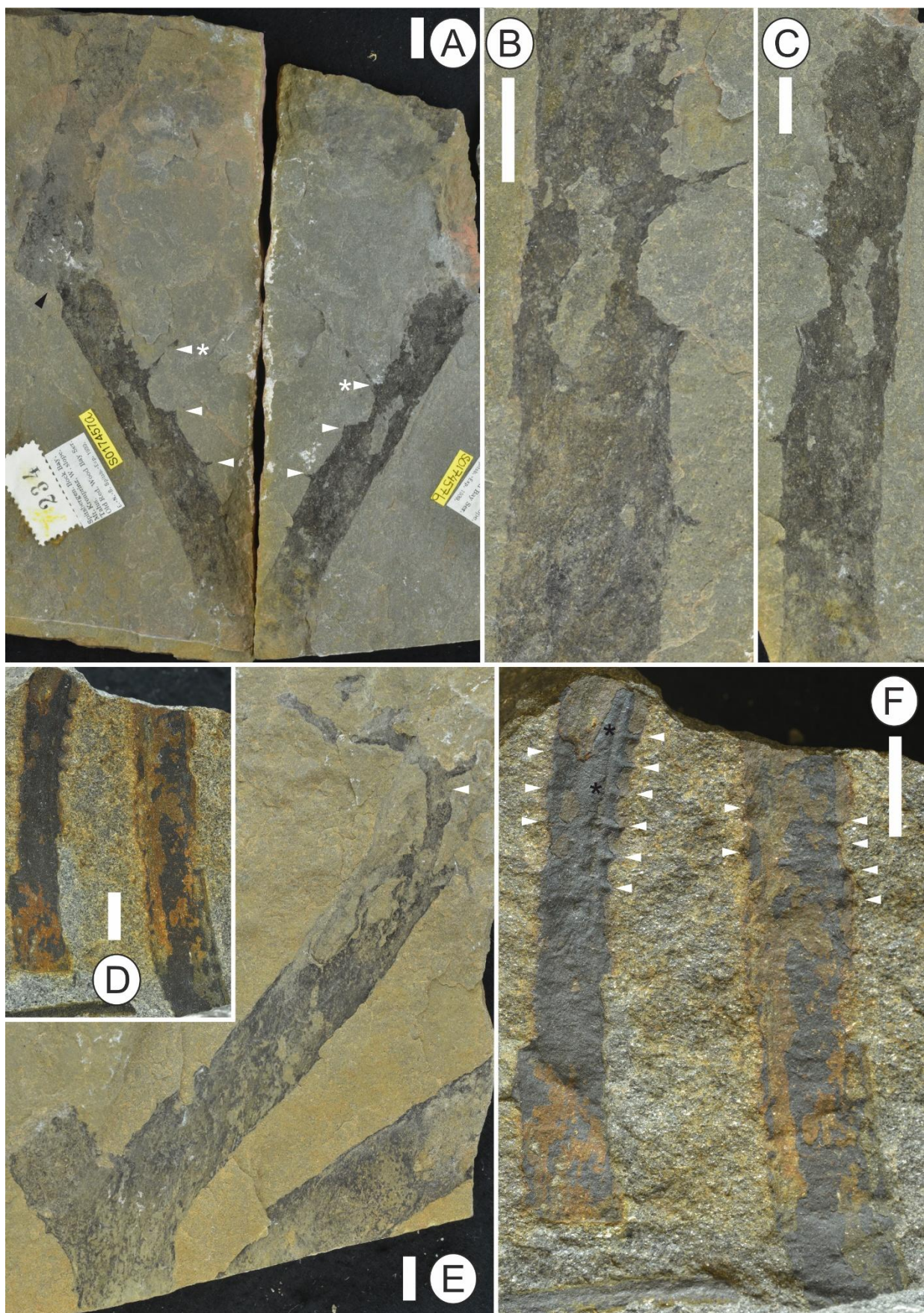


Plate ENS6. cf. *Drepanophycus* KD1 and cf. *Serrulacaulis* KD1 from Kronprinshøgda and Krosspyntdalen, Spitsbergen, collected during the E.N.S. expedition of 1939.

A. cf. *Drepanophycus* KD1. Part (S017457A) and counterpart (S017457B), showing marginal emergences (white arrows); white asterisk marks the longest preserved emergence and black arrow marks an isotomous bifurcation. Kronprinshøgda.

