

This is an Open Access document downloaded from ORCA, Cardiff University's institutional repository:<https://orca.cardiff.ac.uk/id/eprint/127556/>

This is the author's version of a work that was submitted to / accepted for publication.

Citation for final published version:

Stein, William E., Berry, Christopher M. , Morris, Jennifer L. , VanAller Hernick, Linda, Mannolini, Frank, Ver Straeten, Charles, Landing, Ed, Marshall, John E. A., Wellman, Charles H., Beerling, David J. and Leake, Jonathan R. 2020. Mid-Devonian archaeopteris roots signal revolutionary change in earliest fossil forests. *Current Biology* 30 (3) , 421-431.e2. 10.1016/j.cub.2019.11.067

Publishers page: <http://dx.doi.org/10.1016/j.cub.2019.11.067>

Please note:

Changes made as a result of publishing processes such as copy-editing, formatting and page numbers may not be reflected in this version. For the definitive version of this publication, please refer to the published source. You are advised to consult the publisher's version if you wish to cite this paper.

This version is being made available in accordance with publisher policies. See <http://orca.cf.ac.uk/policies.html> for usage policies. Copyright and moral rights for publications made available in ORCA are retained by the copyright holders.



1 **MID DEVONIAN *Archaeopteris* ROOTS**
2 **SIGNAL REVOLUTIONARY CHANGE**
3 **IN EARLIEST FOSSIL FORESTS**

4
5 William E. Stein^{1,6,7,*}, Christopher M. Berry^{2,6}, Jennifer L. Morris^{2,6}, Linda VanAller Hernick³,
6 Frank Mannolini³, Charles Ver Straeten³, Ed Landing³, John E. A. Marshall⁴, Charles H.
7 Wellman⁵, David J. Beerling⁵, and Jonathan R. Leake⁵

8
9 ¹Department of Biological Sciences, Binghamton University, Binghamton NY 13902

10 ²School of Earth and Ocean Sciences, Cardiff University, Cardiff, CF10 3AT, UK

11 ³New York State Museum, Albany, NY 12230

12 ⁴School of Ocean and Earth Science, University of Southampton, Southampton SO14 3ZH, UK

13 ⁵Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK

14 ⁶These authors contributed equally

15 ⁷Lead Contact

16 *Correspondence: stein@binghamton.edu (W.E.S.), BerryCM@cardiff.ac.uk (C.M.B.),
17 drjenlmorris@gmail.com (J.L.M.).

18

19 SUMMARY

20 **The origin of trees and forests in the Mid Devonian (393-383 Ma) was a turning point in**
21 **Earth history marking permanent changes to terrestrial ecology, geochemical cycles,**
22 **atmospheric CO₂ levels and climate. However, how all these factors interrelate remains**
23 **largely unknown. From a fossil soil (palaeosol) in the Catskill region near Cairo NY, USA**
24 **we report evidence of the oldest forest (mid Givetian) yet identified worldwide. Similar to**
25 **the famous site at Gilboa NY, we find treefern-like *Eospermatopteris* (Cladoxylopsida).**
26 **However, the environment at Cairo appears to have been periodically drier. Along with a**
27 **single enigmatic root system potentially belonging to a very early rhizomorphic lycopsid,**
28 **we see spectacularly extensive root systems here assigned to the lignophyte group**
29 **containing the genus *Archaeopteris*. This group appears pivotal to the subsequent**
30 **evolutionary history of forests due to possession of multiple advanced features and likely**
31 **relationship to subsequently dominant seed plants. Here we show that *Archaeopteris* had a**
32 **highly advanced root system essentially comparable to modern seed plants. This suggests a**
33 **unique ecological role for the group involving greatly expanded energy and resource**
34 **utilization, with consequent influence on global processes much greater than expected from**
35 **tree size or rooting depth alone.**

36 INTRODUCTION

37 Trees play an exceedingly complex structural and biotic role within modern terrestrial forest
38 ecosystems [1]. Although Carboniferous (359-299 Ma) fossil forests included tree-sized
39 lycopsids, sphenopsids and ferns [2,3], seed plants have overwhelmingly populated terrestrial
40 forests since the late Paleozoic. However, during the critical interval of initial establishment of
41 Earth's earliest forests, the Mid Devonian, all trees have uncertain evolutionary relationships [4]
42 and are incompletely understood. As a result, direct fossil evidence is critically needed to
43 understand factors relating to initial terrestrial ecosystem assembly, including data on habitat
44 specificity, spatial distributions, ecological tolerances, rooting behavior, and plant interactions
45 [5,6]. Paleosols mapped in plan view potentially provide some of this key information. From

46 Riverside Quarry, Gilboa, New York, trees identified as *Eospermatopteris* [7], with *Wattieza*
47 foliage (belonging to extinct order Pseudosporochneales, class Cladoxylopsida) [8], were
48 previously shown to occur as forest dominants associated with other tree-sized forms including
49 procumbent to lianoid aneurophytaleans (cf. *Tetraxylopteris*, class Progymnospermopsida) and at
50 least one arborescent probably cormose lycopsid [9]. All root systems at Gilboa were simple
51 sparsely branched linear structures generally typical of plants of this and earlier age. However,
52 archaeopteridaleans were conspicuously missing. Commonly placed within the single genus
53 *Archaeopteris* (= *Callixylon*), the group shows significant variation, and very likely represents a
54 taxonomically diverse as well as ecologically significant forest element [10]. Moreover,
55 archaeopteridaleans possess an impressive set of seed plant features assembled together for the
56 first time in the fossil record, including large upright habit, eustelic primary vascular system,
57 bifacial vascular cambium producing conifer-like secondary tissues, laminate leaves,
58 heterospory, delayed development involving bud-like behavior, and endogenous root production
59 [11-13]. Macrofossil and microfossil evidence suggests appearance of *Archaeopteris* worldwide
60 by the early Givetian (388-383 Ma), with apparent rise to dominance in the Catskill region by the
61 Famennian (372-359 Ma) [14,15]. Reconstructed with conifer-like form [16,17] and given its
62 widespread occurrence, *Archaeopteris* has commonly been assumed to occupy drier habitats
63 compared to potentially more ecologically restricted *Eospermatopteris* [10], but direct evidence
64 for the ecological amplitude for either tree, and consequent influence on global processes,
65 remains unknown.

66 **RESULTS**

67 From a paleosol in an abandoned quarry in the Plattekill Formation of the Hamilton Group near
68 Cairo, NY (42°19'09.23"N, 74°02'40.16"W), we have uncovered evidence for a strikingly

69 different paleoenvironment than Riverside Quarry Gilboa, that now includes *Archaeopteris*
70 (Figure 1). Strata at the site are interpreted to be correlative with the marine Ludlowville
71 Formation to the west, which is early mid Givetian (ca. 385 Ma) in age [18] and ca. 2-3 Ma older
72 than Riverside Quarry in the Cooperstown (Moscow) Formation, dependent on time scale used
73 [19,20]. Plant fossils found over many years of collecting in the quarry include the common
74 major groups of Middle Devonian plants (aneurophytaleans, archaeopteridaleans,
75 cladoxylopsids, lycopsids) [21,22], as well as restricted horizons containing liverworts and
76 vertebrate fragments [23,24]. A portion of the quarry floor provides an extensive plan exposure
77 of a siltstone horizon interpreted as the upper part of a paleosol containing spectacular *in situ*
78 root systems (Figure 1C).

79 **Paleosol Description and Interpretation**

80 To date approximately 3000 m² surface of the paleosol has been uncovered. Most regions show
81 complex texture with heavy fracturing into small 1-3 cm blocks as a result of recent weathering
82 and past quarrying. This pattern is superimposed on larger slickensided curvilinear fractures that
83 form semi-spheroidal features 10-30 cm in diameter. In addition, the surface undulates, with
84 many small to larger-scale holes and semi-circular depressions, some of which may represent
85 smaller paleofloral elements that cannot be identified as such, or variations in surface
86 topography. There is also considerable lateral variation in color across the mapped paleosol
87 surface. In the north part of the exposure (Figure 1C, region I), the root systems penetrate a
88 siltstone predominantly dusky to weak red in color (Munsell colors 10R 5/4 – 10R 3/3), with
89 patchy bluish-gray mottling (10B 6/1). This mottling is related in part to the occurrence of
90 nearby root systems, and many root traces exhibit bluish-gray haloes (Figures 3C-F). To the
91 south-southwest (Figure 1C, region II), the mottling intensifies until the siltstone becomes

92 entirely gray (10B 6/1 - N 6/). In these areas, the siltstone contains abundant organic plant
93 material showing by far the best-preserved roots. Occurring here is a spectacular tree root
94 system showing conspicuous limonite (iron oxide) surface incrustations and numerous exposed
95 smaller roots (Figures 4C, 5). Further in the same direction (Figure 1C, region III), abundant
96 limonite appears within the paleosol matrix (Figure 4C). In both occurrences, limonite has
97 intensified in color (5YR 6/4) after uncovering and almost certainly represents modern oxidation
98 of early diagenetic pyrite. In another region (Figure 1C, region IV), a thin siltstone layer with a
99 distinctive greenish color (10G 6/1) overlies the mottled paleosol surface. It is at least 10 cm
100 thick to the east, but feathers out to the north and southwest. In this area, root systems appear on
101 the underlying paleosol, but are invested by the greenish siltstone forming partial molds (Figures
102 3A-B, 4A-B). Beyond the region of continuous deposition, the same greenish siltstone occurs as
103 isolated patches apparently trapped by root systems of the largest plants near their center (Figure
104 5A). The greenish siltstone has scattered vertebrate fragments (placoderms, agnathans,
105 chondrichthyans) on the surface (Figure 4D) and several well-articulated fish have been
106 recovered near the largest trees, seemingly impounded by them. This siltstone is interpreted as
107 overwash from a flood event that penetrated the forest from the east, likely killing many trees
108 and preserving root systems as trace fossils.

109 From data derived from cores drilled at the site, the surface-mapped paleosol (Figures 2A-B, PII)
110 ranges between 1.20 and 1.66 m in thickness, with a gradational lower boundary into either
111 finely-laminated grayish-red (10R 5/3) 'heterolithics' (interbedded mudstone, siltstone and fine-
112 grained sandstone Figure 2B, R), or an underlying paleosol profile (Figures 2A-B, PIII-PIV).
113 The paleosol is capped with the same overwash siltstone seen on the surface, with sharp lower
114 boundary but without a significant change in grain size or evidence of a significant erosional

115 surface. Within the paleosol (Figure 2B, PII), 3 horizons (A-C), with variants: A(g), (AE), B,
116 Btss, Bt, C, are recognized across the mapped area, all with abundant evidence of rooting.
117 Horizon A is a siltstone between 12 and 25 cm thick, has a massive structure, and granular to
118 sub-angular blocky texture of peds. It is either red, partially gleyed to a bluish-gray color from
119 the surface downwards, or is entirely gleyed (Ag), where small patches of pyrite have been
120 found. In a few cores, an additional subhorizon, AE, occurs at the base of Horizon A where the
121 matrix is significantly lighter in color (10R 6/4). Horizon B is between 56 and 118 cm thick, and
122 is characterized by increased clay content and larger, more angular, blocky to columnar peds
123 separated by significant cracks. Conspicuous is subhorizon Btss, a clay-rich layer comprising
124 blocky, wedge-shaped peds with slickensided argillaceous cutans. Horizon C, between 11 and 40
125 cm thick, is characterized by a clayey siltstone with a massive texture, root traces and incipient
126 bedding.

127 From observations of both surface and cores, the mapped surface (Figures 1C; 2, PII) is
128 interpreted as a single vertisol, based on horizon properties, specifically sub-horizon Btss which
129 is indicative of this soil order [25,26]. Movement along pseudo-anticlinal slip planes produced
130 the slickensided wedge-shaped peds and the semi-spheroidal features observed at the surface.
131 These slip planes developed with the shrinking and swelling of clays, as a result of wetting and
132 drying seasonal cycles [27]. Variable gleying at the top of the paleosol is interpreted as
133 reflecting variable short term surface waterlogging across the forest, likely associated with
134 flooding with emplacement of fish, localized topographic differences, or proximity to a water
135 source.

136 **Identified Root Systems**

137 *Eospermatopteris*

138 Three root systems, two unique to this site, have been identified to date. The first type (Figures
139 1C, arrows a-b; 3) is fully equivalent in form and detail to root systems at Gilboa [7-9], with that
140 site also including stem casts previously identified as *Eospermatopteris* [7-8]. At Cairo, bowl-
141 shaped depressions 20-50 cm in diameter were made by expanded bases of an upright trunk.
142 Roots, inserted on the bottom and sides of the base, radiate sub-horizontally and form a densely
143 imbricate pattern that disappears below the paleosol surface 1-2 m from the center. Roots are
144 0.7–1 cm in diameter, smooth to longitudinally plicate, and rarely if at all branched. One
145 exceptional example (Figures 1C, arrow a; 3A-B) shows a well-preserved external mold of the
146 trunk base directly seated on the PII paleosol with root surface features partly cast by the
147 overlying greenish overwash siltstone. Roots extend from the base into the overwash and also
148 downward into the underlying paleosol suggesting that the tree remained erect during the flood
149 and may have remained viable for sometime thereafter. Other individuals in the overwash region
150 show much less evidence of siltstone envelopment possibly related to differences in original pre-
151 flood surface topography, flood sediment thickness or post-flood establishment of some trees.
152 Outside the overwash region (Figures 1C, arrow b; 3C-F), *Eospermatopteris* root systems show
153 somewhat less depressed central bowls surmounting raised mounds on the paleosol surface
154 (Figures 3C-D). In several cases, a partial to nearly complete boundary in the root mass is
155 marked by near vertical slickensided surfaces (Fig. 3A, arrows; 3D, arrows), although roots from
156 the trees penetrate into the paleosol well beyond this distance and up to 30 cm depth. The
157 slickensided boundary is interpreted as recording differences in paleosol shrink-swell movement
158 between sediment bound within the root mat versus less cohesively bound peripheral regions.

159 (See the supplemental data for measurements of *Eospermatopteris* root systems found at the
160 site.)

161 *Archaeopteris*

162 By far the most conspicuous root systems at Cairo have radial dimensions as much as 11 m
163 across the paleosol surface and show great complexity (Figure 1C, arrows d-e; 5-6). As many as
164 10-15 primary roots resulting from numerous divisions diverge from what were probably bases
165 of single central trunks. Some root systems appear essentially symmetrical (Figure 4A) whereas
166 others show marked directionality (Figure 4C). The primary roots range between 6-16 cm in
167 diameter, although fidelity of preservation and casting by overlying sediment contribute to
168 imprecision in measurement. Root pattern, primary root diameters, and radial extent of primary
169 roots suggest trees of different sizes (See Supplemental Figure S6, Supplemental Table S1).
170 Root systems in the overwash region of the site (Figures 1C, arrow d; 4A-B) are especially
171 conspicuous due to casting by the overlying greenish siltstone. However, these roots are
172 evidently seated upon the PII paleosol below, and show only the largest surficial roots with
173 occasional dichotomous branching. Associated root traces in the cores penetrate the paleosol to
174 a depth of 1.2-1.6 m, with positive association between depth and estimated tree size (Figures
175 2C-D).

