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Supplementary Table	1	SI Appendices 1-10.xls	Appendices 1-10: Tables of spore diversity and disparity

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4 **Low tropical diversity during the adaptive radiation of early land plants**

5

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16

17 The latitudinal biodiversity gradient, with tropical regions acting as ‘evolutionary cradles’, is a
18 cornerstone of current biogeographical and ecological theory¹. In the modern world floral
19 biodiversity and biomass is overwhelmingly concentrated in the tropics, and it is often assumed that
20 the tropics were evolutionary cradles throughout land plant evolutionary history. For example, the
21 origination and diversification of angiosperms is believed to have taken place in the Cretaceous
22 tropics² and modern gymnosperms in the Permian tropics³. Here we show that during the first major
23 diversification of land plants, in the late Silurian-Early Devonian, land plant biodiversity was much
24 lower at the equator compared to medium-high southern latitudes. Throughout this crucial interval
25 of plant evolution tropical vegetation remained depauperate and of very low taxonomic biodiversity,
26 although with similar morphological disparity to the more diverse higher latitude floras. Possible
27 explanations for this low tropical floral biodiversity include palaeocontinental configuration or
28 adverse palaeotropical environmental conditions. We discount the possibility that it was simply a
29 fortuitous feature of the biogeographical spread of the earliest vascular land plants.

30

31 The land plants (embryophytes) are a monophyletic group, which are believed to have evolved as an
32 adaptive response to the invasion of the land (non-marine environments), probably from an aquatic
33 multicellular green algae ancestor⁴⁻⁵. Molecular clock analyses suggest that they evolved sometime
34 in the Cambrian-Ordovician⁶, but the first convincing fossil evidence, in the form of dispersed spores,
35 does not appear until the Mid Ordovician (470-458 Ma)⁷. These first land plants appear to have been
36 palaeogeographically widespread generalists, which were widely distributed by subaerially dispersed
37 spores, and rapidly colonised the planet’s continents. However, a rather intriguing 40 million year
38 period of stasis (‘slow fuse’) followed, during which the cryptospore-producing stem-group eophyte
39 plants⁸ appear to have remained diminutive with very little morphological and anatomical
40 innovation⁷⁻¹⁰. It was not until the late Silurian-Early Devonian (433-393 Ma) that land plants
41 underwent their first major adaptive radiation. This is attested to by both the dispersed spore and
42 plant megafossil records of the interval^{4,7}, which document how trilete spore-producing vascular
43 plants first appeared alongside the eophytes and then radiated into the rhyniophytes, zosterophylls,
44 lycopsids and trimerophytes⁴, concurrent with dramatic increases in morphological innovation and
45 maximum plant size.

46 Historically, research on the early land plant fossil record (plant megafossils and their
47 dispersed spores) has been concentrated at mid-high southerly palaeolatitudes. This is in part an
48 artefact of palaeogeography because the two main supercontinents (Gondwana and Laurussia¹¹)
49 were positioned largely in the southern hemisphere in the late Silurian-Early Devonian, and northern
50 hemisphere land masses consisted only of a series of islands (the microcontinents of Siberia,
51 Kazakhstan, North China and South China) (Fig. 1a). This configuration has resulted in a historic
52 palaeogeographical bias in palaeobotanical research towards mid-latitude regions of Laurussia (i.e.,
53 modern day North America and Europe). At the same time, palaeobotanical analysis of deposits that
54 straddle the late Silurian-Early Devonian palaeoequator has been hugely neglected, because it
55 passed through Laurussia and Gondwana only in modern day Arctic Canada-Greenland (where
56 sampling has been limited by inaccessibility) and Australia (where fossil preservation is poor due to

57 Cenozoic deep desert-tropical weathering). As a consequence, until now there has been a persistent
58 knowledge gap in our understanding of how the late Silurian-Early Devonian adaptive radiation of
59 land plants manifested in palaeoequatorial regions.

60 Here we report on Lower Devonian (Lochkovian) early land plant megafossils and dispersed
61 spores from the present day Arctic island of Spitsbergen in Svalbard, accessing a previously
62 unutilized window onto the palaeo-tropics of Laurussia (Fig. 1). The collections come from the
63 extensive 3400-3750 m thick Red Bay Group (typical 'Lower Old Red Sandstone' terrestrial-fluviatile-
64 lacustrine deposits (Fig. 1c))¹²⁻¹³, which is well age-constrained by fish fossils (including
65 biostratigraphically useful thelodonts)¹⁴⁻¹⁶. Palaeocontinental reconstructions locate the deposition
66 of the Red Bay Group to northern Laurussia; at, or very close to, the palaeoequator in late Silurian-
67 Early Devonian times (Fig. 1a)¹². From these deposits we have recovered numerous assemblages of
68 abundant and well-preserved dispersed spores and a number of rich plant megafossil horizons (Fig.
69 2; Table 1).