B. cf. *Drepanophycus* KD1. Close-up of the part. Specimen number: S017457A. Kronprinshøgda.

C. cf. *Drepanophycus* KD1. Close-up of the counterpart. Specimen number: S017457B. Kronprinshøgda.

D. cf. *Serrulacaulis* KD1 from Krosspyntdalen. Specimen number: S017458.

E. cf. *Drepanophycus* KD1. Reverse side of counterpart S017457B, showing two axis fragments; one bifurcates isotomously and bears a possible root-like emergence distally (white arrows). Kronprinshøgda.

F. cf. *Serrulacaulis* KD1 from Krosspyntdalen. White arrows indicate marginal tent-like emergences; black asterisk indicates the ribbon-like surface depression interpreted as a possible vascular strand. Specimen number: S017458.

Scale bar = 10 mm in all panels.

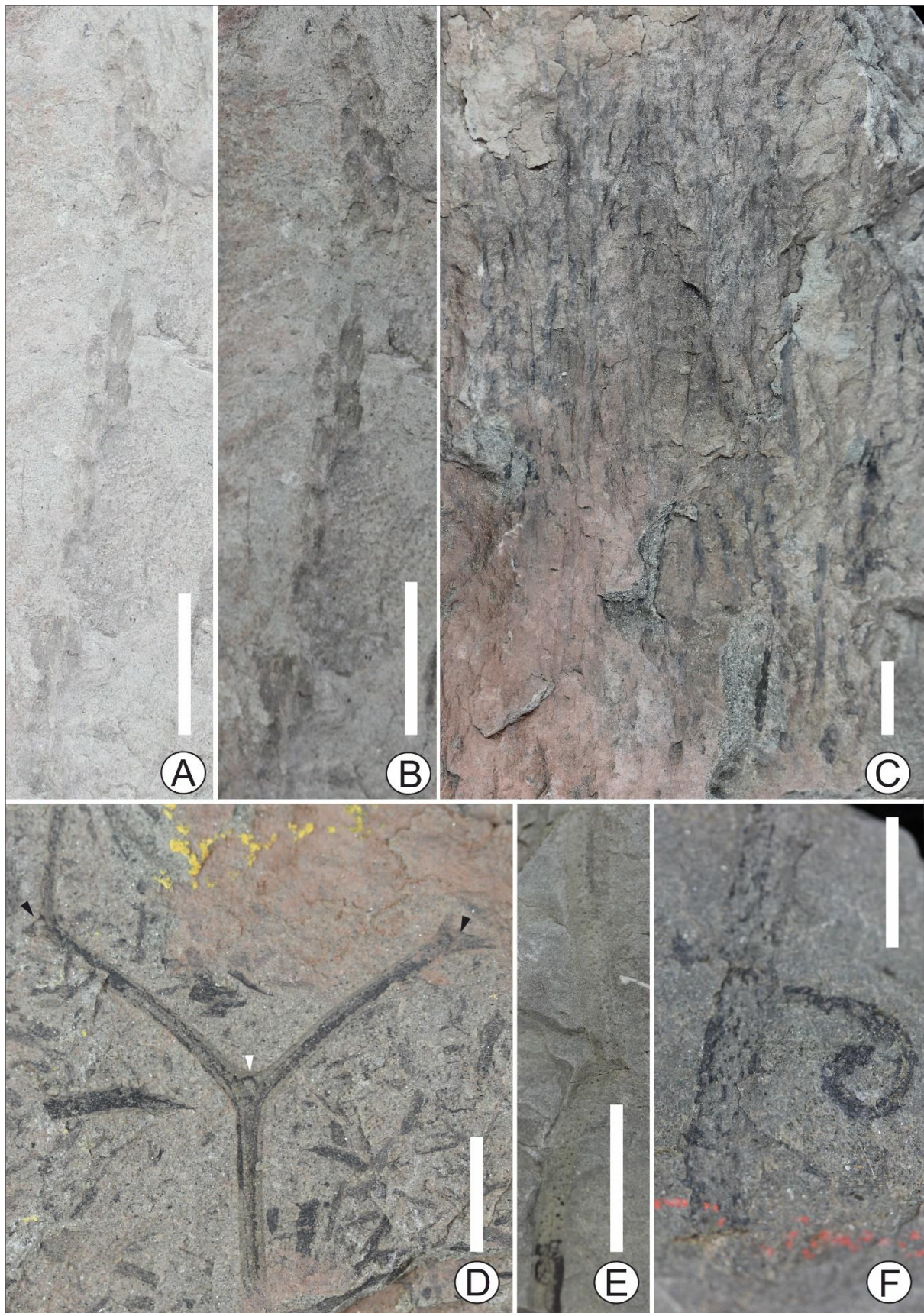


Plate ENS7. Plant remains from Dickson's Bay, Spitsbergen, collected during the E.N.S. expedition of 1939.