176 The most fully articulated detail of this type of tree is provided by a directional root system in
177 gray paleosol diverging mostly to the south-southwest (Figures 1C, arrow e; 4C). Center of the
178 root system is an irregular region with large primary roots as much as 15 cm in diameter. A
179 small region of red-gray mottled paleosol occurs in high relief likely forced upward from the
180 original rooting surface by the tree's weight (Figure 5A, arrows). In addition, a small amount of
181 overwash siltstone caps the highest surfaces suggesting accumulation against the standing tree

182 some 7 m beyond the limit of contiguous overwash. Away from the center, the primary roots are
183 observed to branch both equally and unequally, producing a highly ramified system that is only
184 partly exposed on the surface (Figures 5B-C). Root cloning is suggested by radiating patterns of
185 larger and smaller root systems both here and elsewhere at the site (Figure 4C, arrow), but
186 definitive evidence for this is lacking. Working outward 2, 4, 6, and 8 m from the center, roots
187 show progressive diminishment in root diameters (6-7 cm, 5-6 cm, 4-5 cm, 2.5-3.5 cm
188 respectively) with individual root segments sometimes also showing modest taper between
189 apparent branch points. Some surfaces show limonite incrustations (Figures 5C), and some have
190 blocky transverse-longitudinal in-filled cracks (Figure 5G) reminiscent of wood checking. At ca.
191 4-6 m from the center, anisodichotomous branching predominates in the root system, resulting in
192 numerous lateral roots typically 1-1.5 cm in diameter. Some of these (Figures 5D, 5F) exhibit
193 many small 1-2 mm diameter attached rootlets that diverge at angles ranging from acute to near
194 90°. At more than 8 m from the center, the terminus of one major root is observed. Here, a
195 raised semi-circular fan is evident on the paleosol surface bounded by a subvertical slickenside
196 distal margin (Figures 5E, arrows), again interpreted as the boundary between root-bound
197 sediment and adjacent paleosol. Extending at least 10 m from the center of this individual, and
198 observed associated with another root system of this type nearby (Figure 1C, arrow f), are ca. 1
199 mm diameter rootlets apparently comprising a dense three-dimensional mat. Rootlets typically
200 enclose 1-3 cm diameter ped-like elements of the paleosol and are interpreted as the finest
201 portions of a still largely intact, feeder root system. (See Supplemental data for measurements,
202 and Table S1 estimates of tree sizes).

203 Although our understanding of the relationship between Devonian plant body fossils and the
204 trace fossils left by their root systems in paleosols is currently rudimentary, all features match

205 what we know or reasonably presume to be present in *Archaeopteris* and no other taxon so far
206 identified in the Middle Devonian flora of the Catskills or worldwide. Notable is the presence of
207 structural roots showing taper suggesting secondary development. Significant inequality in
208 branching is consistent with production of laterals of different ages with differing amounts of
209 secondary xylem. The presence of numerous small rootlets associated and attached to distal
210 portions of an evident system of structural roots suggests continuous production of a feeder
211 system consistent with previously described endogenous root development in *Archaeopteris*
212 from anatomically preserved material [11,13,28].

213 **Stigmarian Isoetalean Lycopsid?**

214 A third and currently enigmatic type of tree is represented by a single well-preserved root system
215 occurring largely within the dark grey paleosol region (Figures 1C, arrow c; 6). This system has
216 a nearly circular raised root mound 1.9 m in diameter that is marked at the periphery by a
217 slickensided distal margin similar to that described above for *Eospermatopteris* (Figure 6C,
218 arrows). However, the center also exhibits a low 3-4 ridged depression 80 cm in diameter and
219 clearly attached primary roots with diameters of 12, 15 and 25 cm at their insertion, the largest
220 representing a proximal dichotomy (Figure 6B, arrows). A densely imbricate system of rootlets
221 ca. 1 cm in diameter is well preserved as casts, and several show direct attachment to the primary
222 roots toward the periphery of the root mound (Figure 6D). Other rootlets appear to radiate from
223 the central depression suggesting direct attachment to the stem base. Beyond the root mound,
224 the large primary roots, 5-6 cm in diameter, are observed in organic connection stretching along
225 the paleosol surface as much as 13 m (Figure 6A). The primary roots show sparse equal
226 dichotomies resulting in a lax distal system of secondary roots ca. 3-5 cm in diameter, with some
227 extending into the limonitic region III to the south-southwest. Occasional carbon flecks

228 occurring in regular patterns along a secondary root length suggest attachment sites of rootlets at
229 most levels (Figure 6E, arrows). In one instance, a secondary root was followed to the root tip.
230 At this level it is invested by attached, but fragmentary, 0.7 cm diameter rootlets with fine scale
231 longitudinal surface striations diverging at acute angles (Figure 6F, arrows).

232 Although observed from only a single occurrence at Cairo, evidence for a third type of tree at the
233 site is nevertheless convincing. Among known Mid Devonian plants, nothing yet shows
234 comparable features. However, as our terminology suggests, comparison with stigmarian
235 isoetalean lycopsids of the Carboniferous seems the closest match.

236 **DISCUSSION**

237 **Environmental Setting of the Riverside Quarry Gilboa and Cairo Sites**

238 The Gilboa and Cairo sites, close in age but showing contrasting paleosol evidence, provide
239 important glimpses into the general ecology of some of the Earth's early forests. Both sites
240 occur within a familiar range of sediment types preserved in the Catskill Delta complex [29], and
241 it seems likely that both are components of the same distal floodplain system in a subtropical to
242 temperate wetland environment during an interval of relatively high sea level in the Appalachian
243 Basin [19,30]. Multiple stacked ca. 1m thick sandstone horizons at the Riverside Quarry Gilboa,
244 sometimes bearing rooted *Eospermatopteris*, likely indicate a terrestrial wetland environment for
245 the trees, punctuated by disturbance [9]. At somewhat larger scale, the Schoharie valley,
246 containing both Riverside Quarry and nearby Manorkill Falls [31], shows incursions of fully
247 marine waters as indicated by intercalated units with marine invertebrates [32]. However, fish
248 fragments are rare, and within the Riverside Quarry itself the massive sandstones lack any
249 evidence of marine influence. Micro- and macro-morphological studies of the Gilboa and

250 Manorkill Falls forest soils [9,28,31] suggest poor drainage and high water tables as indicated by
251 extensive gleying, drab colors, large amounts of organic carbon, and abundant pyrite.

252 At Cairo, low angle cross-bedded sandstones exposed in the quarry walls occur immediately
253 above a mudstone containing the acritarch *Veryhachium*. The latter indicates some marine
254 influence from, perhaps, tidal and wave-affected channels [33]. However, marine macrofossils
255 are absent anywhere in the quarry. Based on our observations, it seems likely that a single event
256 of flooding brought sediment and fish into an otherwise tree-dominated terrestrial ecosystem.
257 The presence of chondrichthyans in the greenish overwash suggests marginal marine or brackish
258 origin, and this is further supported by the presence of leiospheres [34] known to be abundant in
259 near shore and lagoonal environments [33]. Several horizons, including an extensive black shale
260 unit bearing conchostrachans and liverworts in another part of the quarry (Fig. 1B, arrow),
261 suggest the presence of nearby lacustrine environments. In contrast to Gilboa, the red vertisols
262 underlying part of the Cairo forest (Fig. 1C, regions I & IV) indicate well-drained soils with
263 periodic wet/dry seasonality, but less disturbance overall. In addition, a wetter local environment
264 is suggested by sediments with more extensive gleying (Fig 1C, regions II-III), perhaps
265 supported by preferred directions of root systems in the direction of greatest pyrite deposition
266 (Fig. 1C, c and e, region III).

267 **Role of Major Groups in the Catskill Early Terrestrial Ecosystem**

268 **Cladoxylopsids** - The presence of *Eospermatopteris* at Riverside Quarry, Manorkill Falls, and at
269 Cairo suggest that these plants had the capacity to live in several different ecological settings
270 rather than being restricted to wetter environments as has been previously interpreted. Their
271 upright habit includes extensive augmentation of tissues by means of extended lateral meristem
272 development [35], but limited sclerified tissues. Thus, it seems more likely that these plants

273 were weedy in habit, relatively fast growing, and able to disperse to a variety of locations in the
274 ancient forest as chance, local disturbance, or openings in the forest canopy might have allowed.

275 **Aneurophytaleans** - By contrast, aneurophytaleans observed at Gilboa, and generally common
276 in Catskill sediments as aerial shoots, produced both secondary xylem and phloem [36] similar to
277 that seen in seed plants. Developmental evidence, however, suggests that secondary tissue
278 production was probably limited [37], and it seems likely that most specimens found so far
279 represent determinate portions of the plants that completed development with sterile or
280 reproductive ultimate units, or a mixture of the two [38]. However it remains uncertain how
281 these plants actually grew. The Gilboa paleosol provides evidence that aneurophytaleans were
282 scrambling to ascendant tree sized forms with a rhizomatous to lianoid main axis not yet
283 identified from anatomical material [9]. Aneurophytalean aerial shoots are represented as both
284 compressions and pyrite permineralizations at Cairo [21,22], but main axes with surface features
285 as observed at Gilboa have not been recognized from the paleosol horizon itself. This may be
286 due to insufficient preservation of diagnostic details (see especially blocks L26-P29 in Fig. 1C
287 from a probably wetter environment perhaps more similar to that Gilboa).

288 **Lycopsids** - Despite commonly held perspective holding to a *Lycopodium*-like interpretation for
289 most Devonian lycopsids, rhizomes and root structures remain largely unknown. Many if not
290 most of the most conspicuous occurrences in Catskills sediments appear to be detrital in origin
291 [39,40]. Similar to aneurophytaleans, this leaves open how Middle Devonian lycopsids should
292 be reconstructed, how big most of them were, and what roles they may have played in the
293 structure of early forests. A tree-sized lycopsid was recovered from the paleosol at Riverside
294 Quarry Gilboa and, although incomplete, probably had a cormose base [9]. This type of base is
295 well preserved in *Lepidosigillaria* from the mid Frasnian of New York [41], and in individuals

296 from a newly described lycopsid forest from the early Frasnian of Svalbard [42]. By contrast,
297 stigmarian lycopsid root systems involving elongate roots with appendicular rootlets make their
298 body-fossil appearance in the Late Devonian (Famennian) [43]. Although wetland
299 specializations are famous for both groups in the Carboniferous [2], there seems to be little if any
300 evidence for similar environments in the Middle Devonian. The potential lycopsid root system
301 observed at Cairo seems consistent with what one might expect of a stigmarian isoetalean
302 lycopsid and would be the oldest occurrence yet described worldwide. Although suggestive, it
303 must be admitted that evidence remains inconclusive pending confirmation with body fossils. If
304 true, however, lycopsids may have been much larger and far more important as trees in forests
305 much earlier than generally recognized, but in environments at least spanning those observed at
306 Gilboa and Cairo.

307 **Pivotal Role of *Archaeopteris* in Emerging Terrestrial Ecosystems**

308 *Eospermatopteris* bases as at Gilboa and Cairo indicate that their roots were typically shallow
309 (Figure 2E), and although the individual roots may have been meters in length, there is little
310 indication that these were multi-year perennial structures. Thus with continued growth of the
311 tree, active roots would have required regular replacement at a rate commensurate with
312 augmentation of aerial tissues. However, new roots and the root system as a whole would have
313 been largely restricted to reworking soils in the vicinity of the plant's main axis. Although
314 rhizomatous and clonal plants would have permitted some lateral movement across the
315 landscape, nevertheless similar restrictions appear characteristic of Devonian plants in general.
316 In striking contrast, the root systems here assigned to *Archaeopteris* mark a dramatic departure
317 from this pattern and, moreover, appear essentially indistinguishable from what might be
318 observed in modern seed plants [44,45]. In modern woody trees there is typically a two-fold

319 investment strategy that includes progressive recruitment, extension, and maintenance of
320 perennial structural roots along with seasonal renewal of smaller ephemeral feeder rootlets in a
321 flexible and potentially ever-expanding array. Evidence at Cairo suggests that the root system of
322 *Archaeopteris* probably functioned in much the same way, signaling a dramatic increase in
323 rooting complexity and extent compared with contemporaneous land plants. Moreover, it seems
324 likely that supplying an ever increasing distal root biomass over the lifetime of the individual
325 would only be possible given augmentation of vascular system via indeterminate secondary
326 tissues. The innovation of leaves, also in *Archaeopteris*, suggests greatly increased
327 photosynthetic receptive surface area per unit biomass compared to contemporaneous plants with
328 non-laminate appendages. This, combined with other derived features occurring together for the
329 first time in *Archaeopteris*, points to tight developmental integration producing a clade-specific
330 quantum leap in physiological capacity of these trees involving rates of energy capture and local
331 resource utilization. Thus, it seems likely to us that this change was fundamental to the
332 subsequent success of *Archaeopteris* and the entire lignophyte clade including seed plants in
333 most terrestrial environments.

334 Previous work has emphasized the importance of roots in “bioengineering” important
335 geochemical cycles associated with “afforestation” of the Earth [46-50]. We see at Cairo that
336 maximum root depth for *Archaeopteris*, but not *Eospermatopteris*, is indeed related to tree size
337 and root lateral extent (Figure 1C-E), as previously suggested [11]. However, since these trees
338 co-occur within the same paleosol, it is clear that the effect of rooting patterns on paleosol
339 development and potential weathering should now be seen to be taxon specific. Beyond that, the
340 enhanced physiological package observed in *Archaeopteris* suggests multiplicative effects on
341 both local environments and global processes well beyond that scaled to forest tree size or

342 rooting depth alone. As a result, it now becomes especially important to consider more fully
343 how these enhanced trees flourished on the ancient Devonian landscape, and changed in both
344 geographic range and ecological amplitude over time. In our opinion, previous ecological
345 interpretations of *Archaeopteris*, and indeed all Mid Devonian plant groups, needs to be
346 reassessed. Given extensive root systems supported by woody tissues, it seems likely that a
347 stable soil environment, perhaps periodically wet and dry as seen at Cairo, would be necessary
348 for *Archaeopteris* to grow to tree size and significant forest dominance. Just as today, it seems
349 likely that these trees plus other plants in early forests, local topography, geographic setting,
350 weathering, and geochemical cycling had multifaceted interrelationships. Thus, understanding
351 what effect the energetic revolution represented by *Archaeopteris* may have had at global scale,
352 including climatic change or extinction, needs to be informed by a more realistic appraisal of
353 these factors in both local ecosystems and at regional scales. Understandably, unraveling all
354 these factors is a tall order! However, what is clear from the occurrence of *Archaeopteris* at
355 Cairo is that this is a Middle Devonian problem, far earlier than previously suspected. In
356 addition, linking different environments based on paleosols with specific plant assemblies as
357 done with Riverside Gilboa and Cairo may provide an enhanced tool for regional landscape and
358 forest reconstructions. The latter is seemingly a prerequisite for assessing temporal changes in
359 larger scale processes. Clearly two examples of this type from sites only 40 km apart are not
360 enough. The essential point is that taxon-specific physiology and ecosystem composition, not
361 just tree size, must now be considered vital keys to understanding the dramatic effect the origin
362 of forests had on planet Earth.

363 **ACKNOWLEDGEMENTS**

364 Drilling costs were met by Natural Environment Research Council (NERC of Great Britain)
365 Grants NE/J007471/1, NE/J007897/1 and NE/J00815X/1. Authors thank the Town of Cairo, and

366 Town of Cairo Highway Department for granting access and enthusiastic help with their site,
367 also thanks to Khudadad for assistance in the field.

368 **AUTHOR CONTRIBUTIONS**

369 L.V.H. and F.M. were responsible for field collections and specimen sampling, W.E.S., L.V.H.
370 & F.M. constructed the map. W.E.S, C.M.B, J.L.M., C.v.S., E.L., J.E. A.M., C.H.W., D.J.B. &
371 J.R.L contributed to palaeoecological and geological interpretation. J.L.M, J.R.L, D.J.B
372 organized and oversaw drilling operations, W.E.S. led writing of the paper with substantial
373 contributions from C.M.B and J.L.M.