70 The dispersed spore assemblages are remarkable in their simplicity in terms of taxonomic
71 biodiversity and the prevalence of simple laevigate forms (Table 1; Fig. 2). They are dominated by
72 simple smooth-walled retusoid (*Retusotriletes* spp.) and crassitate (*Ambitisporites* spp.) trilete
73 spores comprising between 88.0- 93.5% of the assemblages. Rudimentary ornamented spores have
74 grana, coni and verrucae that are seldom larger than 1 μm in height (*Acinosporites* spp.,
75 *Aneurospora* spp., *Apiculiretusispora* spp.). There are rare forms (comprising less than 0.5% of the
76 assemblages and generally not featuring in counts) with proximal radial ribbing (*Emphanisporites*
77 spp.), reticulate sculpture (*Dictyotriletes* sp.) or more complex zonate structure (*Breconisporites* sp.
78 and *Camptozonotriletes* sp.). Notable is the near absence of cryptospores. Rare tetrads possibly
79 represent cryptospore permanent tetrads but are more likely tetrads of trilete spores that have
80 failed to dissociate. In terms of diversity only 18 species in 10 genera are present.

81 We have tabulated dispersed spore distribution in coeval Lochkovian deposits from the
82 southern mid-high latitudes: Scotland (Supplementary Table 1), the Anglo-Welsh Basin
83 (Supplementary Table 2) and the Ardenne-Rhenish region (Supplementary Table 3) from Laurussia;
84 Iberia (Supplementary Table 4) and North Africa (Supplementary Table 5) from Peri-Gondwana and
85 Gondwana. This database demonstrates that certain distinctive trilete spore morphotypes
86 characteristic of coeval Lochkovian spore assemblages are absent from the Spitsbergen assemblages,
87 such as those with patinate structure (*Archaeozonotriletes*, *Chelinospora*, *Cymbosporites*), those with
88 biform ornament (*Dibolisporites*, *Biornatispora*), and various highly distinctive taxa such as
89 *Brochotriletes*, *Iberoospora*, *Perotriletes* and *Scylaspora*. In terms of diversity, the Spitsbergen
90 assemblages contain only 18 species in 10 genera of trilete spores. In coeval Lochkovian mid-latitude
91 dispersed spore assemblages from the same palaeocontinent (Laurussia) both cryptospores and
92 trilete spores are highly diverse. The absence of cryptospores is intriguing and would appear to
93 reflect a complete absence of stem group eophyte plants⁸, despite the cryptospores being abundant
94 and diverse in coeval spore assemblages from higher latitudes. In contrast, in terms of trilete spores
95 67(17) species(genera) have been reported from Scotland¹⁷, 99(25) from the Anglo-Welsh basin¹⁸
96 and 119(29) from the Ardennes-Rhenish region¹⁹. In coeval high latitude assemblages from Peri-
97 Gondwana and Gondwana 66(21) species(genera) of trilete spore have been reported from Iberia²⁰⁻
98 ²¹ and 93(24) from North Africa²²⁻²³.

99 All of the trilete spores in our diversity database (see above) have also been scored using a
100 system recently utilised for quantifying trilete spore disparity⁷(Supplementary Tables 6-10). The
101 average Disparity Index score for the Spitsbergen assemblage is 11.7 (Supplementary Table 11)
102 compared to that from the Anglo-Welsh basin (12.0), Scotland (11.9), the Ardennes-Rhenish region
103 (12.8), Iberia (12.0) and North Africa (11.7) (see Table 2). It is interesting that, despite the absence of
104 some notable genera, the Spitsbergen trilete spore assemblages appear to be of a similar level of
105 morphological complexity to the other trilete spore assemblages. A common feature of adaptive
106 radiations is an early burst of morphological novelty and our disparity data may be picking up this
107 pattern among spores during the adaptive radiation of vascular plants.

108 South China is considered to have represented an isolated island that lay on or very close to
109 the equator during the late Silurian-Early Devonian (Fig. 1a)¹¹ and is one of the very few other
110 locations from where Lower Devonian (Lochkovian) equatorial dispersed spore and plant megafossil
111 assemblages have been described. Traditionally the floras (mega and micro) of this isolated island
112 have been considered to be highly endemic²⁴⁻²⁷. However, inspection of the Lochkovian dispersed
113 spore floras from South China shows that they consist of abundant low diversity assemblages of
114 simple spores, with a very high proportion of laevigate spores (Supplementary Table 12). The
115 Chinese spore assemblages share all of the genera reported from Spitsbergen, with many species in
116 common, except they appear to lack the zonate forms *Camptozonotriletes* and *Breconisporites*. The
117 similarity of composition and morphotypes between the South China and Spitsbergen assemblages
118 demonstrates that an abundance of simple forms is a common motif in all known, albeit rare,
119 samples from the Silurian-Devonian palaeotropics²⁸⁻²⁹.