A. cf. *Zosterophyllum* D1. Fertile spike with sporangia arranged in two rows, placed in the subgenus *PlatyZosterophyllum*. Scale bar = 10 mm.

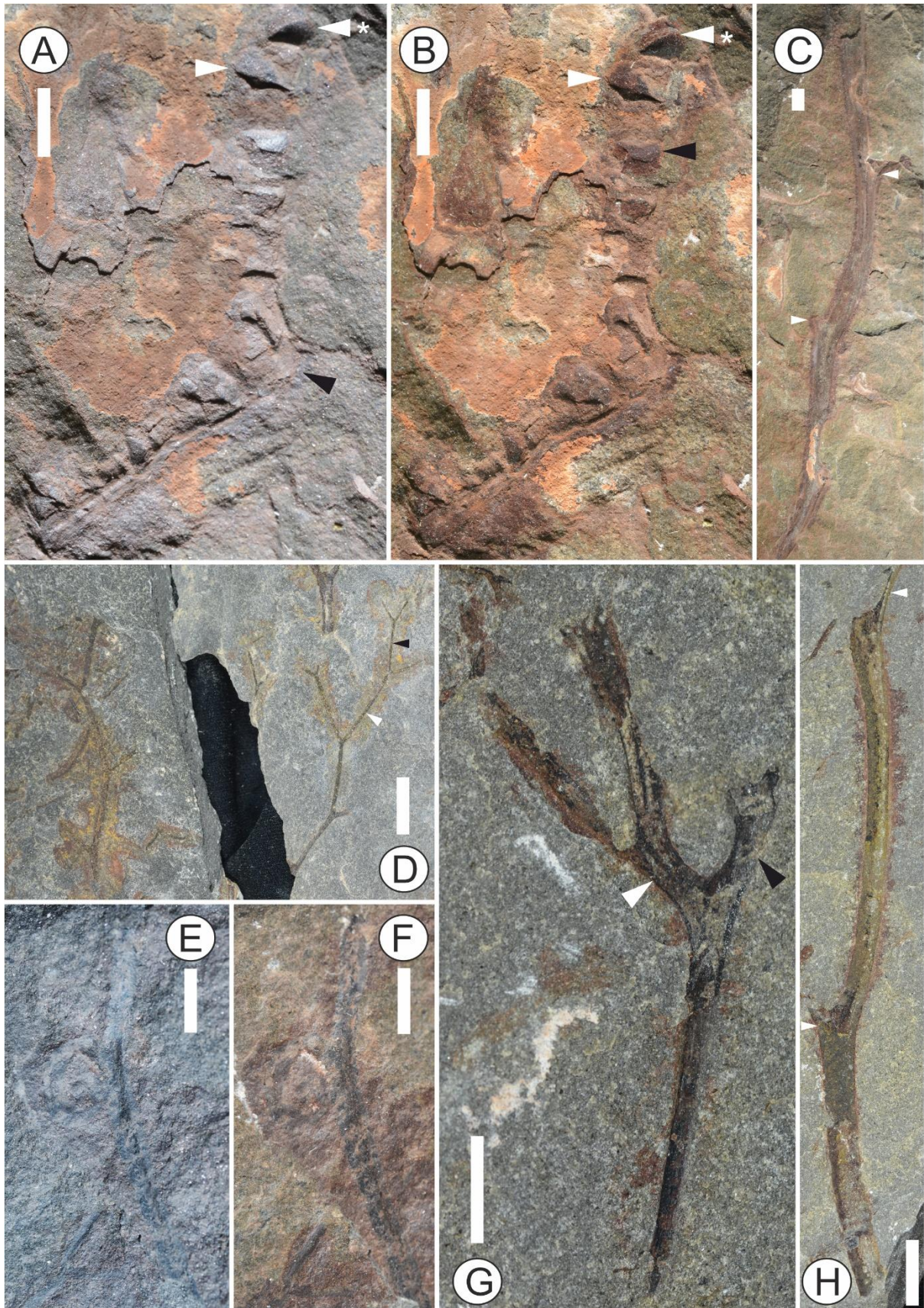
B. Same fertile spike as A, photographed under different lighting conditions. Scale bar = 10 mm.