374 **DECLARATION OF INTERESTS**

375 The authors declare no competing interests.

376 **REFERENCES**

- 377 1. Shugart, H. H., Saatchi, S. & Hall, F. G. (2010). Importance of structure and its measurement
378 in quantifying function of forest ecosystems. *J Geophys. Res.* *115*, G00E13,
379 doi:10.1029/2009JG000993.
- 380 2. Greb, S. F., DiMichele, W. A. & Gastaldo, R. A. (2006). Evolution and importance of
381 wetlands in earth history. *Geol. Soc. Am. Special Papers* *399*, 1–40.
- 382 3. DiMichele, W. A. & Falcon-Lang, H. J. (2011). Pennsylvanian “fossil forests” in growth
383 position (T0 assemblages): origin, taphonomic bias and palaeoecological insights. *J. Geol.*
384 *Soc. (London)* *168*, 585–605.
- 385 4. Meyer-Berthaud, B. & Soria A, Decombeix, A-L. (2010). The land plant cover in the
386 Devonian: a reassessment of the evolution of the tree habit. *Geol. Soc. London Spec. Publ.*
387 *339*, 59–70.
- 388 5. DiMichele, W. A., Falcon-Lang, H. J., Nelson, W. J., Elrick, S. D. & Ames, P. R. (2007).
389 Ecological gradients within a Pennsylvanian mire forest. *Geology* *35*, 415–418.
- 390 6. Wang, J., Pfefferkorn, H. W., Zhang, Y. & Feng, Z. (2012). Permian vegetational Pompeii
391 from Inner Mongolia and its implications for landscape palaeoecology and
392 palaeobiogeography of Cathaysia. *Proc. Natl. Acad. Sci. USA* *109*, 4927–4932.
- 393 7. Goldring, W. (1924). The Upper Devonian forest of seed ferns in eastern New York. *N.Y.*
394 *State Mus. Bull.* *251*, 50-72.
- 395 8. Stein, W. E., Mannolini, F., Hernick, L. V., Landing, E. & Berry, C. M. (2007). Giant
396 cladoxylopsid trees resolve the enigma of the Earth’s earliest forest stumps at Gilboa. *Nature*
397 *446*, 904–907.
- 398 9. Stein, W. E., Berry, C. M., Hernick, L. V. & Mannolini, F. (2012). Surprisingly complex
399 community discovered in the mid-Devonian fossil forest at Gilboa. *Nature* *483*, 78-81.

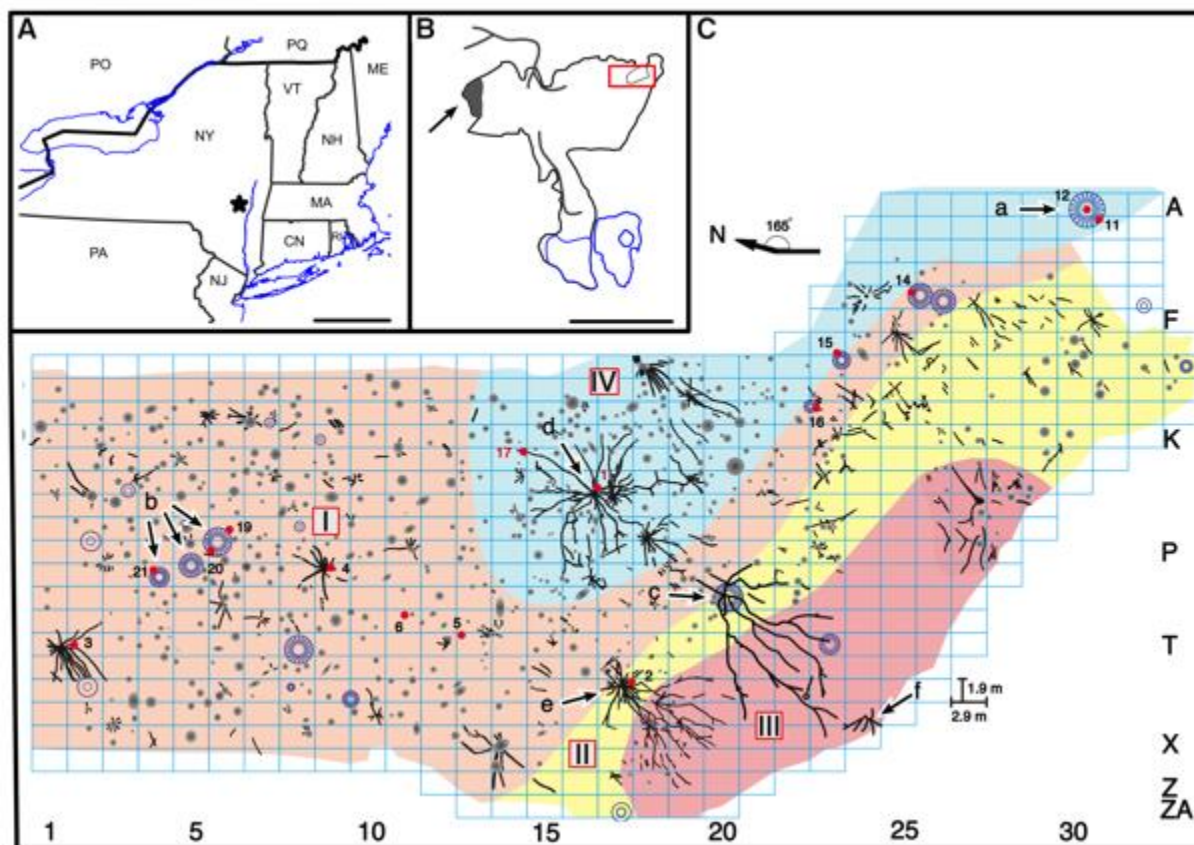
- 400 10. Retallack, G. J. & Huang, C. (2011). Ecology and evolution of Devonian trees in New York,
401 USA. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 299, 110–128.
- 402 11. Algeo, T. J. & Scheckler, S. E. (1998). Terrestrial-marine teleconnections in the Devonian:
403 links between the evolution of land plants, weathering processes, and marine anoxic events.
404 *Philos. Trans. (London) Biol. Sci.* 353B, 113-130.
- 405 12. Meyer-Berthaud, B., Scheckler, S. E. & Bousquet J-L. (2000). The Development of
406 *Archaeopteris*: New Evolutionary Characters from the Structural Analysis of an Early
407 Famennian Trunk from Southeast Morocco. *Am. J. Bot.* 87, 456-468.
- 408 13. Meyer-Berthaud, B., Decombeix, A-L. & Ermacora, X. (2013). Archaeopterid Root Anatomy
409 and Architecture: New Information from Permineralized Specimens of Famennian Age from
410 Anti-Atlas (Morocco). *Int. J. Plant Sci.* 174, 364–381.
- 411 14. Marshall, J. E. A. (1996). *Rhabdosporites langii*, *Geminospora lemurata* and *Contagisporites*
412 *optimus*: an origin for heterospory within the progymnosperms. *Rev. Palaeobot. Palynol.* 93,
413 159–189.
- 414 15. Berry, C. M. & Fairon-Demaret, M. (2001). Middle Devonian flora revisited. In *Plants*
415 *Invade the Land: Evolutionary and Environmental Perspectives* P. G. Gensel & D. Edwards,
416 eds. (New York: Columbia Univ. Press), pp. 120-139
- 417 16. Beck, C. B. (1962). Reconstructions of *Archaeopteris*, and Further Consideration of its
418 Phylogenetic Position. *Amer. Jour. Bot.* 49, 373-382.
- 419 17. Beck, C. B. (1970). The appearance of gymnospermous structure. *Biol. Rev.* 45, 379–399.
- 420 18. Brett, C.E. & Baird, G.C. (1994). Depositional sequences, cycles, and foreland basin
421 dynamics in the late Middle Devonian (Givetian) of the Genesee Valley and western Finger
422 Lakes region. In *Field trip guidebook*, C.E. Brett & J. Scatterday, eds. (New York State
423 Geological Association 66th Annual Meeting, Rochester), pp. 505-585.
- 424 19. Brett, C. E., Baird, G. C., Bartholomew, A., DeSantis, M. K., & Ver Straeten, C. A. (2011).
425 Sequence stratigraphy and revised sea level curve for the Middle Devonian in eastern North
426 America. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 304, 21-53.
- 427 20. Becker, R. T., Gradstein, F. M., & Hammer, O. (2012). The Devonian Period, In *The*
428 *Geologic Time Scale 2012*, F. M. Gradstein, J. G. Ogg, M. D. Schmitz, & G. M. Ogg eds.
429 (New York: Elsevier), pp. 559-601.
- 430 21. Matten, L. C. (1968). *Actinoxylon banksii* gen. et sp. nov.: A progymnosperm from the
431 Middle Devonian of New York. *Am. J. Bot.* 55, 773–782.
- 432 22. Matten, L. C. (1975). Additions to the Givetian Cairo flora from eastern New York. *Bull.*
433 *Torrey Bot. Club* 102, 45–52.
- 434 23. Hernick, L.V., Landing, E. & Bartowski, K. E. (2008). Earth’s oldest liverworts—

- 435 *Metzgeriothallus sharonae* sp. nov. from the Middle Devonian (Givetian) of eastern New
436 York, USA. *Rev. Palaeobot. Palynol.* 148, 154–162.
- 437 24. Potvin-Leduc, D. (2015). Middle Devonian (Givetian) sharks from Cairo, New York (USA):
438 Evidence of early cosmopolitanism. *Acta. Palaeontol Pol.* 60, 183-200.
- 439 25. Soil Survey Staff (1999). *Soil Taxonomy: A basic system of soil classification for making*
440 *and interpreting soil surveys* (Natural Resources Conservation Service, U.S. Department of
441 Agriculture Handbook, 2nd ed.).
- 442 26. Retallack, G. J. (2001). Soil classification. In *Soils of the past: an introduction to*
443 *palaeopedology* (Malden, MA:Wiley-Blackwell 2nd ed), pp. 63-76.
- 444 27. Wilding, L. P. & Tessier, D. (1988). Genesis of vertisols: shrink-swell phenomena. In
445 *Vertisols: Their Distribution, Properties, Classification, and Management*, L.P. Wilding & R.
446 Puentes, eds. (College Station, TX: A&M University Printing Center), pp. 55-79.
- 447 28. Meyer-Berthaud, B., Scheckler, S.E. and Bousquet J-L. (2000). The development of
448 *Archaeopteris*: New evolutionary characters from the structural analysis of an early
449 Famennian trunk from Southeast Morocco. *Amer. J. Bot.* 87, 456-468.
- 450 29. Mintz, J.S, Driese, S.G. and White J.D. (2010). Environmental and ecological variability of
451 Middle Devonian (Givetian) forests in Appalachian basin paleosols, New York, United
452 States. *Palaios* 25, 85-96.
- 453 30. Bridge, J.S. (2000). The geometry, flow patterns and sedimentary processes of Devonian
454 rivers and coasts, New York and Pennsylvania, USA. *Geol. Soc. London Special Publication*
455 *180*, 85–108.
- 456 31. Driese, S.G., Mora, C.I. and Elick, J.M. (1997). Morphology and taphonomy of root and
457 stump casts of the earliest trees (Middle to Late Devonian), Pennsylvania and New York,
458 U.S.A. *Palaios* 12, 524-537.
- 459 32. Bridge, J.S. and Willis, B. (1994). Marine transgressions and regressions recorded in Middle
460 Devonian shore-zone deposits of the Catskill clastic wedge. *Geol. Soc. Am. Bull.* 106, 1440-
461 1458.
- 462 33. Dorning, K.J. (1987). The organic palaeontology of Palaeozoic carbonate environments. In
463 *Micropalaeontology of carbonate environments*, M.B Hart, ed. (Chichester, UK: Ellis
464 Horwood & British Micropalaeontology Society Series), pp. 256-265.
- 465 34. Colbath, G.K. and Grenfell, H.R. (1995). Review of biological affinities of Palaeozoic acid-
466 resistant, organic walled eukaryotic algal microfossils (including “acritarchs”). *Rev.*
467 *Palaeobot. Palynol.* 86, 287-314.
- 468 35. Xu, H-H. et al. (2017). Unique growth strategy in the Earth’s first trees revealed in silicified
469 fossil trunks from China. *Proc. Natl. Acad. Sci. USA* 114, 12009-12014.

- 470 36. Wight, D.C. and Beck, C.B. (1984). Sieve cells in phloem of a Middle Devonian
471 progymnosperm: *Science* 225, 1469-1471.
- 472 37. Stein, W.E. and Beck, C.B. (1983). *Triloboxylon arnoldii* from the Middle Devonian of
473 western New York. *Contr. Mus. Paleont. Univ. Mich.* 26, 257-288.
- 474 38. Dannenhoffer, J.M., Stein, W.E. and Bonamo, P.M. (2007). The primary body of *Rellimia*
475 *thomsonii*: integrated perspectives based on organically connected specimens. *Internat. J. Pl.*
476 *Sci.* 168, 491-506.
- 477 39. Grierson, J.D. and Banks, H.P. (1963). Lycopods of the Devonian of New York State:
478 *Palaeontogr. Am.* 4, 220-295.
- 479 40. Banks, H.P., Bonamo, P.M. and Grierson, J.D. (1972). *Leclercqia complexa* gen. et sp. nov.,
480 a new Lycopod from the late Middle Devonian of eastern New York. *Rev. Palaeobot.*
481 *Palynol.* 14, 19–40.
- 482 41. White, D. (1907). A remarkable fossil tree trunk from the Middle Devonian of New York.
483 *N.Y. State Mus. Ann. Rept.* 107, 327–340.
- 484 42. Berry, C.M. and Marshall, J.E.A. (2015). Lycopoid forests in the early Late Devonian
485 palaeoequatorial zone of Svalbard. *Geology* 43, 1043–1046.
- 486 43. Wang, D. et al. (2019). The most extensive Devonian fossil forest with small lycopsid trees
487 bearing the earliest stigmarian roots. *Current Biology* 29, 2604-2615.
- 488 44. Bauhus, J. & Messier, C. (1999). Soil exploitation strategies of fine roots in different tree
489 species of the southern boreal forest of eastern Canada. *Can. J. For. Res.* 29, 260–273.
- 490 45. Danjon, F. & Reubens, B. (2007). Assessing and analyzing 3D architecture of woody root
491 systems, a review of methods and applications in tree and soil stability, resource acquisition
492 and allocation. *Plant Soil* 303, 1–34.
- 493 46. Algeo, T. J., Scheckler, S. E. & Maynard, J. B. (2001). In *Plants Invade the Land:*
494 *Evolutionary and Environmental Perspectives* P. G. Gensel & D. Edwards, eds. (New York:
495 Columbia Univ. Press), pp. 213-236.
- 496 47. Gibling, M. R. & Davies, N. S. (2012). Palaeozoic landscapes shaped by plant evolution.
497 *Nature Geosci.* 5, 99–105.
- 498 48. Quirk, J., Leake, J. R., Johnson, D. A., Taylor, L.L., Saccone, L. & Beerling, D. J. (2015).
499 Constraining the role of early land plants in Palaeozoic weathering and global cooling. *Proc.*
500 *R. Soc. B* 282, 2015.1115, doi10.1098/rspb.2015.1115.
- 501 49. Morris, J. L. et al. (2015). Investigating trees as geo-engineers of past climates: linking
502 palaeosols to palaeobotany and experimental geobiology. *Palaeontology* 58, 787–801.
- 503 50. Ibarra, D. E. et al. (2019). Modeling the consequences of land plant evolution on silicate

504 weathering. *Amer. J. Sci.* 319, 1-43.

