

The southwesternmost record of late Silurian (Pridolian) early land plants of Gondwana.

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1 **The southwesternmost record of late Silurian (Pridolian) early land**
2 **plants of Gondwana.**

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29 **Abstract**

30 The Silurian constitutes a key period in the evolutionary history of land plants. However, records of
31 Pridolian plants in western Gondwana are scarce, limited to outcrops located in southern Bolivia. In this
32 contribution, an association of fossil plants housed in the Rinconada Formation, San Juan Province,
33 Argentina, is presented. This association corresponds to fossil remains of primitive flora with reproductive
34 structures and sterile axes linked to basal tracheophytes. The fossil assemblage is composed of *Salopella*
35 *marcensis*, *Hostinella* sp, *Aberlemnia caledonica*, *Cooksonia paranensis*, *C. pertoni*, *C. cambrensis*,
36 *Steganoteka striata*, *Isidrophyton* sp, *Caia langii*, two morphotypes of doubtful taxonomy, and graptolites
37 colonies. The association between flora remains and graptolites, represents a parautochthonous fossil
38 assemblage in an inner marine platform, dominated by gravity flows. This fossil record has
39 paleophytogeographic importance since it allows extending the northwest Gondwana-southern Laurussia
40 unit to more southern areas of Gondwana. This expansion would have been favoured by the post-glacial
41 climatic improvement of the late Silurian, together with a great radiation capacity and environmental
42 flexibility of the flora. Furthermore, this contribution extends the biocron of three South American taxa
43 (*A. caledonica*, *C. paranensis* and *Isidrophyton* sp) first known from the Lochkovian, to the Pridoli.

44 **Keywords:** Early land plants, Pridoli, Gondwana, Paleophytogeography, Rinconada Formation.

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49 **Introduction**

50 One of the most important events in the history of Earth is the terrestrialization of plants. The settlement
51 on the continent by the first plants would have taken place during the early Paleozoic, based on the first
52 appearance of cryptospores and trilete spores from early embryophytes, and the first record of spore-
53 bearing fertile structures during the Darriwilian-Hirnantian [1-4]

54 Late Silurian and Early Devonian are critical times for primitive land plants radiation [5]. The fossil record
55 of this time is scarce and restricted to paleotropical environments [6]. However, in recent decades
56 numerous records of land plants in Gondwana high paleolatitudes have been released [7-12].

57 Late Silurian phytogeography is crucial for understanding the global diversity and palaeoecology of early
58 land plants, and also, may yield information concerning the palaeogeography and palaeoclimate of this
59 interval. In addition, the study of late Silurian phytogeography may elucidate the pathway of land-plant
60 radiation during the Silurian-Devonian boundary.

61 The distribution of primitive land plants from the late Silurian has been grouped into four
62 paleophytogeographic units [13]: South Laurussian-Northwest Gondwanian unit; North Laurussian unit;
63 Kazakhstan unit, and East Gondwanian unit. The first is characterised by the predominance of
64 rhyniophytas and rhyniophytoides such as *Steganotheca*, *Pertonella*, *Tarrantia*, and *Cooksonia*, and is
65 located in the temperate climatic zone [14, 13, 12]. The second unit is characterised by the dominance of
66 basal licophytes like *Zosterophylls* (*Zosterophyllum*, *Distichophyllum* and *Bathurstia*) and is located near
67 the paleoequatorial zone [13, 12]. The Kazakhstan unit is characterised by *Jugumella*, *Cooksonella*,
68 *Baragwanathia* and *Taeniocrada* [13, 12]. This unit is located to the north of paleoequator and is
69 established in a subtropical zone [12]. The fourth unit has a position close to the paleoequator and it is
70 characterised by *Zosterophylls* and basal Lycopsids such as *Baragwanathia* [13].

71 Paleobiogeographically, the flora of South America (Bolivia) [9] shows certain similarities with those of
72 southern Laurussia (Great Britain), so they are grouped in the South Laurussian-Northwest Gondwana
73 paleophytogeographic unit that extends from subtropical zones to peripolar zones [13]. Despite the

74 climatic differences between both units, paleo-Antarctic Circle for Bolivian and subtropical paleolatitude
75 for Laurasian assemblages, the similarities may result from a wide-ranging dispersal ability and/or from
76 morphological simplicity of late Silurian land-plants macrofossils, a wide climatic tolerance of plants [9,
77 13] or even the result of paleogeographic proximity between the southernmost zone of Laurasia and the
78 northernmost zone of Northwestern Gondwana [9, 13].