C. Mat of poorly preserved, parallel axes of cf. *Zosterophyllum* D1. Scale bar = 10 mm.

D. *Hostinella* M3 with a poorly preserved axillary tubercle at the first bifurcation. Specimen number: V32370. Scale bar = 10 mm.

E. cf. *Psilophytites* M2. Poorly preserved bifurcating axis with spine bases. Specimen number: V32367. Scale bar = 10 mm.

F. Axis of cf. *Zosterophyllum* D1 showing circinate vernation. Scale bar = 5 mm.



Høeg Plate 1. Plant remains from Locality 1 (III), west side of Klaas Billen Bay, collected during the Høeg expedition of 1939. All specimens are housed at the Natural History Museum, Oslo (Naturhistorisk museum).

A. *Zosterophyllum* L2. Fertile spike with sporangia arranged in two rows. Black arrow marks the bend in the fertile axis; white arrows indicate the best-preserved distal sporangia and the white asterisk marks the best-preserved example. Specimen number: PMO.250.066. Scale bar = 5 mm.

B. Same fertile spike as A, photographed under cross-polarised light. White arrows indicate the best-preserved distal sporangia; black arrow indicates a compressed sporangium. Specimen number: PMO.250.066. Scale bar = 5 mm.

C. *Aphylopteris* M1 with at least two bifurcations (white arrows) and a poorly preserved central vascular strand. Specimen number: PMO.250.066. Scale bar = 10 mm.

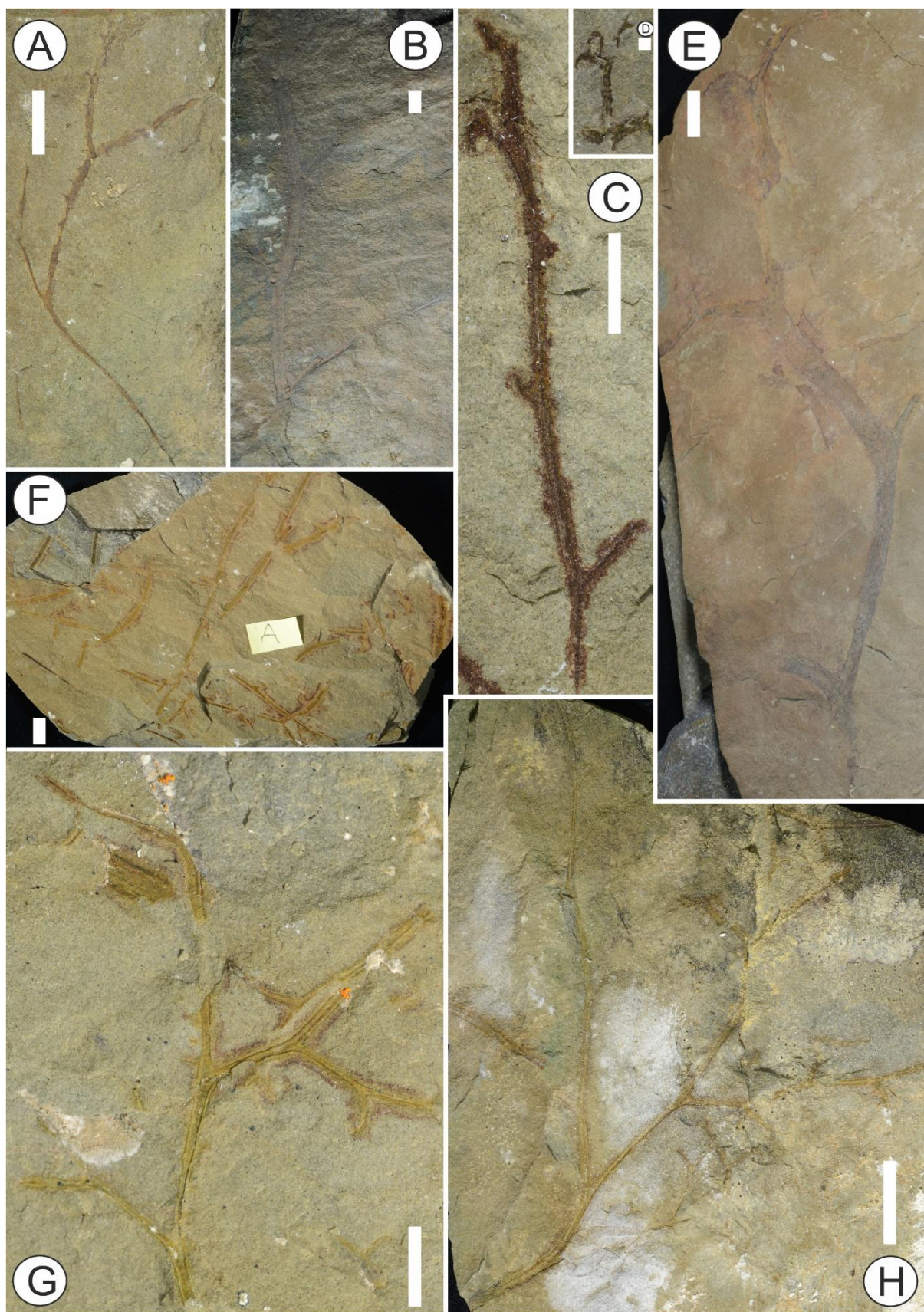
D. *Hostinella strictissima*. Part and counterpart of a bifurcating axis. White arrow marks the longest internode and black arrow the shortest. Specimen number: PMO.250.078. Scale bar = 10 mm.