505



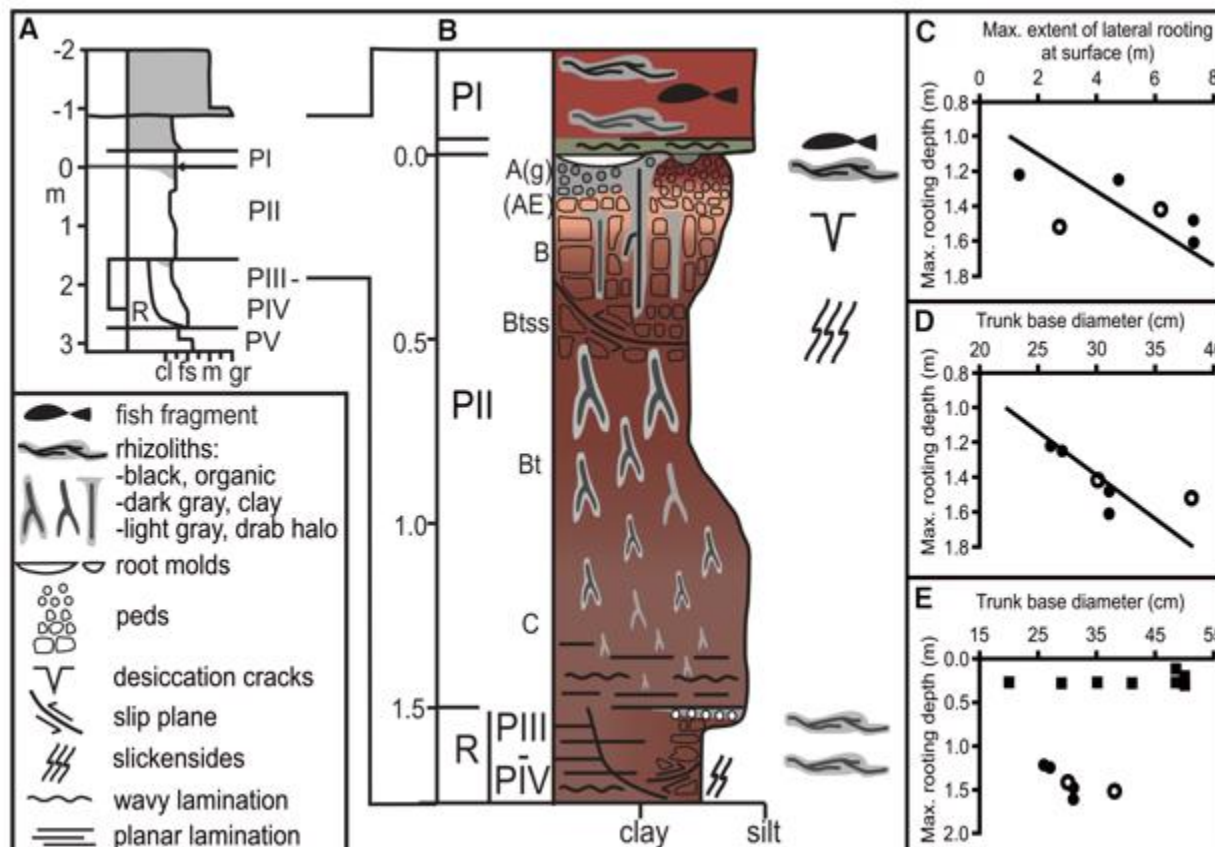
506

507 **Figure 1. Location and plan map of the Cairo site.**

508 (A) General location. Scale bar 160 km (100 mi).

509 (B) Cairo Quarry. Blue outlines water ponds; shaded region (arrow) dark shale; red rectangle
510 mapped region. Scale bar, 213 m (700 ft).

511 (C) Plan map. Color-shaded regions I-IV indicate approximate extent of differing surface
512 features of paleosol PII in [Figure 2B](#), and as described in the text. Identified *Eospermatopteris*
513 root systems are indicated by blue double circles with stylized radiating lines indicating
514 approximate radial extent of roots observed on the paleosol surface when present. Black lines
515 indicate identified *Archaeopteris* root systems and isolated linear roots. Numbers and red circles
516 indicate some of the cores drilled at the site (not all cores were drilled on the mapped surface).
517 Gray shaded circles/ellipses indicate surface depressions indicating original paleosol topography
518 or potential floral elements that could not be positively identified. Arrows indicate specific
519 individuals also identified in other figures: a, partially cast *Eospermatopteris* ([Figures 3A, 3B](#);
520 [Supplemental Figures 1A, 2A, 2C](#)); b, three well-preserved *Eospermatopteris* seated directly on
521 mottled paleosol ([Figures 3C-F](#); [Supplemental Figures 1, 2B](#)); c, unidentified root system,
522 potentially lycopsid, with large primary roots bearing rootlets ([Figure 6](#); [Supplemental Figures 1,](#)
523 [5](#)); d, partly cast *Archaeopteris* root systems associated with vertebrate remains ([Figures 4A-B](#);
524 [Supplemental Figure 1](#)); e, best preserved *Archaeopteris* showing extensive articulated root
525 system ([Figures 4C, 5](#)); f, smaller *Archaeopteris* root system preserved entirely within the
526 limonite-stained region ([Supplemental Figure. 1A](#)).



527

528 **Figure 2. Schematic sections of paleosols at Cairo Quarry, interpreted from cores taken**
 529 **across the fossil forest surface.**

530 (A) Generalized sequence of stacked paleosols (PI to PV) and parent material (R). PII = paleosol
 531 beneath mapped surface. Quarry floor and top of PII = 0 m, cl = clay, fs = fine-grained
 532 sandstone, m = medium-grained sandstone, gr = gravel.

533 (B) Paleosol (PII) beneath mapped surface, capped by overwash bed bearing fish (PI). Paleosol
 534 horizons (A(g)-AE-B-Btss-Bt-C) in PII overlies either parent material (R) or additional paleosols
 535 PIII-PIV.

536 (C) Maximum rooting depths in cores of rhizoliths beneath individual *Archaeopteris* roots at the
 537 surface versus maximum extent of lateral rooting at the surface. Open circles = roots apparently
 538 extend beyond base of the cores.

539 (D) Maximum rooting depth in cores for *Archaeopteris* versus estimated trunk base diameter.

540 (E) Comparison of maximum rooting depths of rhizoliths beneath *Archaeopteris* (circles) and
 541 *Eospermatopteris* (squares) root systems at the surface against estimated trunk base diameter.

542



544 **Figure 3. *Eospermatopteris* root systems**

545 (A) Individual a in [Figure 1C](#), partly cast by greenish siltstone (overwash sediment), showing
546 deep water-filled central depression where the tree base once sat surrounded by preserved roots
547 radiating from the center. Arrows indicate a distinct boundary in the paleosol, characterized by
548 subvertical slickenside surfaces. Scale bar, 20 cm.

549 (B) Magnified view of radiating roots near left arrow in (A). The root mass forms an imbricate
550 system with individual roots occurring on the surface as impressions. Scale bar, 10 cm.

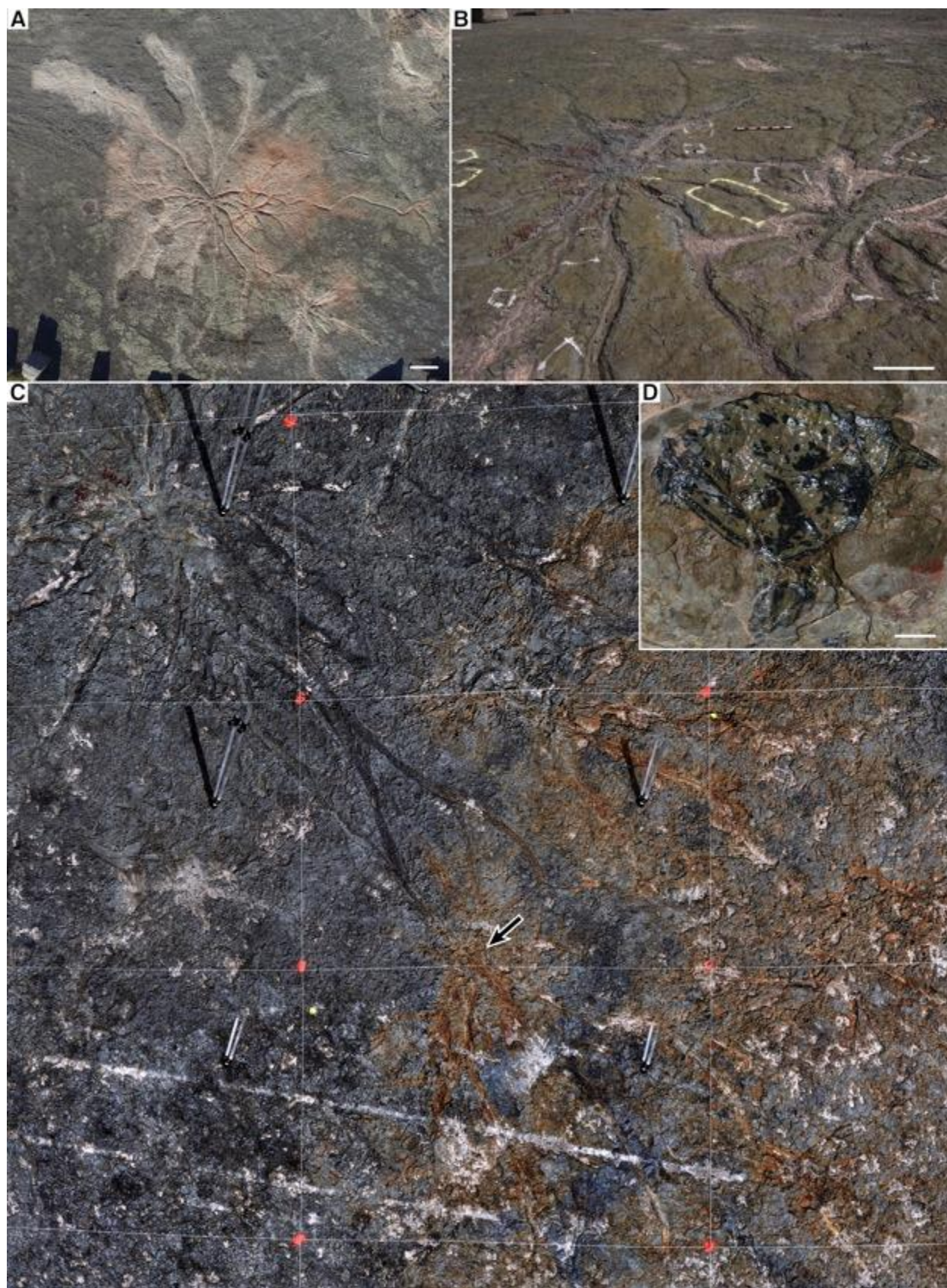
551 (C) Three individuals indicated by arrows b in [Figure 1C](#) occurring on the surface of the mottled
552 paleosol. Central depressions, marked by orange cones, surmount shallow mounds bearing
553 numerous roots. The arrows mark paleosol boundary with slickenside surfaces. Scale bar, 50
554 cm.

555 (D) Right-hand individual indicated by arrows b in [Figure 1C](#), showing root mound with distinct
556 boundary, arrows, with subvertical slickenside surfaces. Scale bar, 10 cm.

557 (E) Magnified portion of root mound of left-most individual indicated by arrows b in [Figure 1C](#).
558 Center of root system is toward the top of the image with roots showing reduced halos. Scale bar,
559 5 cm.

560 (F) Magnified view of root halos in (E). Scale bar, 3 cm.

561



563 **Figure 4. *Archaeopteris* Root systems**

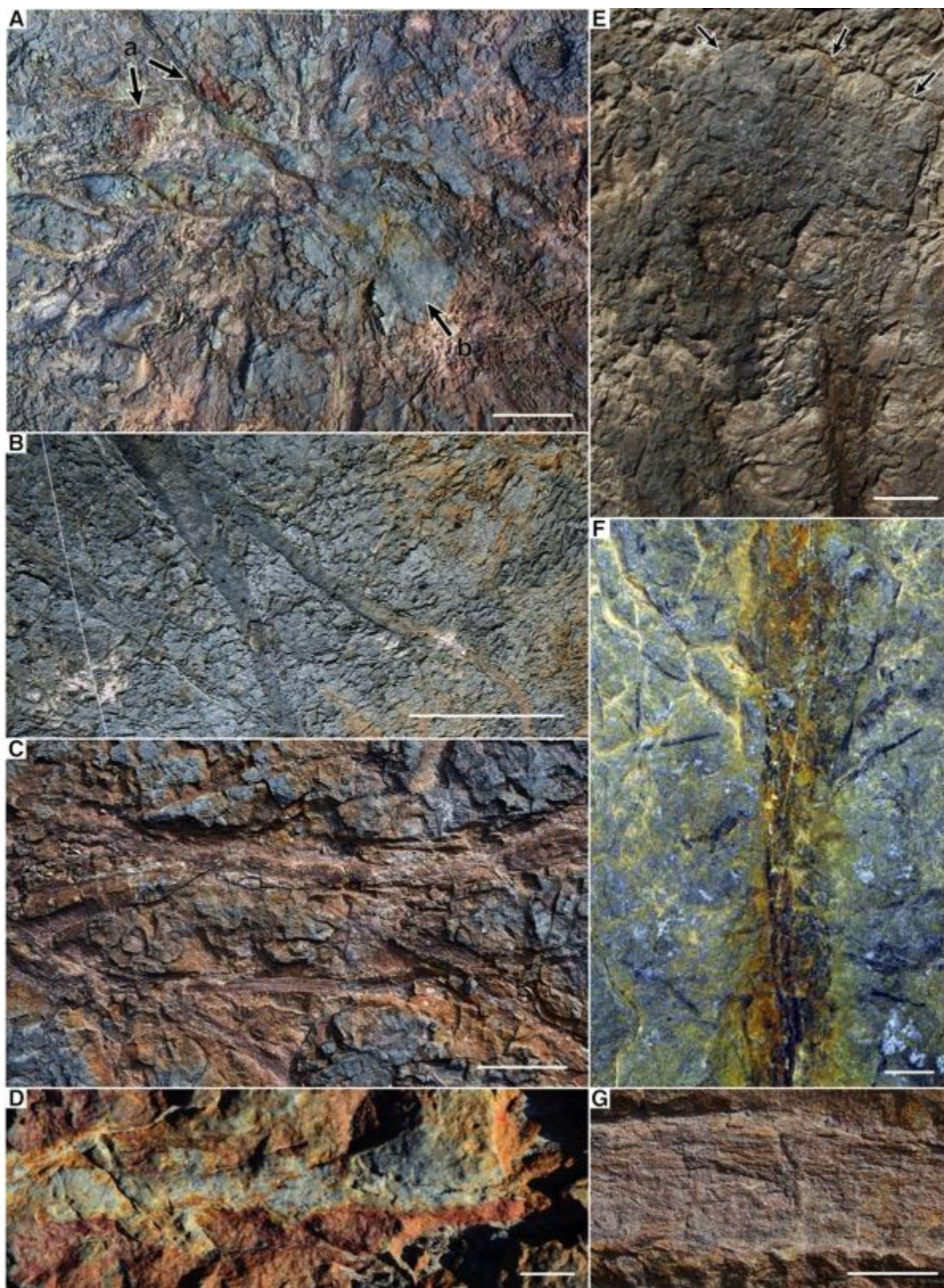
564 (A) Aerial view of a conspicuous pair of bases partly cast by greenish overwash siltstone (region
565 IV), indicated by arrow d in [Figure 1C](#). Scale bar, 1 m.

566 (B) Same pair with only the largest structural roots seen on the surface and reddish surface
567 mottling near root system centers. Yellow polygons on the paleosol indicate fish remains. Scale
568 bar, 50 cm.

569 (C) Stitched view from 6 photographs of best-preserved individual showing its highly ramified
570 root system, indicated by arrow e in [Figure 1C](#). Center of root system is at upper left. Primary
571 structural roots trend mostly to the southwest in organic connection throughout most of this
572 view. Roots are dark impressions in the dark gray palaeosol region ([Figure 1C, region II](#)),
573 becoming increasingly encrusted with limonite toward and into the limonite stained palaeosol
574 region ([Figure 1C, region III](#)). Arrow indicates possible root clone individual. The 1.9 X 2.9m
575 map grid with red paint intersections provides scale.

576 (D) Vertebrate (fish) fossil shown here as example of multiple specimens found on the surface of
577 the overwash sediment ([Figure 1C, region IV](#)). Scale bar, 2 cm.

578



580 **Figure 5. Details of *Archaeopteris* individual in Figure 4C.**

581 (A) Center of root system showing complex branching of primary structural roots, red palaeosol
582 pushed up from below at arrows a, and isolated patch of overwash siltstone at arrow b. Scale bar,
583 20 cm.