120 Plant megafossil assemblages were recovered from three rich plant beds from the Red Bay
121 Group, two horizons previously reported in the small ravine near Frænkelryggen³⁰ and a new locality
122 on Buchananhalvøya (Fig. 2). Plant/fungal taxa previously reported from the Red Bay Group by Høeg
123 are the nematophytes *Pachytheca* cf. *fasciculata* Kidston & Lang and *Prototaxites* sp., the
124 rhyniophytes *Taeniocrada* (?) *spitsbergensis* Høeg and *Hostinella* sp., and the zosterophyll
125 *Zosterophyllum* sp.³⁰. Despite extensive searching our collections (Fig. 2) did not add to this
126 depauperate flora. Plant megafossil assemblages from coeval mid-high latitude assemblages of
127 Laurussia and Gondwana are notably more diverse^{4,7}. For example, the Lochkovian of the Anglo-
128 Welsh Basin has yielded 32 species placed within 25 genera³¹. It is clear that notable plant groups
129 are absent including the Rhyniophytoids with terminal sporangia (e.g. *Cooksonia*, *Salopella*,
130 *Tortilicaulis*, *Uskiella*), more complexly- branched zosterophylls (e.g. definite *Gosslingia*) and early
131 trimerophytes.

132
133 It is evident from the above discussion that the tropical Early Devonian Spitsbergen flora is
134 significantly less taxonomically diverse and morphologically disparate than coeval higher latitude
135 floras. Comparison with other potential tropical floras is limited. The enigmatic *Baragwanathia* flora
136 of Australia is poorly age constrained and it is unclear if any of the plant assemblages are of
137 Lochkovian age³². Dispersed spore assemblages of Lochkovian (and indeed Early Devonian) age are
138 unknown from Australia. The South China microcontinent was located in tropical latitudes (see
139 above) but was an isolated island that appears to have harboured a highly endemic flora³³.
140 Lochkovian plant megafossils described to date consist entirely of zosterophylls and in this respect
141 resemble the Spitsbergen flora³⁴⁻³⁷. The similarity between Lochkovian dispersed spore assemblages
142 from South China and Spitsbergen is noted above and this includes a dominance of the simple
143 retusoid spore *Retusotriletes* spp. that is known to be produced by many zosterophylls.

144 There are a number of possible explanations for the low taxonomic biodiversity of Early
145 Devonian (Lochkovian) tropical floras. One possibility is that it is a consequence of palaeocontinental
146 configuration. During the critical late Silurian-Early Devonian interval there was only limited land
147 mass in tropical regions: the northern extremities of the supercontinents Laurussia and Gondwana,
148 in addition to isolated island microcontinents such as South China. Potentially the lack of space and
149 biotic interaction hindered the potential of the tropics to act as an 'evolutionary cradle' resulting in
150 low biodiversity. Conversely, the much larger land areas in the southern mid-high latitudes may have
151 provided the required space and interconnectivity to facilitate land plant diversification leading to
152 higher biodiversity.

153 A second possibility is that the Lower Devonian (Lochkovian) witnessed extreme
154 environments at the tropics that were detrimental to plants thriving and thus retarded evolutionary
155 innovation and biodiversity. Obvious candidates for environmental stress are adverse climatic and
156 atmospheric conditions. For example, high temperatures coupled with low atmospheric oxygen
157 levels has been posited as an explanation for low tropical biodiversity during the Permian-Triassic³⁸.
158 However, this time also witnessed low fish diversity due to the same stresses, whereas the fish
159 biotas of tropical Spitsbergen are both abundant and diverse¹⁴⁻¹⁶, and are comparable in their
160 abundance and diversity to those of the southern mid-high latitudes. Interestingly, the Lochkovian
161 fish biotas of tropical South China are also abundant and diverse³⁹. It should also be pointing out
162 that sedimentological evidence for climate extremes in the Spitsbergen sequences is lacking¹²⁻¹³
163 with the stratigraphic sequence comprising typical continental 'Lower Old Red Sandstone' sediments
164 similar to those from mid-high southerly palaeolatitudes of Laurussia.