E. *Zosterophyllum* L2. Poorly preserved axis fragment showing circinate veneration. Specimen number: PMO.250.067. Scale bar = 5 mm.

F. Same specimen as E, photographed under cross-polarised light. *Zosterophyllum* L2. Specimen number: PMO.250.067. Scale bar = 5 mm.

G. *Aphylopteris* L1. Axis fragment with two closely spaced bifurcations. Black arrow marks the first bifurcation; white arrows mark the second bifurcation into two narrower daughter axes. Specimen number: PMO.250.076. Scale bar = 5 mm.

H. *Aphylopteris* M1. Bifurcating axis fragment. Specimen number: PMO.250.076. Scale bar = 10 mm.



Høeg Plate 2. Plant remains from several localities on the west side of Klaas Billen Bay, collected during the Høeg expedition of 1939. All specimens are housed at the Natural History Museum, Oslo (Naturhistorisk museum).

A. *Psilophytites* M2. Anisotomously bifurcating, spiny axis fragment. Specimen number: PMO.250.106. Scale bar = 10 mm.

B. *Psilophytites svalbardensis*. Axis with at least five anisotomous bifurcations, spine bases and axillary tubercles. Specimen number: PMO.250.125. Scale bar = 10 mm.

C. *Psilophytites* N1. Poorly preserved axis fragment with possible recurved distal tips. Specimen number: PMO.250.137. Scale bar = 5 mm.

D. *Psilophytites* N1. Smaller axis fragment with recurved distal projections, from the same slab as C. Specimen number: PMO.250.137. Scale bar = 1 mm.

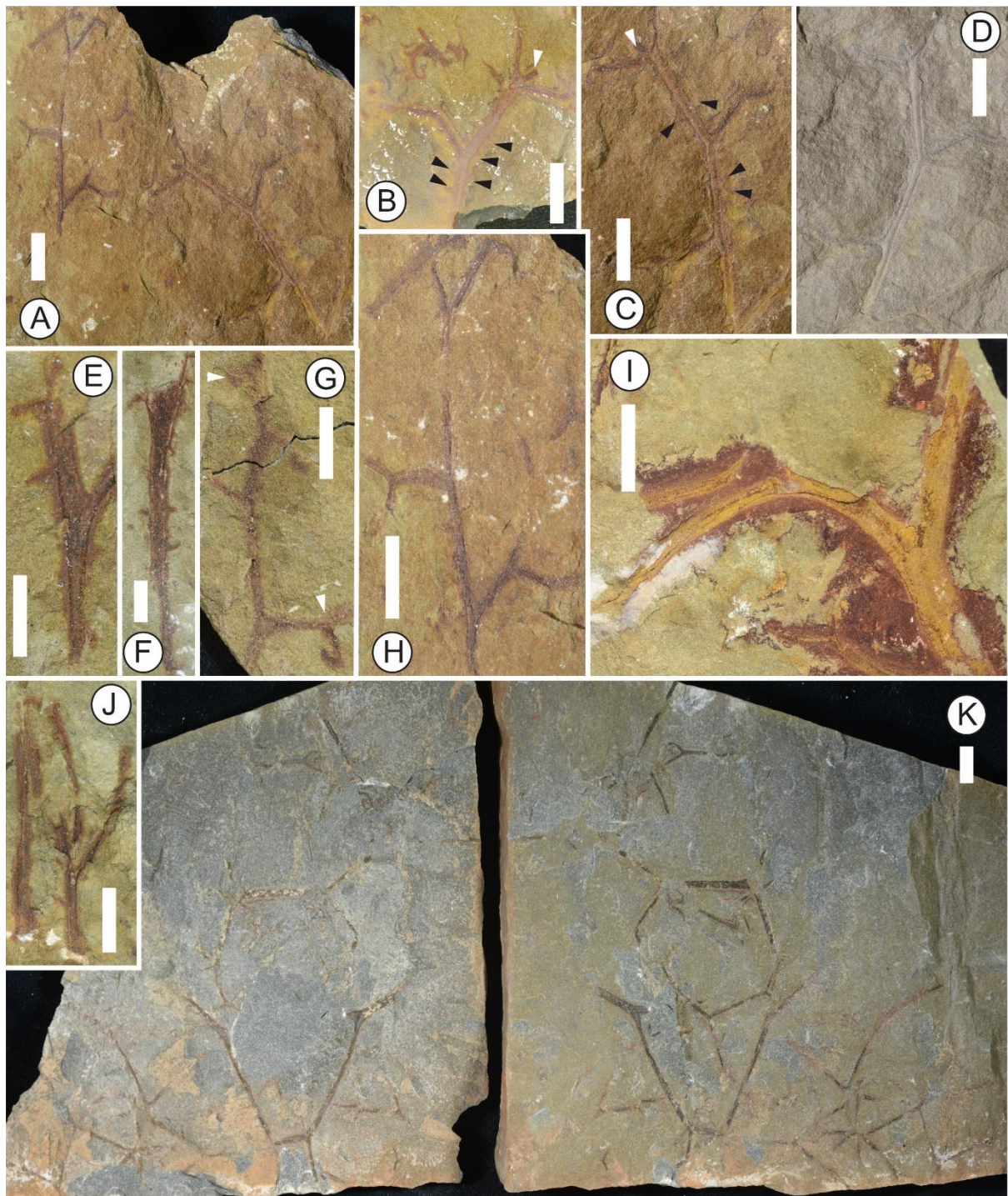
E. *Aphyllopteris* M1. Anisotomously bifurcating axis fragment. Specimen number: PMO.250.128. Scale bar = 10 mm.