584 (B) Region near center of Figure 4C showing more-or-less equal dichotomies of some of the
585 largest structural roots. Scale bar, 50 cm.

586 (C) Unequal branching of structural roots ca. 3 m from the center at left. Scale bar, 10 cm.

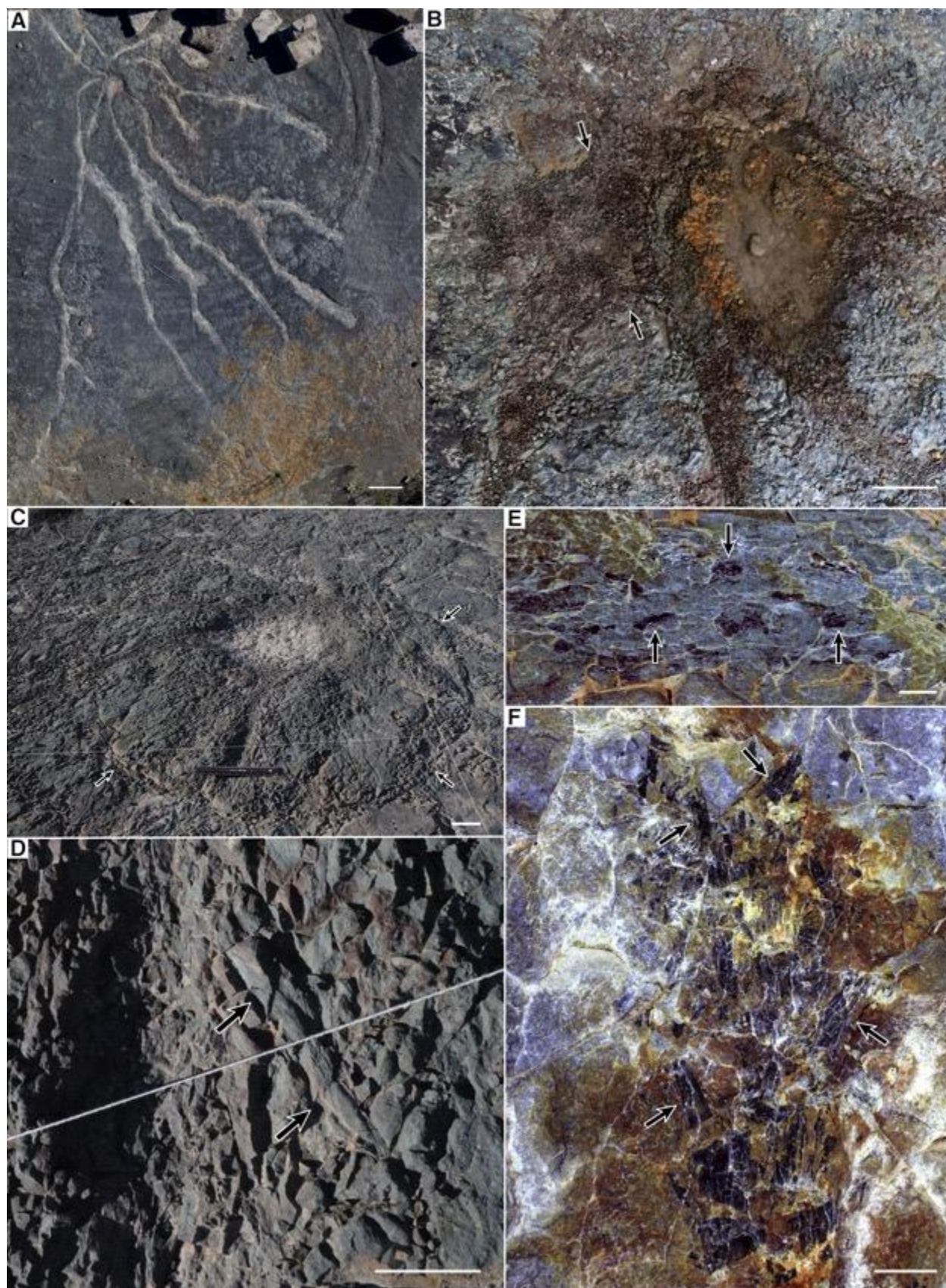
587 (D) Detail of smallest scale structural roots apparently giving off multiple rootlets. Scale bar, 1
588 cm.

589 (E) Primary structural root near termination, distal end up. Arrows mark boundary with
590 slickensides between root-bound and non-bound palaeosol. Scale bar, 10 cm.

591 (F) Small root showing attached and associated finest-scale rootlets, photographed at night with
592 cross-polar light. Scale bar, 1 cm.

593 (G) Detail of distal root with limonite-filled transverse cracks. Scale bar, 1 cm.

594



596 **Figure 6. Root system, potentially lycopsid, showing large primary roots with radiating**
597 **rootlets, indicated by arrow c in Figure 1C.**

598 (A) Aerial view showing root system center upper left, with sparsely dichotomous primary roots,
599 trending toward the limonite stained region at lower right. Scale bar, 1 m.

600 (B) Center of root system, wet, with limonite incrustated center, and red-stained primary roots.
601 Arrows indicate lateral limit of the largest primary root that appears bifurcate at or near
602 attachment to the base. Scale bar, 20 cm.

603 (C) Root system, dry, showing root mound in oblique view. Arrows indicate nearly circular
604 boundary with subvertical slickensides. Scale bar, 10 cm.

605 (D) Magnification of root spanned by ruler in C, with attached lateral rootlet, one of several,
606 indicated by arrows. Scale bar, 5 cm.

607 (E) Secondary root approximately midway between center and observed tip, at night in cross-
608 polar light. Arrows indicate black carbon flecks in regular array likely at attachment points of
609 lateral rootlets. Scale bar, 1 cm.

610 (F) Secondary root at or near terminus in cross-polar light, distal end up. Remnants of rootlets
611 with fine longitudinal striations appear to diverge distally outward, indicating attachment and
612 better preservation near the root tip. Scale bar, 1 cm.

STAR*METHODS

KEY RESOURCES TABLE

LEAD CONTACT AND MATERIALS AVAILABILITY

Requests for further information should be directed to Corresponding Authors, William Stein (stein@binghamton.edu), Chris Berry (berryCM@cardiff.ac.uk), or Jennifer Morris (drjenlmorris@gmail.com). Access to materials should be directed to the New York State Museum or Cardiff University.

Cairo Quarry and Materials

The large Cairo quarry ([Figure 1B](#)) comprises multiple loci of excavation at different topographic levels, but local faulting restricts interpretation of the stratigraphic correlation between exposures within the site. Quarry walls show 1-3 stacked sets of low-angle cross-bedded sandstones, whereas lower excavations expose thinly bedded fine-grained siltstones associated with multiple inter-bedded shale and paleosol horizons. In one part of the quarry, a ca. 1.5 m thick dark weakly fissile shale yields conchostrachans and plant debris and is tentatively interpreted by us as remains of a fresh-water lake ([Figure 1B, arrow](#)). Access to this site is by permission only.

The Cairo quarry occurs approximately 122-152m below the base of the Manorkill Formation [1], and roughly in the middle of the Plattekill Formation, which is estimated to have a maximum thickness of ca. 305m at the Catskill Front [2]. The boundary between the Plattekill and Manorkill Formations in the study area is a chronostratigraphic boundary, marked by a same-age conglomerate event bed, which correlates with a basal sandstone to limestone of the marine Moscow Formation in central to western New York State. By contrast, the Riverside quarry at Gilboa occurs either in strata correlative with the lower Moscow Formation (locally the lower part of the nearshore Cooperstown Formation) [3,4] or in the upper lower to middle part of the Cooperstown Formation in the Schoharie Valley (upper part of the fourth of seven Moscow subsequences, correlative with a unit called the Bear Swamp Beds) [5]. At this time the viability of Rickard's versus Bartholomew's correlations of the Riverside Quarry is unclear. Nevertheless, the Cairo Quarry is definitely older than the Riverside quarry at Gilboa.

Based on sequence stratigraphic analyses of the Middle Devonian Hamilton Group, and estimated duration of Milankovitch cyclicity in the Givetian Stage, a 1.8 Ma duration for the Ludlowville Formation, and 1.2 Ma duration for the lower to middle Moscow Formation up through the Bear Swamp Beds has been estimated, giving a total duration of ca. 7.5 Ma for the stage [6]. If, as presented above, the Cairo quarry occurs in mid-Plattekill position correlative with the base of the marine Ludlowville Formation to the west, and the Riverside Quarry occurs in mid-Moscow strata correlative with the Bear Swamp Beds, then the time span between deposition of the Cairo quarry and Riverside quarry forests would approximate 3 Ma. However, another recent Devonian time scale estimates only 5.0 Ma for the Givetian Stage [7]. This and lack of clarity on exact stratigraphic correlations may shorten the estimated time between the Cairo and Gilboa forests to approximately 2 Ma.

Surface samples have been taken for laboratory study. In addition, 7.6 cm (3-inch) cores (numbered 1-6 in 2012 and 11-22 in 2013) were drilled across and beyond mapped area to depths ranging between 1 to 3 m (Figure 1C). In all cases, care was exercised to leave important features of root systems and the entire site relatively intact for further *in situ* study and potential conservation by local authorities. All surface collections now belong to the New York State Museum (NYSM) in Albany NY. The cores were cut in half longitudinally, with half conserved at the NYSM, the other half sampled for further study at the University of Sheffield and National Oceanography Center, Southampton, and now permanently housed at Cardiff University, UK.

METHOD DETAILS

When originally discovered in 2009, some root systems were partly revealed on a hard surface with regularly arrayed blast fractures exposed by quarrying operations some 40+ years earlier. Careful uncovering of loose fragments and exogenous gravel was performed in stages followed by laying down a grid system with individual blocks measuring 1.9m by 2.9m for complete photographic coverage (Figure 1C). A photographic record of the surface was then made at grid intersection points using a specially constructed 4m tripod, boom, digital camera and lens covering the grid system with sufficient overlap. When a drone became available, portions of the site were uncovered again and photographed at varying heights (Figures 3C, 4A, 6A; Supplemental Figures S1, S3A). Root systems were imaged both dry and wet during the day, taking advantage of natural light at different angles to emphasize features. Other details were photographed at night using cross-polar light (Figure 5F, 6E-F).

Measurements

Individual root base locations may be identified using the 2.9m x 1.9m grid system with grid rows given consecutive letters A-Z + ZA and grid columns numbered 1-33 (Figure 1C). Two tree bases assignable to *Eospermatopteris* occur within grid E26, and provide the only instance of ambiguity. These are further labeled in the table as E26a for the left-hand base, and E26b for the right-hand base in the tables respectively.

Eospermatopteris - Individuals offer differing certainty depending on what was observed in the field (see downloadable [datafile](#)). As a result, they are broadly classified as C for “certain”, versus Cp for “possible or probable” as done previously at Riverside Quarry, Gilboa. Where considered meaningful, measurements were collected of the central depression in the palaeosol made by the plant base (D), with minimum (Da) and maximum (Db) values indicating major and minor axes of an ellipse circumscribing the depression respectively. In well-preserved examples, the floor of the central depression rises outward to a circular to elliptical ridge, presumably representing upward displacement of the palaeosol by trunk weight and growth. Dimensions across the ridges have also been measured (R), using minimum (Ra) and maximum (Rb) values, and provides a different assessment of plant base size. In addition, the surrounding root masses observed on the palaeosol surface were measured (S), with minimum (Sa) and maximum (Sb) values in cases where preservation permitted potentially useful data. Specific features observed in each case are indicated by columns a-d (with features defined in the dataset), where 0 = not observed, and 1 = observed.

Archaeopteris - All curvilinear structures that are likely roots are shown in black on the map (Figure 1C). Among the best candidates for assignment to *Archaeopteris* are those identified by unique number, grid location, and trunk base diameters (ID, Loc, and TBD in datafile). However, determining exact boundaries between trunk base and the largest lateral roots is imprecise due to minimal preservation of details in the palaeosol directly relating to the trunk above. Potentially more precise measurements include diameters of lateral roots (LR) and maximum observed diameters of lateral roots (LRD) (also in the datafile). Although the data points are few, a positive relationship is seen between measured trunk base diameter TBD and LRD (Supplemental Figure S6B).

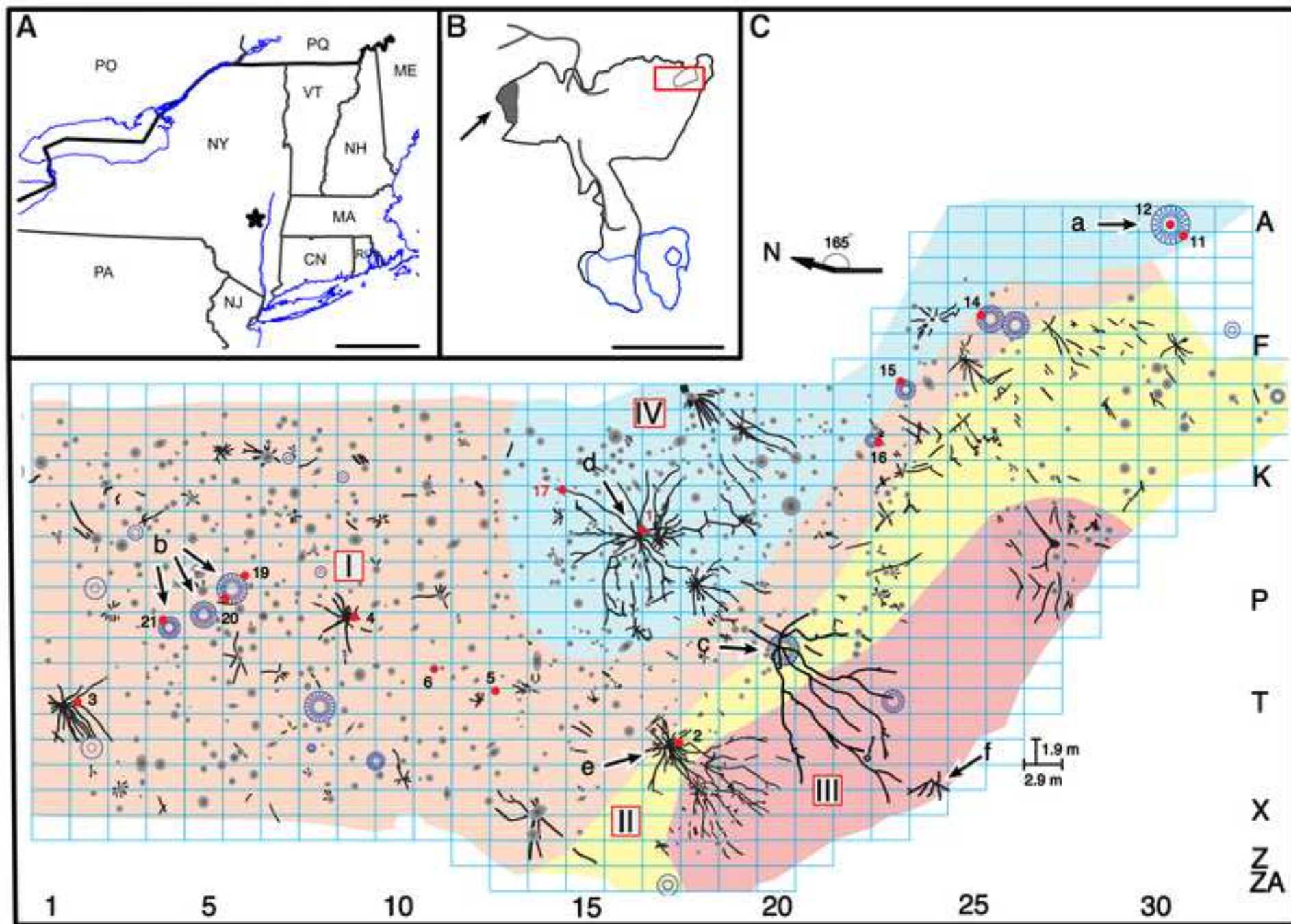
Estimating *Archaeopteris* Tree Sizes at Cairo