165 A third possibility is that the pattern of biodiversity/disparity simply reflects an inherent
166 (perhaps fortuitous) pattern of early land plant evolution. For example, land plants, particularly
167 vascular plants, may have originated much further south in Laurussia or Gondwana⁷ and biodiversity
168 may simply have taken longer to migrate to the equatorial northern extremities of these continents.
169 However, this explanation seems less plausible given that vascular plants appeared in the Late
170 Silurian (Pridoli), at the very latest, giving them an adequate period of time, at least several million
171 years, to migrate across the continents by Lochkovian times.

172

173 **Methods**

174 **Fieldwork expedition**

175 Samples were collected during fieldwork in northern Spitsbergen undertaken in August 2018 by
176 CMB, ND, F-JL, JEAM and CHW. The boat MS Farm was used for transport and accommodation. A
177 number of sections in the Lower Devonian (Lochkovian) Red Bay Group sequence, which crops out in
178 the vicinity of Red Bay, were explored (Fig. 1)¹¹⁻¹². These were sedimentologically/stratigraphically
179 investigated and collected for palynological and palaeobotanical samples. Details of the
180 palynological samples and palaeobotanical samples (plant beds) are provided in Online Content
181 (Supplementary Table 13).

182 **Palynology**

183 For each sample 20g of fresh rock was cleaned and demineralised using standard palynological HCl-
184 HF-HCl acid maceration techniques. Sieving was undertaken using a 20 µm mesh. The residue was
185 then subjected to heavy mineral separation, using zinc chloride, to remove any remaining mineral
186 matter. The residues were strew mounted onto glass coverslips and attached to glass slides using
187 Epoxy resin. Rich assemblages of palynomorphs were recovered containing only land plant spores
188 and phytodebris. The palynomorphs were well preserved and of moderate thermal maturity (T.A.I.
189 3.5-5.0 based on a standard colour scheme⁴⁰). Oxidation for between 10 and 60 minutes in fresh
190 Schultz solution lightened the palynomorphs to a translucent yellow-orange suitable for light
191 microscope analysis. All materials are curated in the Centre for Palynology of the University of
192 Sheffield.

193 **Palaeobotany**

194 Extensive collections of land plant megafossil were collected from the 'plant beds' and shipped to
195 Cardiff University. Here they were analysed by CMB and AW and photographed. All specimens are
196 curated in the Department of Earth and Ocean Sciences of Cardiff University and the Natural History
197 Museum Oslo.

198 **Data availability**

199 All data is available from the corresponding author.

200

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203 undertake the fieldwork (RiS-ID 10970).

204

205 **Author contribution** CMB, ND, F-JL, JEAM and CHW participated in the expedition to northern
206 Spitsbergen and were involved in geological-stratigraphical-sedimentological interpretation and
207 collecting samples for palynological/palaeobotanical analysis. CHW undertook the palynological
208 research and created the spore diversity and disparity database. CMB and AW undertook the
209 palaeobotanical research. All authors contributed to the design of the project, the interpretation of
210 the data and the writing of the manuscript.

211

212 **Competing interests** The authors declare no competing interests.

213

214 **Table legends**

215

216 **Table 1** Dispersed spore taxa and their distribution from the Lower Devonian (Lochkovian) Red Bay
217 Group of Red Bay, Spitsbergen.

218

219 **Table 2** A comparison of the diversity (disparity) of the dispersed trilete spore assemblages from the
220 Red Bay Group, Spitsbergen compared to Lochkovian assemblages from elsewhere.

221

222 **Figure legends**

223

224 **Fig. 1 Geology of the Lochkovian Red Bay Group of Spitsbergen.** **a**, Lower Devonian (Lochkovian)
225 palaeocontinental reconstruction after Torsvik & Cocks (2017)¹⁰. Note the position of Spitsbergen at
226 the equator. 1 = Scotland; 2 = Ardenne-Rhenish region; 3 = Anglo-Welsh Basin; 4 = Northern Spain; 5
227 = North Africa (Libya); 6 = South China. **b**, Location map and geological map of the Spitsbergen Red
228 Bay Group. **c**, Stratigraphy of the Late Silurian-Lower Devonian of Spitsbergen and stratigraphical
229 nomenclature for the Red Bay Group. Spitsbergen Silurian-Devonian stratigraphical nomenclature
230 follows Davies et al. (2021)¹². Red Bay Group stratigraphical column after Friend et al. (1997)¹¹. ORS =
231 Old Red Sandstone.