F. *Hostinella strictissima*. Multiple poorly preserved bifurcating axis fragments. Specimen number: PMO.250.108. Scale bar = 10 mm.

G. *Hostinella strictissima*. Isotomously bifurcating axis fragment. Specimen number: PMO.250.130. Scale bar = 5 mm.

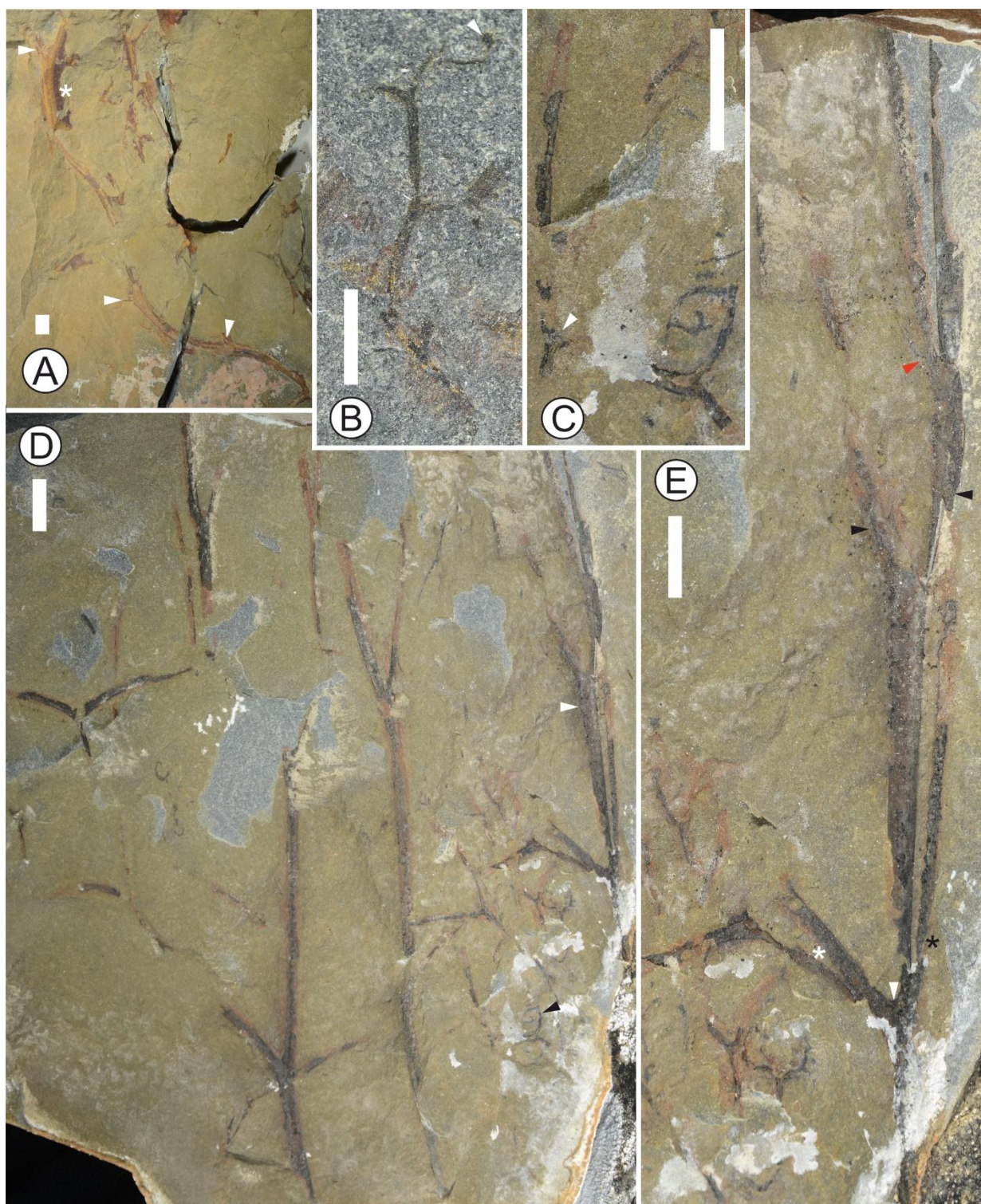
H. *Hostinella strictissima*. Isotomously bifurcating axis fragment. Specimen number: PMO.250.136. Scale bar = 10 mm.