79 The fossil record of early tracheophytes of Pridolian age is abundant and well known in lower
80 paleolatitudes. [15] and [13] presented an excellent summary on the distribution of Silurian flora, with
81 specimens found in China [16], United States [17], Canada [18, 17], Czech Republic [19-22] United
82 Kingdom [23-26], Poland [27], Ukraine [28], Libya [7], Kazakhstan [29-30, 15], and Australia [31-32].
83 In South America, a probable Pridolian age flora was found in Bolivia, nevertheless there are no index
84 faunas to give a more accurate age [9]. Nonetheless, megaflores of this age have not been reported in
85 Argentina until now.

86 This contribution presents the first record of basal tracheophytes of early Pridolian age from Argentina,
87 in the Rinconada Formation, Eastern Precordillera, San Juan province. The fossil assemblage is dated due
88 to the presence of the *Skalograptus parultimus* Zone in the bearing strata [33]. This finding makes it
89 possible to discuss the phytogeographic proposals for early tracheophytes and extend their scope to
90 southwestern areas of Gondwana during the late Silurian.

91

92 **Silurian flora in Argentina**

93 The presence of primitive flora in Argentina is well known in Devonian successions [34-37]. However,
94 the record of Silurian vascular plants is scarce, limited to outcrops in Northwestern Argentina [10]. This
95 flora was found in the upper levels of the Lipeón Formation, exposed in the Subandinas Range of Salta
96 Province. The authors recognized a low-diversity association consisting mainly of fragmentary plant
97 remains, isolated sporangia, and better preserved remains assigned to *Hostinella* sp., *Cooksonia* sp., and

98 cf. *Tarrantia*. Aris *et al.* [10] supported a Ludlovian age for this paleoflora due the presence of
99 *Andinodesma* sp. cf. *A. radicosata*. However, this chronological assignment is conflictive given: 1) the
100 taxon is not found in the flora-bearing beds; 2) *Andinodesma* presents an extensive biochron, also recorded
101 in Devonian (Lochkovian) successions; 3) the taxon is not accompanied by other guide taxa that allow
102 delimiting the beds carrying the flora to the Ludlow.

103 The Lipeón Formation outcrops to the north into Bolivian territory and takes the name of Kirusillas
104 Formation [38]. In the latter, [8] reported the first early tracheophytes with reproductive structures in
105 South America. The authors recognized axes with isotomic branching that culminate in terminal
106 sporangia, assigned to *Cooksonia*. cf. *caledonica* [39]. Subsequently, [9] reported in the Lipeón Formation
107 typical sterile axes of the genus *Hostinella*, non-rhyniophytoid axes with variable diameters probably
108 belonging to algae, axes with dichotomous branching that culminate in terminal sporangia similar to
109 *Cooksonia*. cf. *caledonica*, and isolated sporangia with forms assignable to cf. *Tarrantia*, cf. *Cooksonia*
110 *cambrensis*, cf. *Cooksonia hemisphaerica* and *C. pertyi*.

111 In contrast, the Silurian microflora record in Argentina is well known. In the Precordillera, the Tucunuco
112 Group [40] has been extensively studied [41-44]. This group includes the La Chilca and Los Espejos
113 formations [40], which make up two transgressive-regressive siliciclastic sequences. These units are
114 carriers of palynomorphs between the upper Hirnantian-lower Lochkovian interval, and recognize the
115 Silurian-Devonian boundary in this succession [45, 43].

116 The presence of Pridolian palynomorphs in the Precordillera has been the subject of doubt over the years.
117 [46], proposed a Ludlow-Pridoli? age for the top of the Los Espejos Formation. However this age was
118 later discarded by [41], suggesting that reliable palynological data to suggest Pridolian ages are absent.

119 More recently, [47,45] reveals for the Los Espejos Formation the biozones LP (*Synorisporites libycus*-
120 *Lophozonotriletes poecilomorphus*), RS (*Chelinospora reticulate-Chelinospora sanpetrensis*), and
121 Subzone H (*Chelinospora hemiesferica*), originally recognized by [48] in the upper Silurian of Spain.