232

233 **Fig. 2 Dispersed spores (a-r) and plant megafossils (s-u) from the Red Bay Group of Spitsbergen.**
234 Scale bar = 40 μ m (a-r), 5 mm (s), 1 mm (t), 1 mm (u). **a-r**, dispersed spores. (a) *Retusotriletes* spp.
235 18SPITS07/1 (G29). (b) *Retusotriletes triangulatus* 18SPITS07/1(C25/1). (c) *Retusotriletes maculatus*
236 18SPITS05/1(L40/4). (d) *Retusotriletes* sp. A 18SPITS08/1(T36/4). (e) *Apiculiretusispora* sp. A
237 18SPITS08/1(W44). (f) *Apiculiretusispora* spp. 18SPITS22/1(F32). (g) *Dictyotriletes* sp. A
238 18SPITS05/1(M39/1). (h) *Ambitisporites avitus* 18SPITS07/1(P49/1). (i) *Ambitisporites* spp.
239 18SPITS08/1(Q36/3). (j) *Aneurospora* sp. B 18SPITS07/1(p46/4). (k) *Aneurospora* sp. A
240 18SPITS18/1(J44/3). (l) *Aneurospora* sp. C 18SPITS29/1(B29). (m) *Aneurospora* sp. D
241 18SPITS23/1(K28/2). (n) *Aneurospora* sp. E 18SPITS30/1(D36). (o) *Emphanisporites* sp.
242 A18SPITS24/1(Y47/1). (p) *Acinosporites* sp. A 18SPITS21/1(L26/4). (q) *Camptozonotriletes* sp. A
243 18SPITS23/1(G53/4). (r) *Breconisporites* sp. A 18SPITS08/1(J30/4). **s-u**, plant megafossils. (s)
244 Anisotomous branching in *Zosterophyllum*. The basal portion of the axis exhibits H- branching typical
245 of that found in *Zosterophyllum*. The apical portion of the specimen dichotomises anisotomously,
246 into a further dichotomising axis. PMO 235.642/a. (t) Fertile axis of *Zosterophyllum* with 4 pairs of
247 sporangia. Associated axis can be seen on the most basal pair of sporangia. PMO 235.642/b. (u)
248 Erect, overlapping *Zosterophyllum* axis. PMO 235.643.