All specimens are housed at the Natural History Museum in Oslo (*Naturhistorisk museum*).



Høeg Plate 3. Plant remains from 200 m above the Nordenskiöld Cairn (⊗), west side of Klaas Billen Bay, collected during the Høeg expedition of 1939. All specimens are housed at the Natural History Museum, Oslo (Naturhistorisk museum).

- A. Two bifurcating axes, also shown in C and H. *Psilophytites* L1. Specimen number: PMO.250.103A. Scale bar = 10 mm.
- B. Counterpart of the axis shown in C and D, photographed with water to enhance contrast. Black arrows indicate poorly preserved spine-like emergences; white arrow marks the closely spaced distal bifurcations. *Psilophytites* L1. Specimen number: PMO.250.103D. Scale bar = 10 mm.
- C. Pseudomonopodially branching axis. White arrow marks closely spaced distal bifurcations; black arrows indicate poorly preserved spine-like emergences. *Psilophytites* L1. Specimen number: PMO.250.103A. Scale bar = 10 mm.
- D. Same specimen as C, photographed without cross-polarised light to enhance surface detail. *Psilophytites* L1. Specimen number: PMO.250.103A. Scale bar = 10 mm.
- E. Anisotomously bifurcating axis with distinctive spine-like emergences. *Aphylopteris* N1. Specimen number: PMO.250.105A. Scale bar = 5 mm.
- F. Anisotomously bifurcating axis fragment with distinctive spine-like emergences. *Aphylopteris* N1. Specimen number: PMO.250.105A. Scale bar = 5 mm.
- G. Bifurcating axis with recurved distal tips and pseudomonopodial branching. *Psilophytites* N1. Specimen number: PMO.250.103B. Scale bar = 5 mm.
- H. Bifurcating axis fragment, also shown in A, with pseudomonopodial branching. *Psilophytites* L1. Specimen number: PMO.250.103A. Scale bar = 10 mm.
- I. Wide bifurcating axis fragment with an axillary tubercle between the branches. *Aphylopteris* M1. Specimen number: PMO.250.103C. Scale bar = 10 mm.
- J. Poorly preserved anisotomously bifurcating axis fragments. *Aphylopteris* N1. Specimen number: PMO.250.105B. Scale bar = 5 mm.
- K. Part and counterpart containing multiple bifurcating axis fragments. *Hostinella strictissima*. Specimen number: PMO.250.100. Scale bar = 10 mm.



Høeg Plate 4. Plant remains from the locality “Next to the red bolts (V)”, west side of Klaas Billen Bay, collected during the Høeg expedition of 1939. All specimens are housed at the Natural History Museum, Oslo (Naturhistorisk museum).