122 These biozones would indicate a Ludlovian-early Pridolian age [47]. In addition, the authors reported the
123 existence of the TS Biozone (*Synorisporites tripapillatus*-*Apiculirestusispora spicula*) [49], indicating an
124 early Pridolian-Lochkovian age.

125 Paleogeographically, the marine phytoplankton of the La Chilca and Los Espejos formations show a
126 cosmopolitan distribution, sharing species with Avalonia, Baltica, Laurentia, Armorica, and other
127 Gondwanian regions [50, 44]; while the terrestrial palynomorphs from the Los Espejos Formation show
128 affinities with Gondwanian regions like Brazil and North Africa [51, 44].

129 In Northwestern Argentina, in the Zenta Range, two assemblages of Pridolian palynomorphs were
130 reported by [52] and [53] for the Lipeón and Baritú formations. The first unit is bearer of an association,
131 made up of: *Ambitisporites avitus*, *Amicosporites* sp., *Crassiangulinavaria cornuta*, *Quadrisporites*
132 *variabilis*, *Duvernay sphaera* sp. cf. *D. blanca*, *Eisenachitina* sp. cf. *E. bohémica*, *Margachitina* sp. cf.
133 *M. saretensis*, *Ancyrochitina fragilis*, *Angochitina sinica*, *Angochitina* sp. cf. *A. filosa* [52-53]. This
134 association suggests an Aeronian (middle Llandovery) to a Pridolian-Lochkovian age [52]. The second
135 association, first assigned to the Lipeón Formation [52] and then to the Baritú Formation [53], is made up
136 of: *Crassiangulina variacornuta*, *Quadrisporites variabilis*, *Q. granulatus*, *Duvernaysphaera* sp. cf. *D.*
137 *blanca*, *Onondagaella asymmetrica*, *Verhyachium brave*, *V. downieri*, *Leiofusa banderillae*,
138 *Goniosphaeridium* sp. cf. *G. uncinatum*, *Diexalophasis denticulate*, *Cheilotetras* sp., *Imperfectotriletes*
139 sp., *Dvaspora murusattenuda*, *Synsphaeridium* sp., *Eisenachitina* sp. cf. *E. bohémica*, *Desmochitina*
140 *sphaerica*, *Angochitina chlupaci*, *Angoschitina sinica*, *Conochitina papchycephala* [52-53]. This
141 association suggests a Ludlovian-Pridolian age [52]. Recently, [54] described the first record of Silurian
142 palynomorphs in the Famatina System, Villacorta Formation, La Rioja Province. The palynological
143 assemblage is composed of terrestrial miospores (e.g. *Artemopyra radiata*, *Cheilotetras caledonica*,
144 *Dyadospora murusdensa*, *Gneudnaspora (Laevolancis) chibrikovae*, *Imperfectotriletes vavrdovae*,
145 *Pseudodyadospora petasus*, *Rimosotetras problematica*, *Tetrahedraletes grayae*, *T. medinensis*,

146 *Ambitisporites avitus/dilutus*, *Ambitisporites* cf. *A. eslae*, *Apiculiretusispora* cf. *Apiculiretusispora*
147 *asperata*, *Apiculiretusispora* sp., cf. *Brochotriletes* sp., *Emphanisporites protophanus*, *Scylaspora scripta*
148 and *S. vetusta*) and nematophyte remains (*Cosmochlaina*). The biochronostratigraphic range of the species
149 allowed the authors to propose a Wenlockian-Ludlovian age for the Villacorta Formation.

150

151 **Geological Settings**

152 The Rinconada Formation is a sedimentary succession of 550 metres thick [33] that outcrops on the eastern
153 margin of the Argentine Precordillera, in the Villicum, Chica de Zonda, and Pedernal ranges (Fig. 1).
154 Lithologically, it is characterised by a sedimentary *mélange*, composed of blocks of various sizes, mainly
155 of limestones, black shales, quartzites, and conglomerates, surrounded by a clastic matrix formed by
156 conglomerate lenses, sandstones, and shales that shows an strong synsedimentary deformation. The base
157 of the unit varies depending on the geographical location: in the Villicum Range it is overlying the Don
158 Braulio Formation in an erosive unconformity [55], in the Chica de Zonda Range, it rests unconformably
159 over the Ordovician limestones of the San Juan Formation [56], and finally, in the Pedernal Range, it
160 covered the possible Don Braulio Formation [57]. Regarding its upper contact, it is generally covered by
161 Neopaleozoic or Quaternary deposits in all localities (Jejenes and Loma de Las Tapias formations, or
162 piedmont deposits).