249

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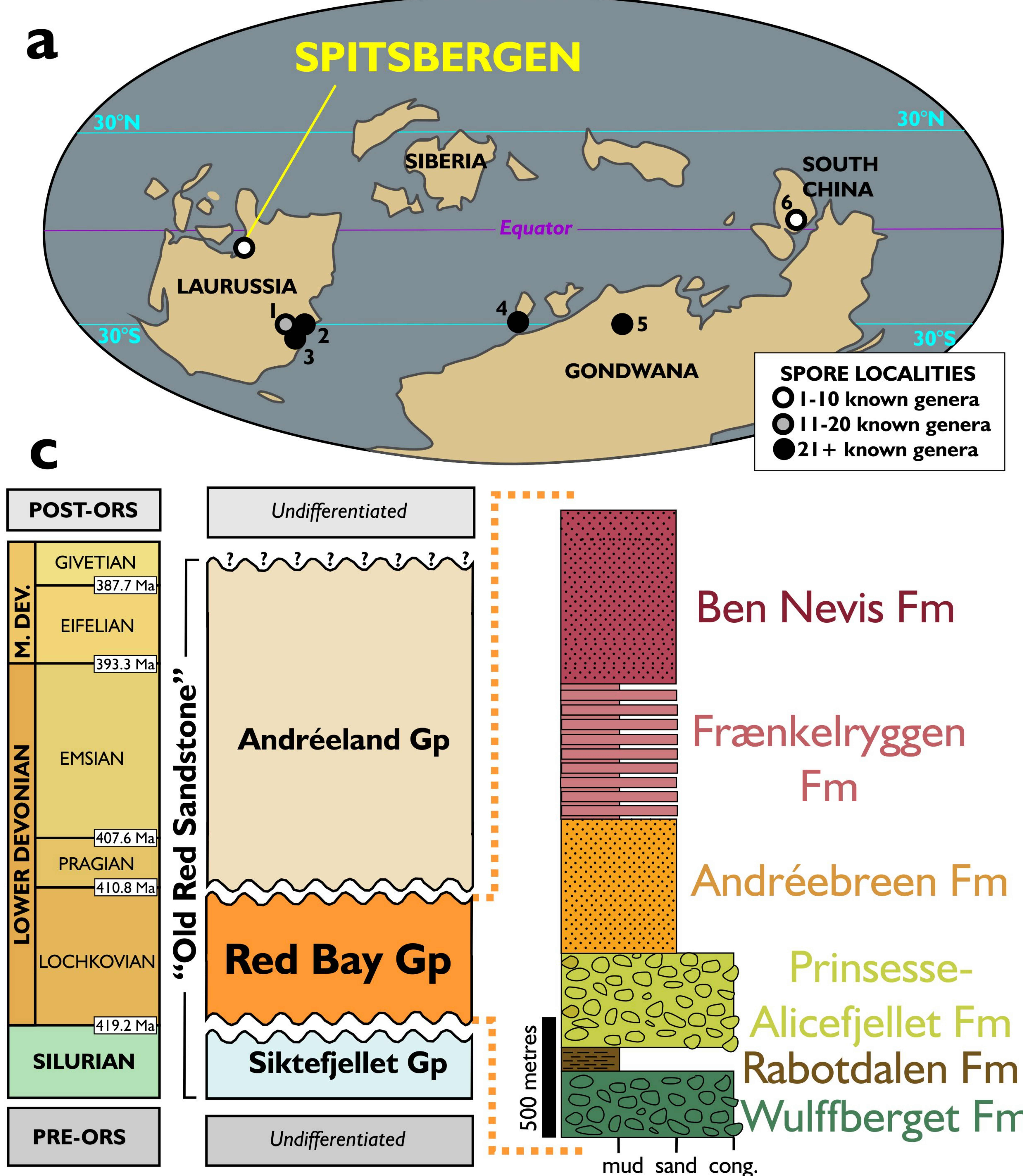
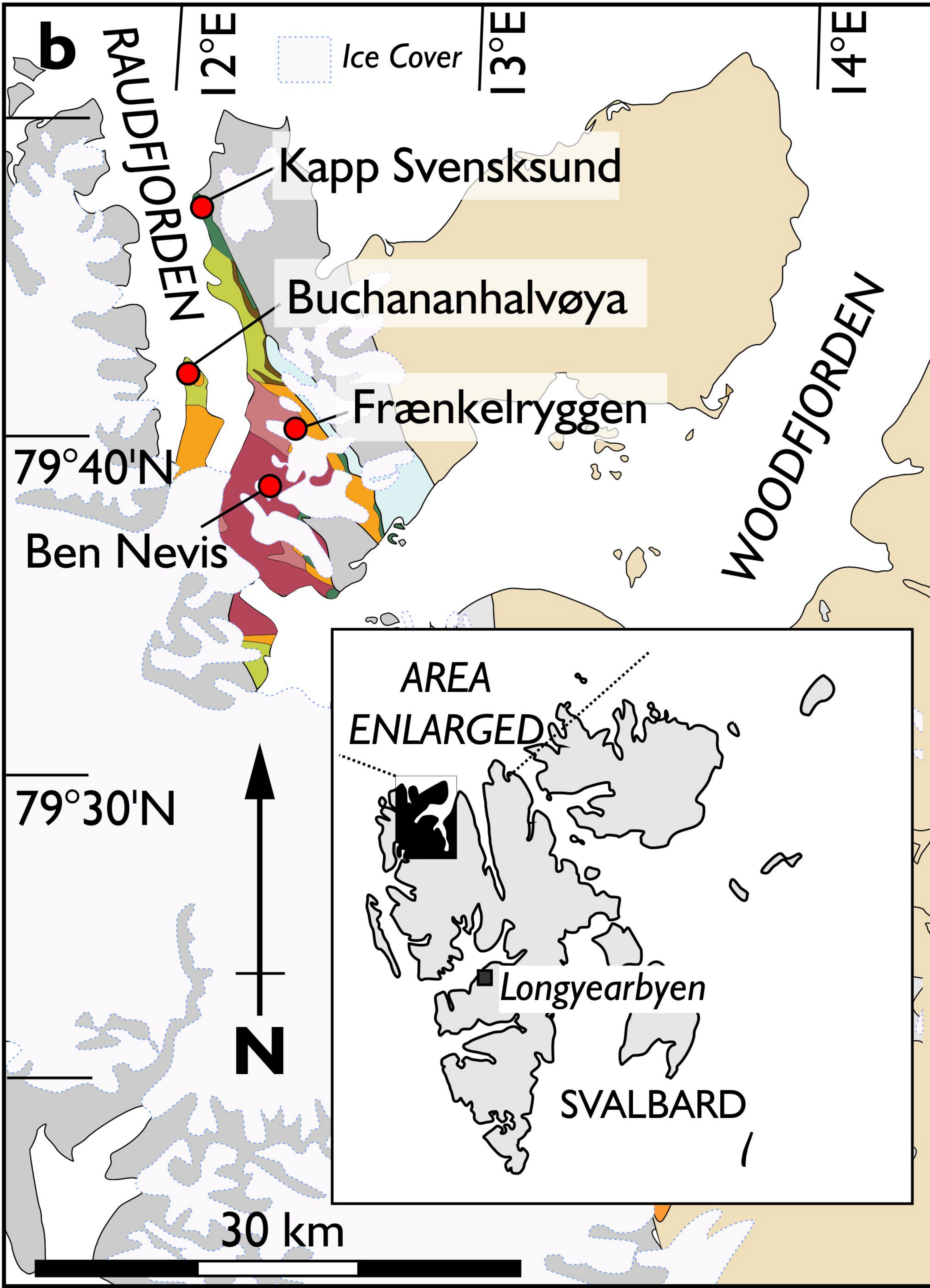
347 **Additional information**