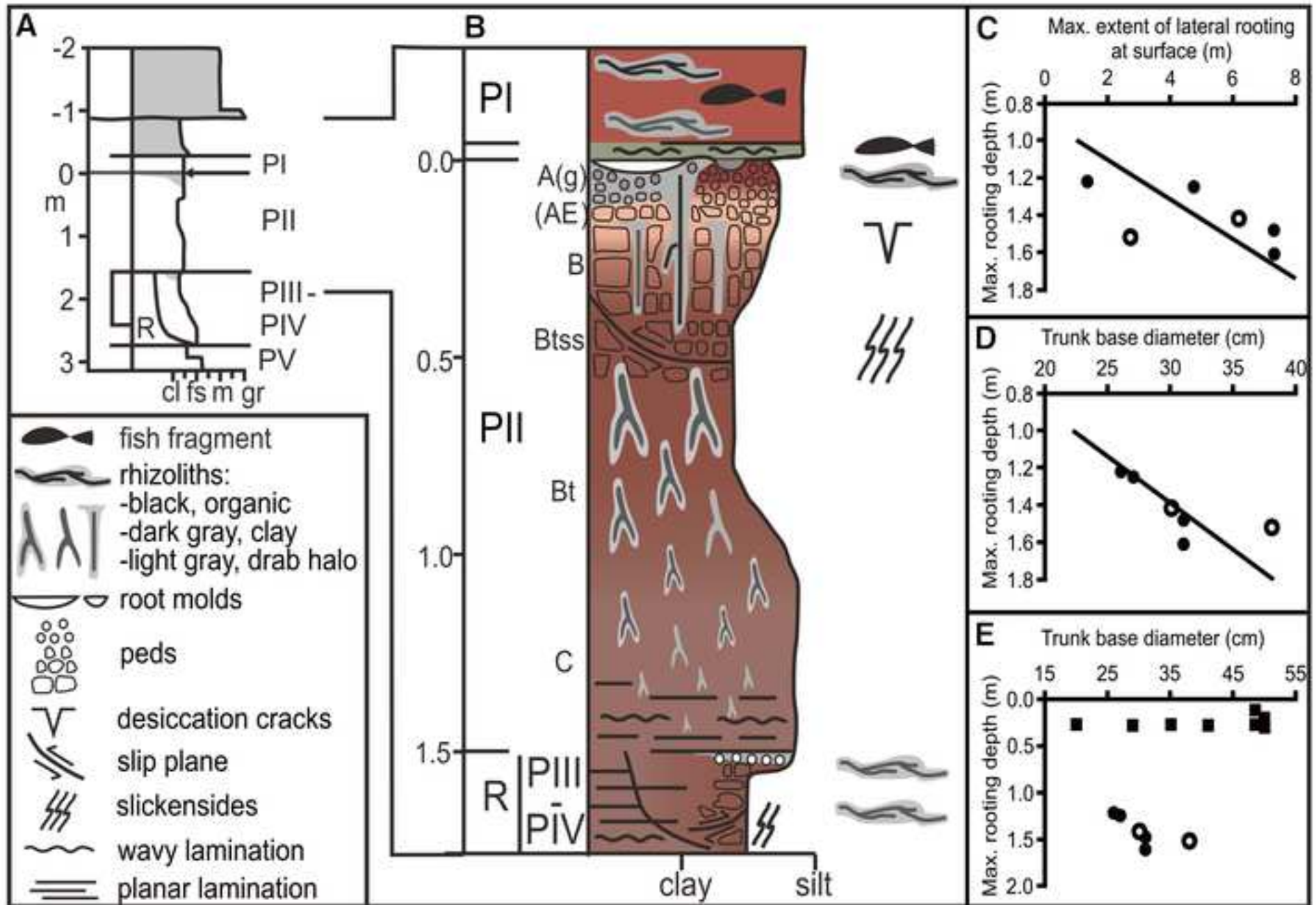
Although the field of plant allometry is large, we have not found directly applicable equations relating variables we can measure from the paleosol surface with diameter of the main trunk at breast height (DBH) commonly encountered in allometric studies, or overall tree height. So here we take a different approach. It is widely assumed that *Archaeopteris* trees more-or-less followed the tapered form seen today among conifers [8], and probably most seed plants, given shared presence of secondary growth. If so, then diameter of the largest roots (LRD) likely has a direct relationship with diameter at breast height (DBH), and from the DBH tree heights can be estimated using published regression parameters. To see whether a relationship might be found in a modern primitive conifer, data comprising LRD observed on a modern soil surface and DBH were collected in 2010 in a pilot dataset for *Araucaria* growing in domestication on the island of O'ahu, Hawaii (see datafile). A positive relationship is seen (Supplemental Figure S6A), supporting use of LRD as a proxy for DBH. Using simple linear (LM) and reduced major axis (RMA) [9] regression parameters from *Araucaria*, estimates of DBH derived from LRD for the Cairo *Archaeopteris* trees were then calculated. These estimates of DBH for *Archaeopteris* were then used to estimate *Archaeopteris* tree height using a very simple power function for conifers [10]: $H = a \cdot \text{DBH}^b$, $a=3.21$, $b=0.6$, where H is in m, DBH in cm. In addition, since *Archaeopteris* trunk base diameters (TBD) measured in the field also show a positive relationship with LRD (Supplemental Figure S6B), tree heights were estimated directly from *Archaeopteris* TBD using the same conifer formula, but here ignoring taper. Analysis was carried out using Microsoft Excel and the R Statistical computing platform. All height estimates (Supplemental Table S1) indicate trees of moderate sizes. However, all estimates should only be considered approximations primarily designed to illustrate the approach taken.

References

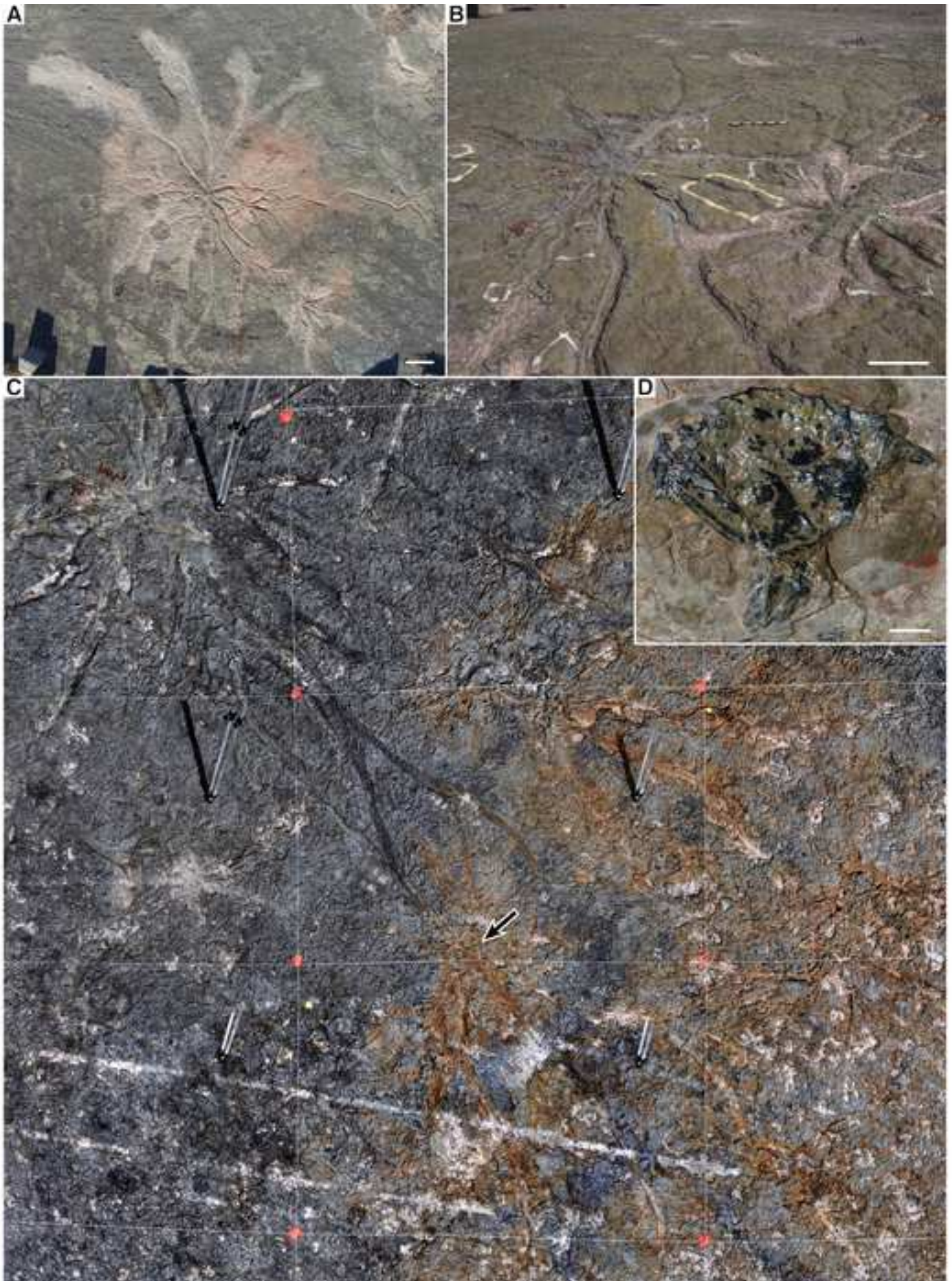
1. Rickard, L. V. (1968a). Bedrock map of the Durham 15' Quadrangle. New York State Museum, Geology Open Files, no. 1g1040.
2. Fletcher, F. W. (1967). Middle and Upper Devonian clastics of the Catskill front, New York. In New York State Geological Association Guidebook, R. H. Wainess ed., 39th Annual Meeting, New Paltz, pp. C1-C23.
3. Rickard, L. V. (1968b). Bedrock map of the Gilboa 15' Quadrangle. New York State Museum, Geology Open Files, no. 1g1601.

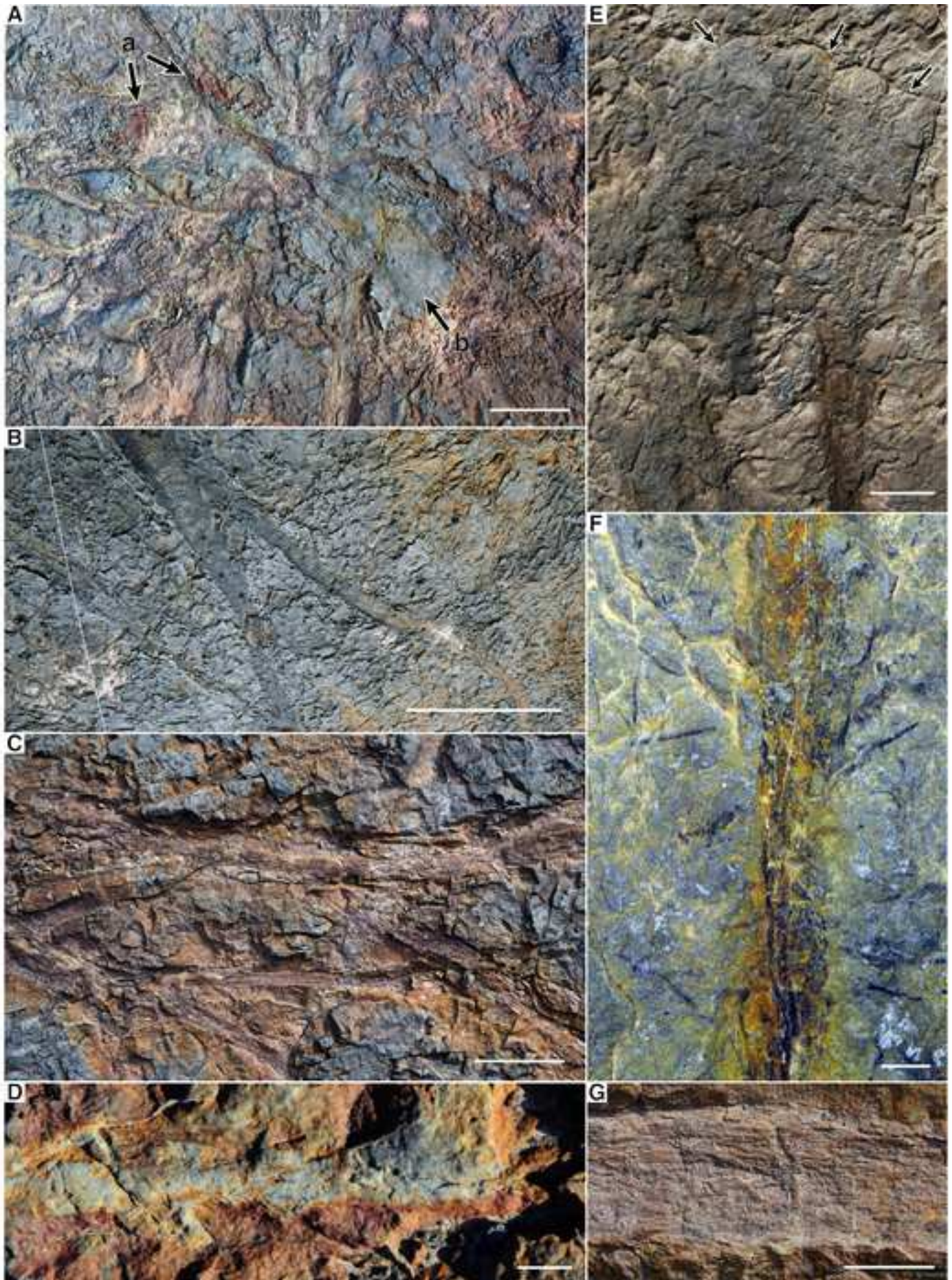
4. Rickard, L.V. (1975). Correlation of the Silurian and Devonian rocks in New York State. (Albany: University of the State of New York)
<https://nysl.ptfs.com/data/Library1/Library1/pdf/1895260.pdf>
5. Bartholomew, A.J. (2002). Correlation of High Order Cycles in the Marine-Paralic Transition of the upper Middle Devonian (Givetian) Moscow Formation, Eastern New York State. M.S. thesis, University of Cincinnati, 93 pp.
6. Brett, C. E., Baird, G. C., Bartholomew, A., DeSantis, M. K., & Ver Straeten, C. A. (2011). Sequence stratigraphy and revised sea level curve for the Middle Devonian in eastern North America. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 304, 21-53.
7. Becker, R. T., Gradstein, F. M., & Hammer, O. (2012). The Devonian Period, In *The Geologic Time Scale 2012*, F. M. Gradstein, J. G. Ogg, M. D. Schmitz, & G. M. Ogg eds. (New York: Elsevier), pp. 559-601.
8. Beck, C. B. (1970). The appearance of gymnospermous structure. *Biol. Rev.* 45, 379–399.
9. Sokal, R. R. & Rohlf, J. (1994). *Biometry: The Principles and Practices of Statistics in Biological Research*. (New York: W.H. Freeman, 3rd ed.).
10. Hulshof, C. M., Swenson, N. G. & Weiser, M. D. (2015). Tree height-diameter allometry across the United States. *Ecol. Evol.* 5, 1193–1204.