163 The relevant area is located in the eastern margin of the Chica de Zonda Range, San Juan, Argentina (Fig.
164 1). The section is 550 metres thick with a lower fault contact, which runs in a N-S direction, while its top
165 is covered by Quaternary sediments (Fig. 2). The fossiliferous level is located 350 metres from the base,
166 lodged in the matrix that is superimposed on a calcareous olistolith (Fig. 2).

167 **Age of the Rinconada Formation**

168 The age of the Rinconada Formation is controversial given the sedimentary complexity of the *mélange*.
169 The age data obtained over the years come mainly from the fossiliferous content collected both from the

170 olistoliths and from the matrix. Several authors have contributed to the resolution of this problem, but
171 there is still no consensus in the geological community.

172 The paleontological content of the Rinconada Formation is made up mainly of marine invertebrates, from
173 the matrix and olistoliths, and para-autochthonous plants remains. In particular, specimens of brachiopods,
174 graptolites, plants, conodonts, trilobites, bivalves, corals, scolecodonts, and icnofossils have been
175 described in the matrix of the unit [58, 56, 59-60, 33]. On the other hand, graptolites, conodonts, trilobites,
176 brachiopods, and nautiloids were described in olistoliths within the Rinconada Formation matrix [56, 61-
177 62]. These paleontological data allowed to date the unit as Wenlockian to early Devonian, presenting
178 olistoliths from the Lower Ordovician (or older) to the lower Silurian (Llandovery) time-lapse.

179

180 **Material and Methods**

181 The paleofloristic assemblage comes from the top of the Rinconada Formation at the homonymous section
182 (Fig. 1). The fossil plants are preserved in a green sandstone, accompanied by colonies of graptolites of
183 early Pridolian age (Fig. 2) [33]. The paleofloristic specimens occur as carbonaceous impression-
184 compression. The specimens were observed with a binocular stereo microscope Leica S9D and
185 photographed with a Leica Flexcam C1 camera. In cases requiring mechanical preparation, needles and a
186 microjack-type pneumatic hammer were used. The descriptions were made using the criteria of [63-66].

187 All of the specimens are housed in the collection of the “Instituto y Museo de Ciencias Naturales,
188 Universidad Nacional de San Juan” under the acronym PBSJ.

189

190 **Results**

191 **Systematic Paleobotanical**

192 Embryophyta Endlicher 1836, emend. Lewis and McCourt 2004

193 Polysporangiophyta Kenrick and Crane, 1997.

194 Genus: *Aberlemnia* Gonez and Gerrienne, 2010

195 Type Species: *Aberlemnia caledonica* (Edwards) Gonez and Gerrienne, 2010

196 *Aberlemnia caledonica* (Fig. 3 a-c)

197 **Description:** The specimens consist of isolated carbonaceous compression of the sporangia and the
198 proximal part of the sporangia axes. The axes are on average 0.94 mm wide, widening towards the
199 sporangium base. The sporangia are oval to reniform in front view, bilaterally symmetrical. The sporangia
200 has a mean width of 2.1 mm and 1.75 mm in height. The sporangium-axis junction is marked by a concave-
201 downward line between the two structures. Nevertheless, this feature is well preserved in only one
202 specimen.

203 Repository: PBSJ 1770-1771

204 **Remarks:** [67] excluded *Cooksonia caledonica* from the genus *Cooksonia* and erected the genus
205 *Aberlemnia*, naming the type species of the genus *A. caledonica* based on the number of sporangium per
206 axis, the sporangium bearing axes widening just before the sporangium-axis junction, a well-defined
207 concave downward curve in the sporangium-axis junction, the shape in the front view of the sporangium
208 (oval, circular or reniform), sporangia formed by two valves attached in their proximal part, and a
209 dehiscence line that meets the sporangium outline at the axis-sporangium junction. Although the
210 Rinconada Formation specimen is a single sporangium with the last part of the axis preserved, most of the
211 characters outlined for the genus *Aberlemnia* were recognized. In addition, the general morphology and
212 measurements of the Rinconada Formation specimen are consistent with the description of the species *A.*
213 *caledonica* (Edwards) [67]. That is why we decided to name our material *Amberlemnia caledonica*.