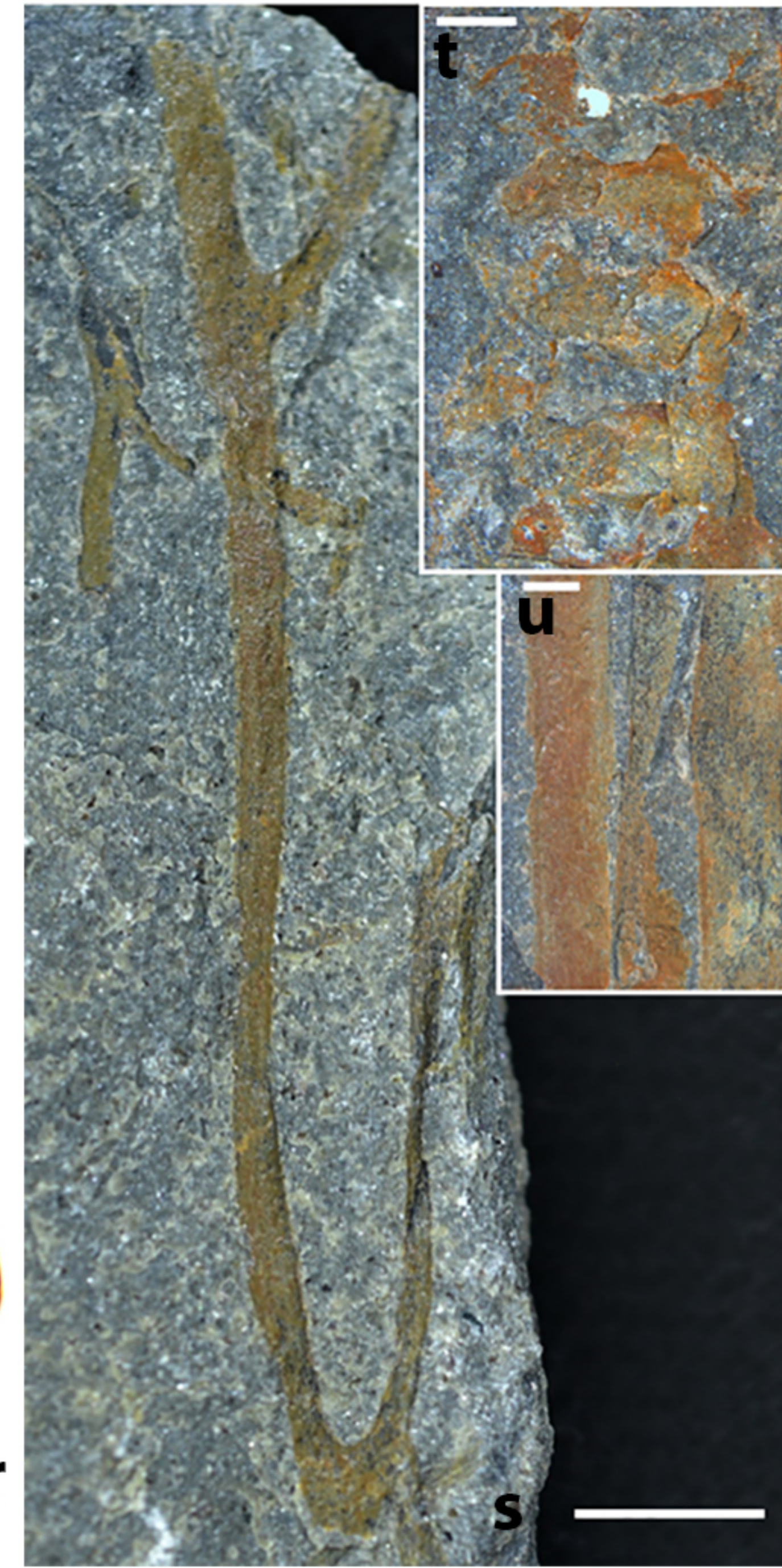
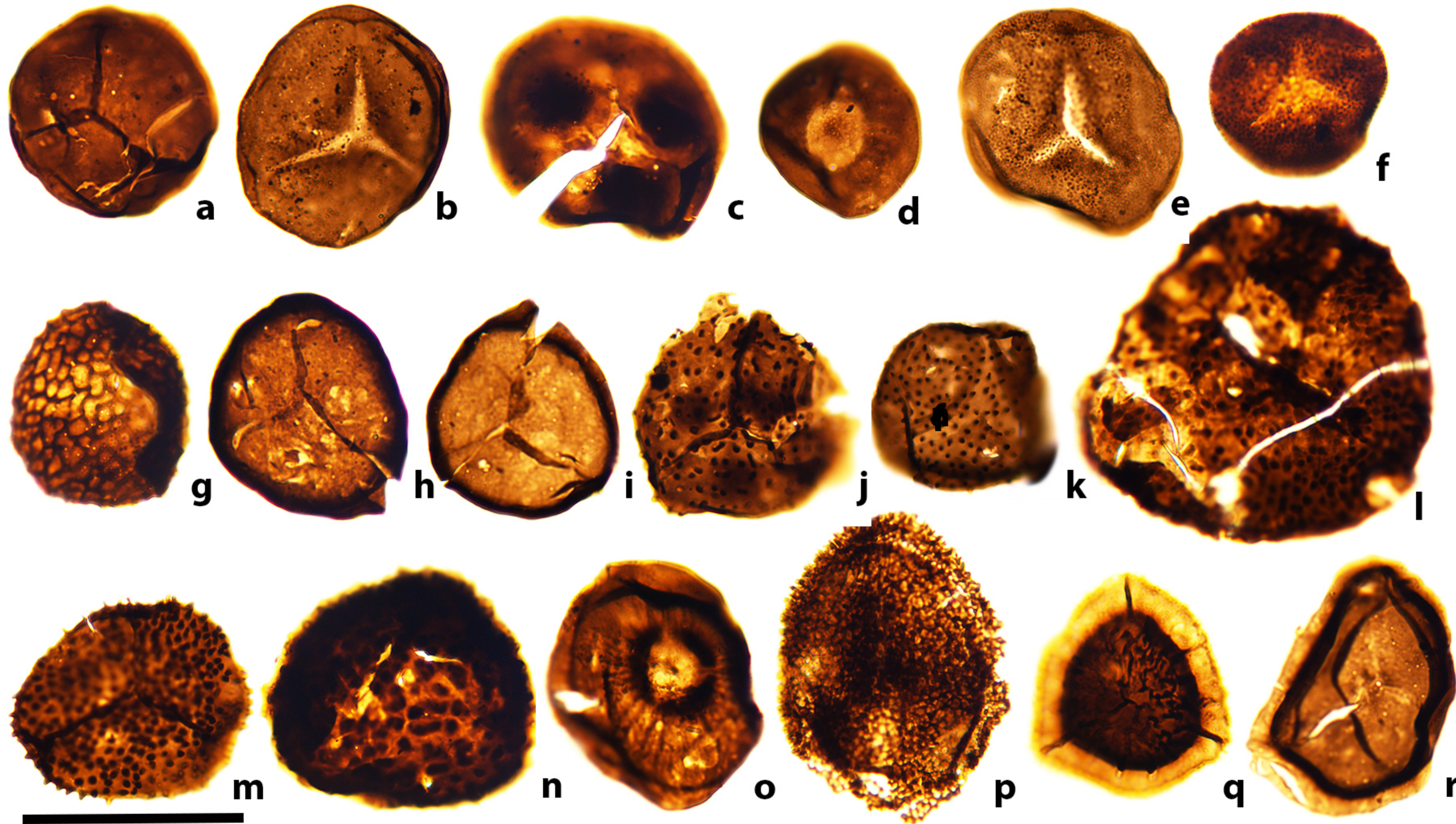
348 **Supplementary information** The online version contains supplementary material available at
349 <https://>

350 **Correspondence and requests for materials** should be addressed to CHW.

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DIVERSITY	11	14	16	11	13	13	12	14	11	6	9	10	11	9	13
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	TRILETE SPORE SPECIES DIVERSITY	TRILETE SPORE GENERIC DIVERSITY	CRYPTOSPORE DIVERSITY	TRILETE SPORE DISPARITY [MIN(AVERAGE)MAX]
SPITSBERGEN	18	10	?1	9(11.7)15
SCOTLAND	67	17	32	9(11.9)15
ANGLO-WELSH BASIN	99	25	54	9(12.0)15
ARDENNE-RHENISH	119	29	Not reported	9(12.8)16
NORTHERN SPAIN	66	21	Not reported	9(12.0)15
NORTH AFRICA	93	24	13	9(11.7)15