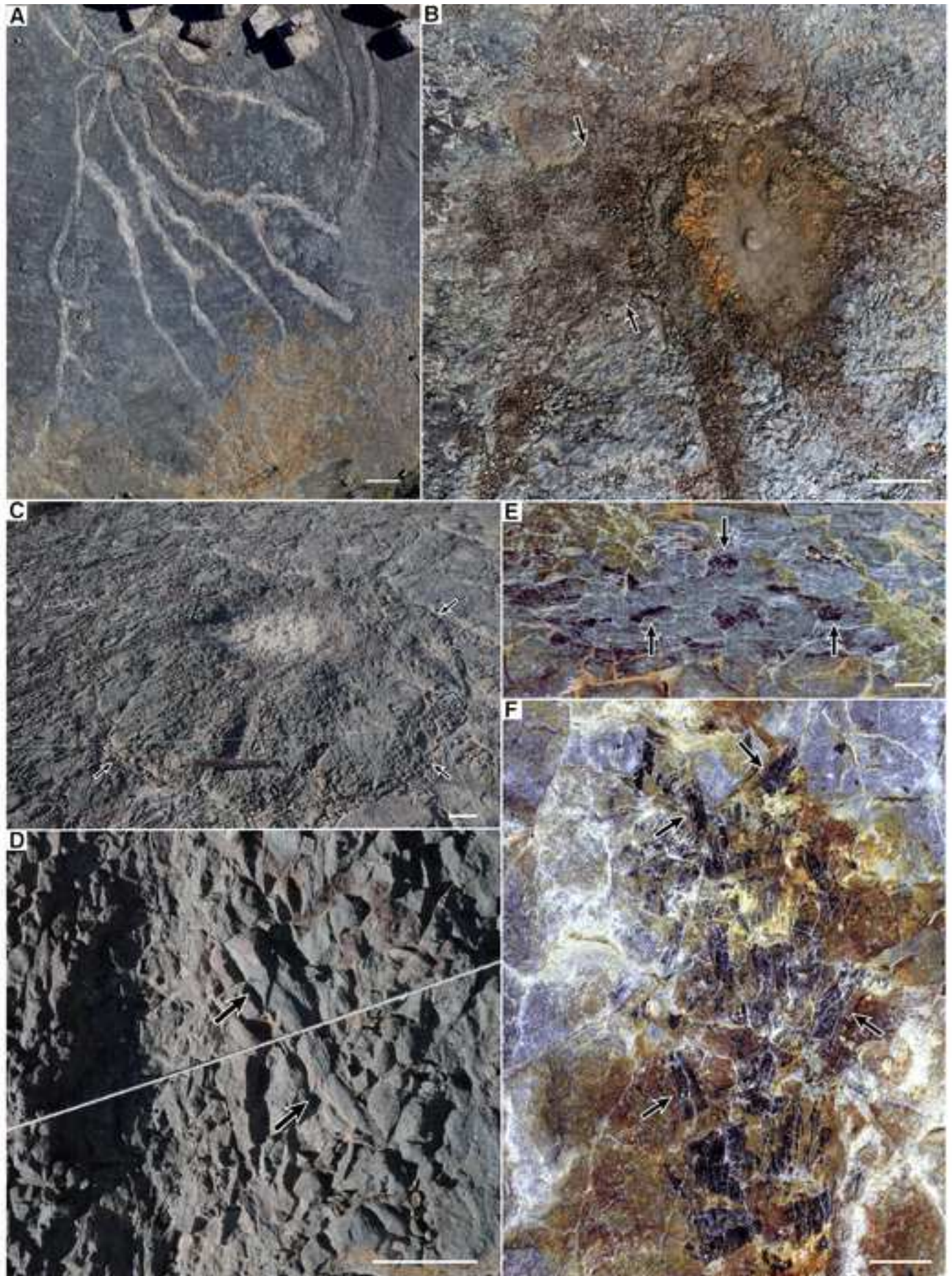




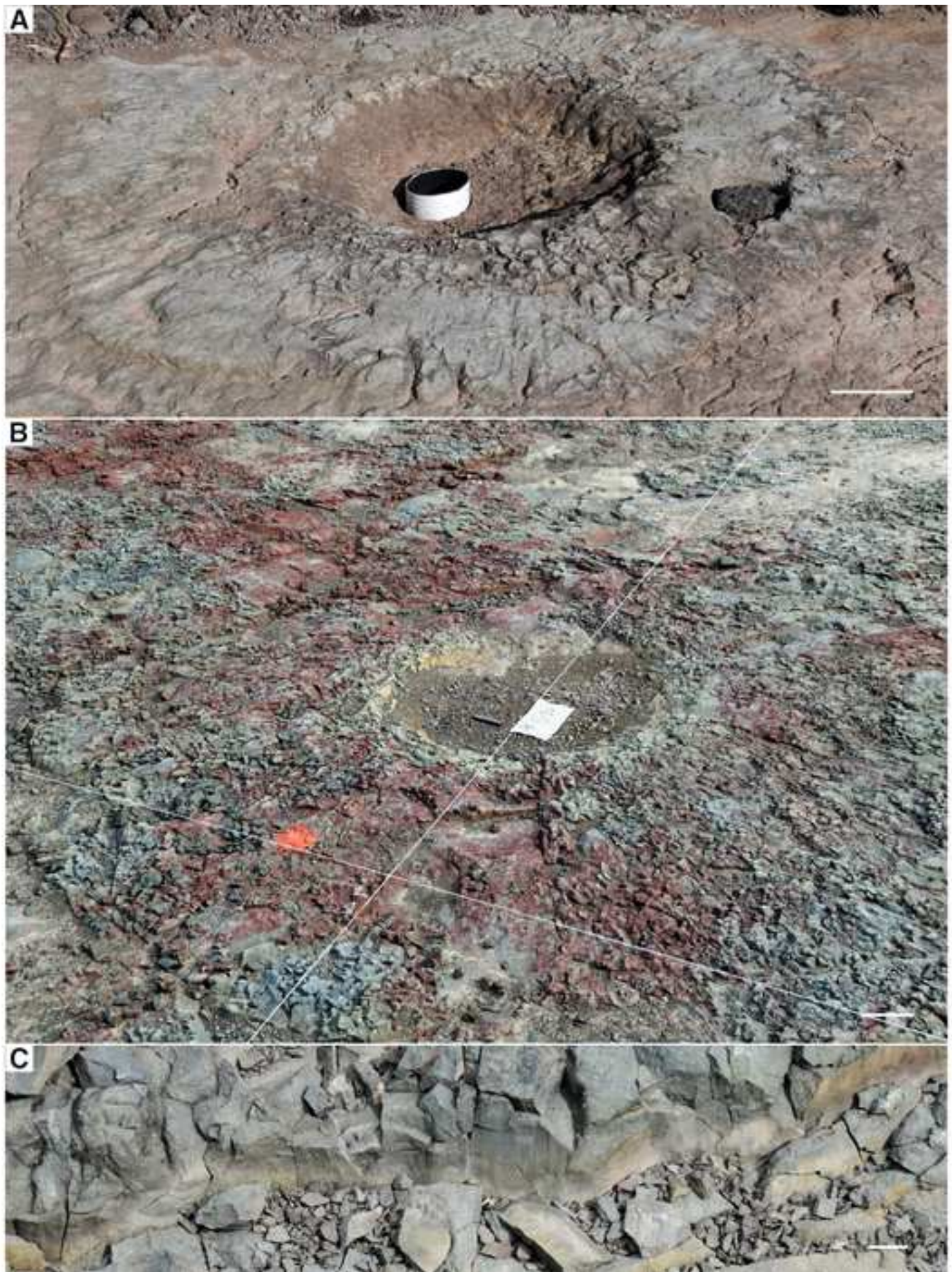




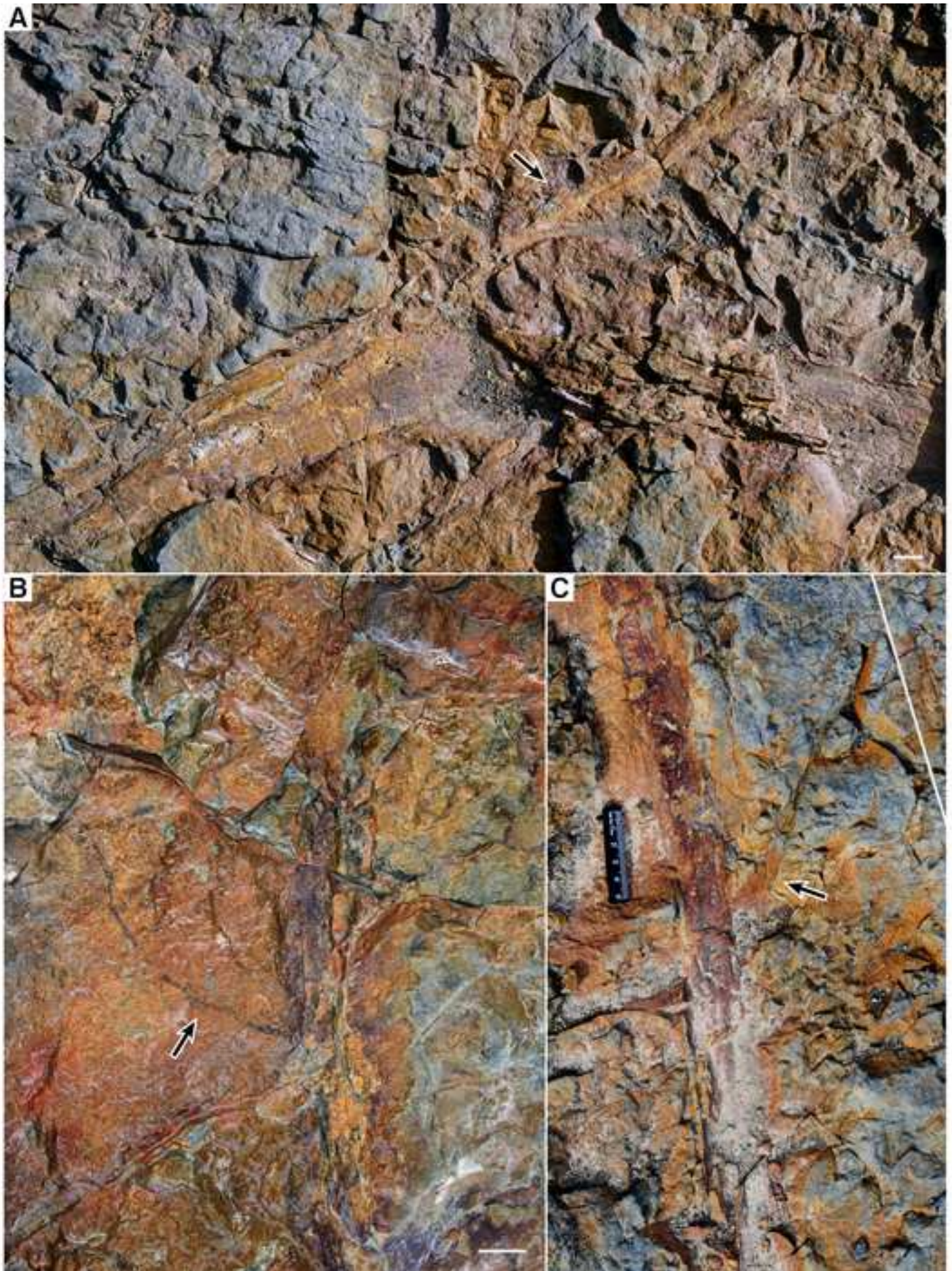


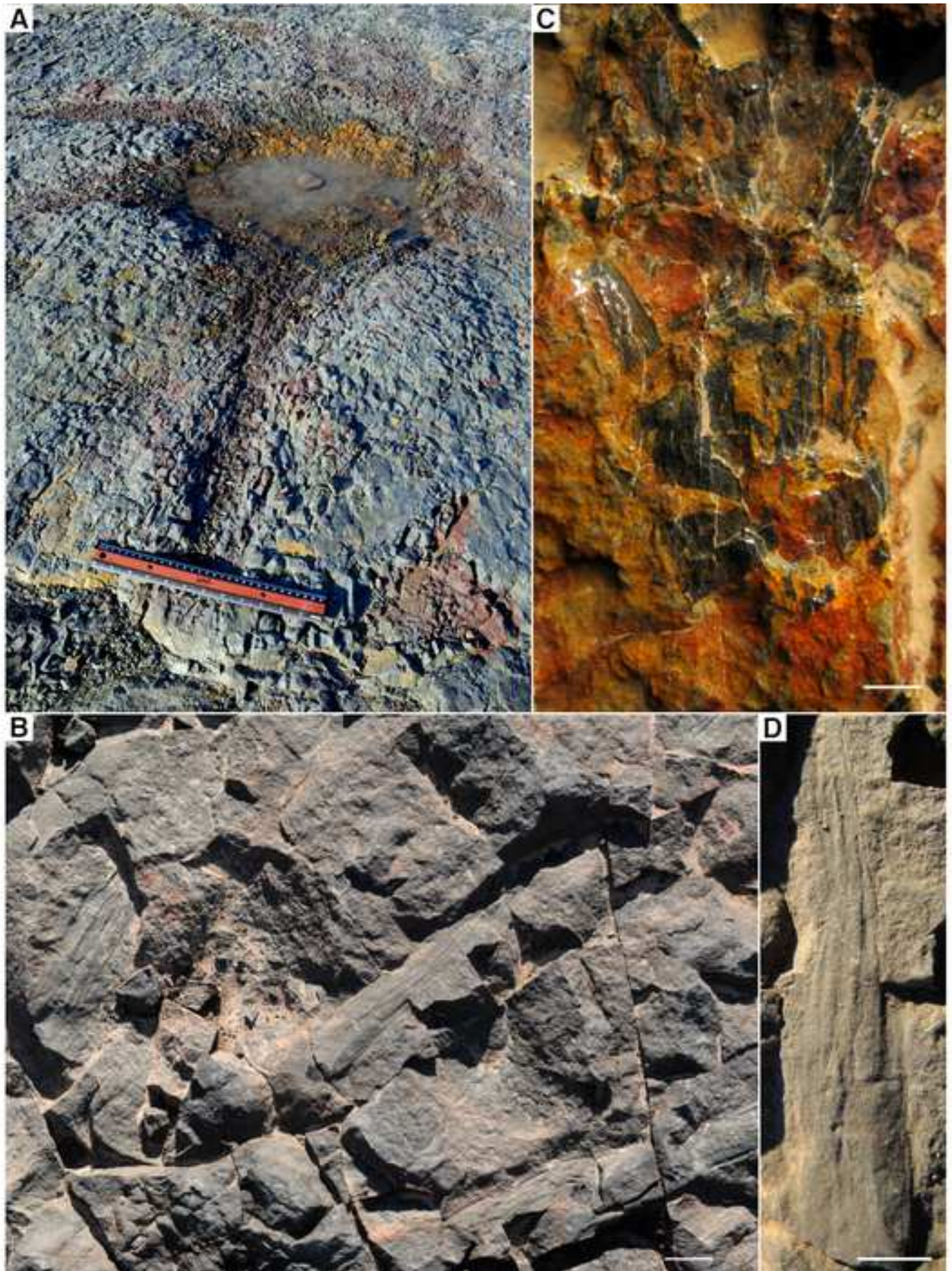












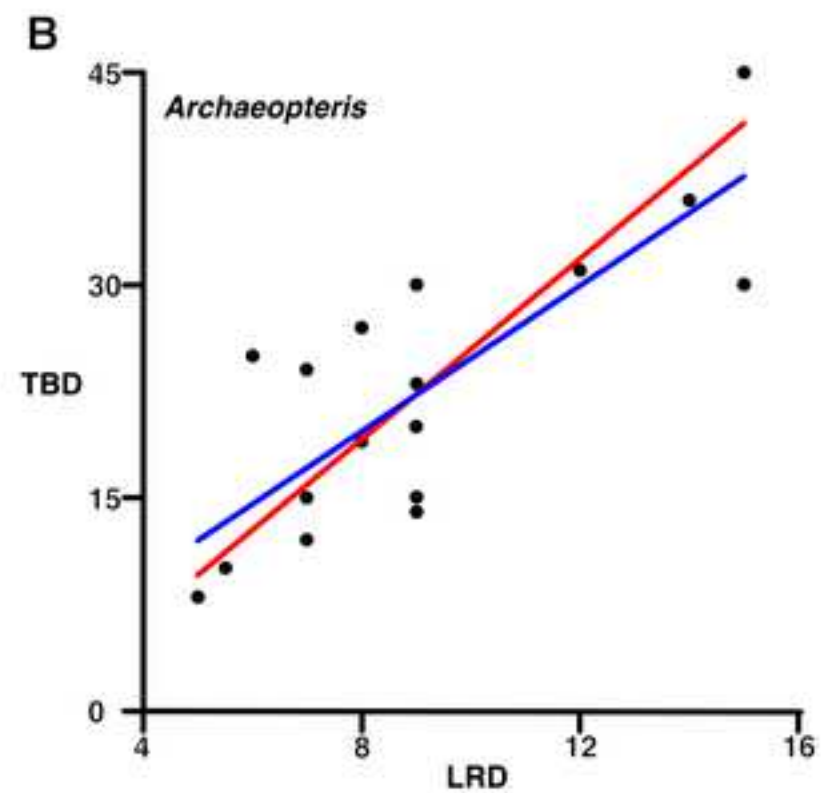
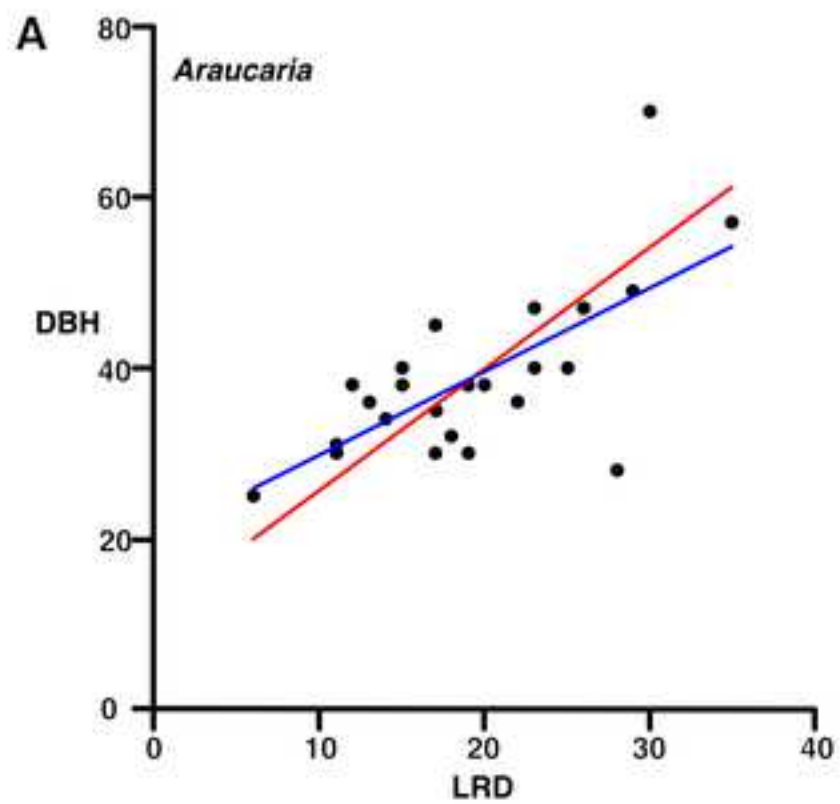




Figure S1. Aerial photographs of the Cairo site

The site now shows new gravel cover and surface weathering. Some root systems were partially re-excavated for views with a drone in order to indicate relative sizes of the individuals identified in [Figure 1C](#). Vehicle is 5.7 m length for scale.

(A) Overhead view with individuals a-f identified, arrows.

(B), Oblique view looking north, individuals b-e identified, arrows.

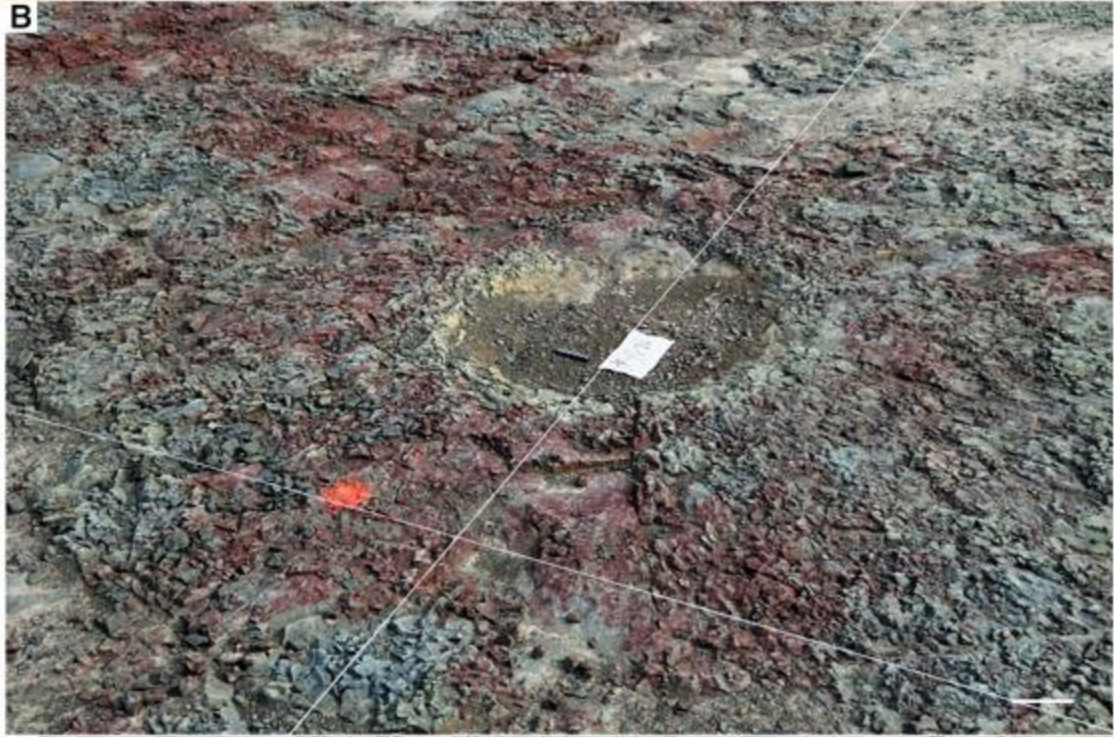


Figure S2. *Eospermatopteris* root systems

(A) Individual within the overwash siltstone (Figure 1C, arrow a within region IV), and also in Figures 3A-B. The image also shows core holes 11 and 12 along with red iron oxide stain derived from drilling the paleosol below. A radiating pattern of roots is apparent on the surface as well as the boundary with subvertical slickened sides marking the boundary of root bound sediment. Scale bar, 10 cm.

(B) Right hand individual in the group labeled b within region I in Figure 1C at the time of mapping. Center of system with 5 cm scale is partly filled with exogenous sediment and has a yellowish limonite stain. The surrounding raised root mass is shows mottling and abundant root halos. Scale bar, 10 cm.

(C) Same individual as (A), showing boundary of root mass with subvertical slickensides. Scale bar, 1 cm.

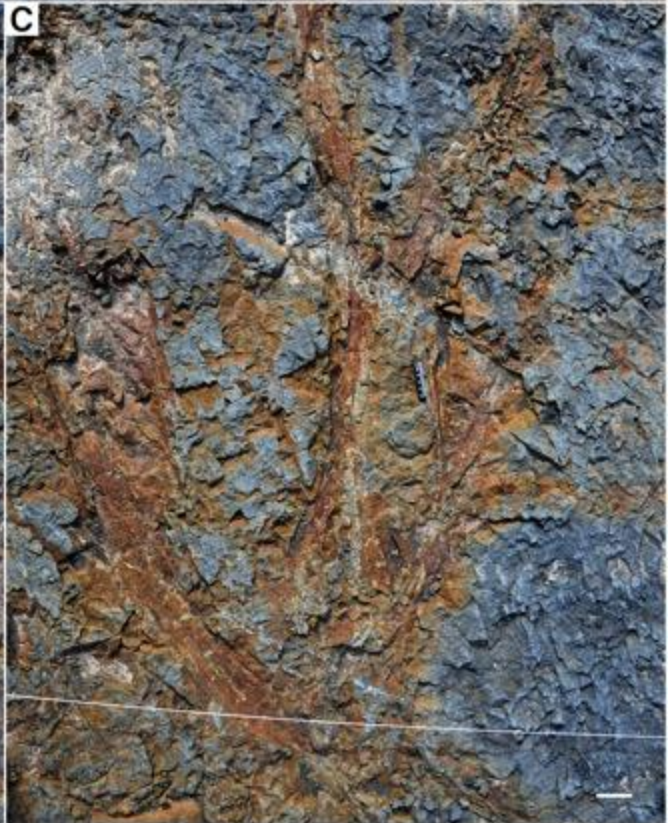


Figure S3. *Archaeopteris* root system, individual e in [Figure 1C](#)

(A) Aerial view of showing root system center, arrow, in region II, with limonite staining of region III to the right, as described in the text. Scale bar, 1 m.

(B) Root system approximately midway between center and tip, showing more-or-less equal dichotomy of a structural root. Scale bar, 3 cm.

(C) Root system near (B), showing complex branching and overlaps of structural roots. Scale bar, 5 cm.



Figure S4. *Archaeopteris* root system, individual e in [Figure 1C](#), showing finer scale roots.

(A) Structural root at mid level showing attachment of smaller root, arrow, similar in size to those bearing lateral small roots interpreted as part of a feeder root system. Scale bar, 2 cm.

(B) Small root bearing very fine root, arrow. Scale bar, 1 cm.

(C) Root similar in size to (B) with attachment of lateral root, arrow. Scale in photo, 5 cm.

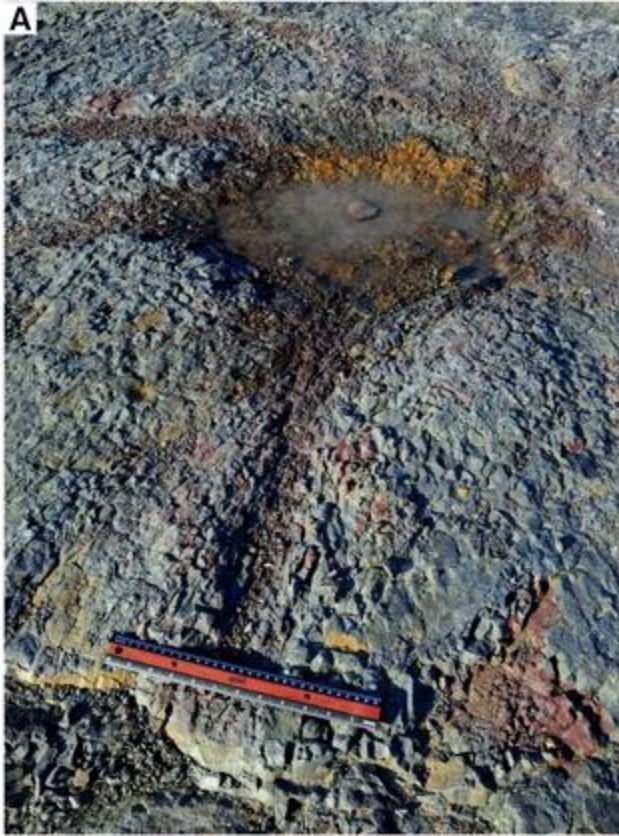


Figure S5. Lycopsid? root system, individual c in [Figure 1C](#)