A. *Aphyllopteris* M1. Large pseudomonopodially branching axis with three anisotomous bifurcations (white arrows); white asterisk marks a poorly preserved central vascular strand. Specimen number: PMO.250.099. Scale bar value not recorded.

B. *Aphyllopteris* S3. Slender pseudomonopodially branching axis with alternate lateral branches; white arrow marks a distal circular constriction. Specimen number: PMO.250.096. Scale bar value not recorded.

C. *Psilophytites* B1. Portion of the complex branching system; white arrow marks an axis that appears to emerge from a larger primary axis. Specimen number: PMO.250.101. Scale bar value not recorded.

D. *Psilophytites* B1. Branch bifurcating isotomously; black arrow indicates a daughter axis recurving back on itself. Specimen number: PMO.250.101. Scale bar = 10 mm.

E. *Psilophytites* B1. Complex branching system; white and black asterisks mark lateral axes at the same branching node and the red arrow marks a further distal branching point. Specimen number: PMO.250.101. Scale bar = 5 mm.

Locality Name	Site Name	Area	Expedition	Taxa found
Sjettedalen	Between Sjettedalen and Purpurdalen	Wood Bay Fm, Dicksonfjorden Mb	ENS 1939	<i>Prototaxites</i> sp. <i>Aphylopteris</i> SJ1 <i>Aphylopteris</i> SJ2 <i>Aphylopteris</i> SJ3 Incertae sedis
Mt Skansen	North coast profile	Wood Bay Fm, Dicksonfjorden Mb	ENS 1939	<i>Aphylopteris</i> M1 <i>Psilophytites</i> M2 <i>Hostinella</i> M3
Sigurd fjellet	Slope towards Hoffnungsglacier	Wood Bay Fm, Dicksonfjorden Mb	ENS 1939	<i>Aphylopteris</i> M1 <i>Psilophytites</i> M2
Prismefjella	SW corner	Wood Bay Fm, Dicksonfjorden Mb	ENS 1939	<i>Aphylopteris</i> P1 <i>Hostinella</i> P2 Incertae sedis (ovate structure)
Verdalen	North side, west part	Wood Bay Fm, Dicksonfjorden Mb	ENS 1939	Large axis V1 <i>Hostinella strictissima</i> V2 <i>Hostinella</i> V3
Krosspyntdalen	—	Wood Bay Fm, Dicksonfjorden Mb	ENS 1939	cf. <i>Serrulacaulis</i> KD1
Kronprins høgda	—	Wood Bay Fm, Dicksonfjorden Mb	ENS 1939	cf. <i>Drepanophycus</i> KS1
Dickson's Bay	—	Wood Bay Fm, Dicksonfjorden Mb	ENS 1939	cf. <i>Zosterophyllum</i> D1 <i>Hostinella</i> M3 cf. <i>Psilophytites</i> M2
Klaas Billen Bay	Locality 1 (III), west side	Wood Bay Fm, Dicksonfjorden Mb	Høeg 1939	<i>Aphylopteris</i> M1 <i>Hostinella strictissima</i> <i>Aphylopteris</i> L1 <i>Zosterophyllum</i> L2
Nordenskiöld cairn	100 m from cairn (∞)	Wood Bay Fm, Dicksonfjorden Mb	Høeg 1939	<i>Hostinella strictissima</i> <i>Psilophytites</i> M2
Nordenskiöld cairn	200 m from cairn (≈)	Wood Bay Fm, Dicksonfjorden Mb	Høeg 1939	<i>Psilophytites svalbardensis</i> (Kapp Petermann morphotype)
Beach section	300 m from the beach (Ø)	Wood Bay Fm, Dicksonfjorden Mb	Høeg 1939	<i>Aphylopteris</i> M1
Nordenskiöld cairn	400 m from cairn (~)	Wood Bay Fm, Dicksonfjorden Mb	Høeg 1939	<i>Hostinella strictissima</i> <i>Psilophytites</i> N1
Nordenskiöld cairn	200 m above cairn (⊗)	Wood Bay Fm, Dicksonfjorden Mb	Høeg 1939	<i>Aphylopteris</i> N1 <i>Aphylopteris</i> M1 <i>Hostinella strictissima</i> <i>Psilophytites</i> L1 <i>Psilophytites</i> N1
Red bolts site	Next to the red bolts (V)	Wood Bay Fm, Dicksonfjorden Mb	Høeg 1939	<i>Aphylopteris</i> M1 <i>Aphylopteris</i> S3 <i>Psilophytites</i> B1