(A) Oblique view of root system center showing a radiating system of primary roots, and slickenside boundary immediately in front of the ruler (1 ft = 30.5 cm) for scale.

(B) Rootlets with longitudinal striations on root mass immediately adjacent and attached to the primary root in the foreground in (A). Scale bar, 1 cm.

(C) Tip of secondary root, as described in the text, with attached rootlets. This region is the same as in [Figure 6F](#), but imaged instead wet with oblique daylight. Scale bar, 5 mm.

(D) Higher magnification of rootlet near that in (B). Scale bar, 5 mm.

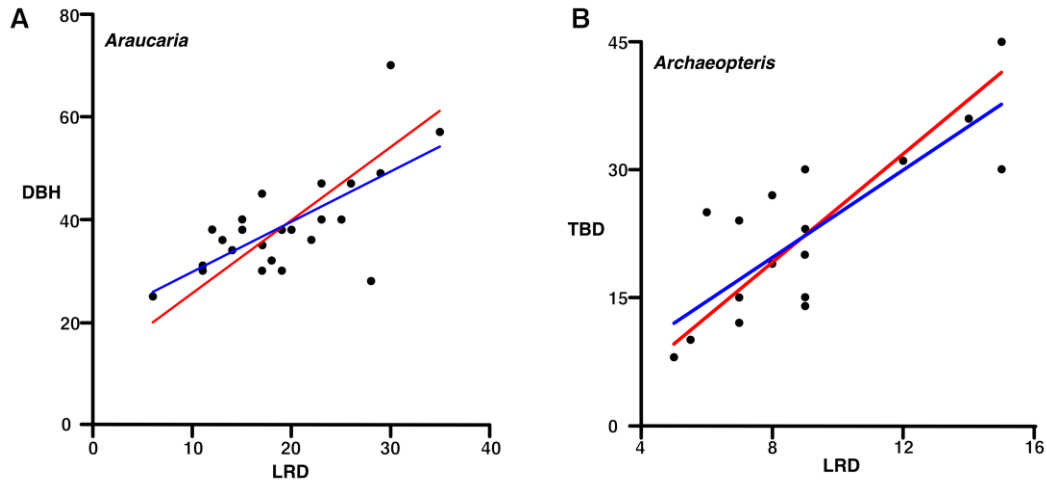


Figure S6. Regressions utilized in estimating size of *Archaeopteris* trees at Cairo Quarry.

(A) Using *Araucaria* as proxy for trunk taper. Diameter of the largest measured lateral root for each tree observed on the soil surface (LRD) versus diameter at breast height (DBH) converted from measured circumference. Regression predictions are represented by red line ($DBH = (1.4206)LRD + 11.392$) for RMA regression, and blue line ($DBH = (0.9772)LRD + 19.984$) for linear regression (LM).

(B) *Archaeopteris* field observations; diameter of the largest measured lateral root for each root system (LRD) versus diameter of the trunk base for each root system (TBD). Regression predictions are represented by red line ($TBD = (3.1859)LRD - 6.4176$) for RMA regression, and blue line ($TBD = (2.5682)LRD - 0.8756$) for linear regression (LM).

Loc	TBD	LRD	RMA DBH	LM DBH	RMA H	LM H	TBD H
X14	45	15	32.70	34.64	26.02	26.93	31.51
Q9	40	14	31.28	33.66	25.33	26.47	29.36
M16	31	12	28.44	31.71	23.93	25.54	25.20
V17	30	15	32.70	34.64	26.02	26.93	24.70
P11	30	9	24.18	28.78	21.70	24.10	24.70
O18	27	8	22.76	27.80	20.93	23.60	23.19
I19	25	6	19.92	25.85	19.32	22.59	22.14
T1	30	7	21.34	26.82	20.14	23.10	24.70
E24	23	9	24.18	28.78	21.70	24.10	21.06
R6	20	9	24.18	28.78	21.70	24.10	19.37
M19	19	8	22.76	27.80	20.93	23.60	18.78
G25	15	9	24.18	28.78	21.70	24.10	16.30
W10	16	7	21.34	26.82	20.14	23.10	16.94
K1	15	7	21.34	26.82	20.14	23.10	16.30
N17	14	9	24.18	28.78	21.70	24.10	15.64
E28	14	7	21.34	26.82	20.14	23.10	15.64
F30	12	5.5	19.21	25.36	18.90	22.33	14.26
Z17	8	5	18.50	24.87	18.48	22.08	11.18

Table S1. Regression estimate of *Archaeopteris* tree heights

Key to columns:

- Loc** Grid location of individual on map (Figure 1C).
- TBD** Trunk base diameter measured in the field (cm).
- LRD** Maximum diameter of roots attached to the tree base (cm).
- DBH** Diameter of trunk at breast height estimated from
RMA or **LM** Regressions of *Araucaria* (cm).
- H** Height of tree derived from DBH as estimated from
RMA or **LM** Regressions of *Araucaria* (m).
- H** Height of tree estimated directly from **TBD** (m).