214 Genus: *Cooksonia* (Lang, *emend.* Gonez & Gerrienne, 2010)

215 Type Species: *Cooksonia pertoni* Gonez & Gerrienne, 2010

216 *Cooksonia paranensis* (Fig. 3 d, e)

217 Repository: PBSJ 1766

218 **Description:** The specimen comprises one coalified compression composed of an sporangia-bearing axe
219 with an apical sporangium. The complete specimen is 6.55 mm in length, the axis is smooth, 5.35 mm in
220 length and 0.7 mm wide, widening upward, marking the axis-sporangium transition progressive. The
221 sporangium is partially preserved, cup-shaped in outline and measures 4.37 mm wide and 1.97 mm in
222 height. The apical part of the sporangium is concave, because of the absence of the operculum.

223 **Remarks:** The general characteristics of the Rinconada Formation specimen matches most of the species
224 *Cooksonia paranensis* [68]. Compared with *C. pertoni*, the transition between the axis and the sporangium
225 is clear-cut in the type species while in *C. paranensis* this transition is more gradual. The sporangium in
226 *C. pertoni* varies from shallowly funnel-shaped to discoidal, in *C. paranensis*, the sporangium is cup-
227 shape. Compared with *Aberlemnia caledonica* described above, the sporangium of *C. paranensis* is cup-
228 shape, in *A. caledonica*, sporangium ranges from sub-circular, oval to reniform shape. In addition,
229 sporangium of *C. paranensis* is considerably larger than *A. caledonica* sporangium. This comparison also
230 includes *Cooksonia* cf. *caledonica* from the Silurian of Bolivia [9] that would be identified as *A.*
231 *caledonica* by [67]. [69] described a new species of *Cooksonia* named *C. banksii*, from the Lower
232 Devonian of Welsh. This specimen was later transferred to the species *Concavatheca banksii* by [70].
233 *Concavatheca banksii* comprises a single sporangium on smooth axes, nevertheless, there is a significant
234 difference in size from the Rinconada Formation specimen. The specimen here described and compared,
235 has morphological similarities with *C. pertoni*, *C. paranensis* and *C. banksii*. From these, the gradual
236 transition between the sporangium and the subtending axes, as well as the cup-shaped of the sporangium
237 are reminiscent of *C. paranensis* and *C. banksii*. [6] point out that the main difference between

238 *Concavatheca banskii* and *Cooksonia paranensis* is related to preservation, which is allowed by the
239 nomenclatural code (Art. 11.1, Shenzhen Code). Until the connection between the two is clarified and
240 given that our samples are preserved as impression-compressions, here we name the material from La
241 Rinconada as *Cooksonia paranensis*.

242

243 *Cooksonia pertoni* (Lang, *emend.* Gonez & Gerrienne, 2010)

244 *Cooksonia pertoni* (Fig. 3 f-h)

245 Repository: PBSJ 1767-1768

246 **Description:** The specimens comprise two isolated sporangia and the last section of the axis-sporangium
247 junction, all preserved as lateral compressions. The axis is 0.38 mm wide and 1.14 mm in length, and the
248 junction axis-sporangium is transitional, with the axis widening upwards. The sporangia are trumpet-
249 shaped, 1.77 mm wide, and 1.25 mm in length. Both specimens have a distal flattening towards the
250 lateral top of the sporangia.

251 **Remarks:** Most of the characters named by [67] for the sporangia of *Cooksonia pertoni* are present in
252 the specimens from the Rinconada Formation. Despite the incomplete nature of the Rinconada
253 specimens, we could compare our specimens sporangia with most of the genus *Cooksonia*. Sporangia of
254 *C. cambrensis* and *C. hemisphaerica* do not have a trumpet-shaped form. In *C. crassiparietilis*, the shape
255 of the sporangia is bivalve. *C. paranensis* has cup or bowl shape sporangia and a more gradual transition
256 sporangium-axes than *C. pertoni*. Other species of the genus *Cooksonia*, such as *C. banski* were
257 transferred to the genus *Concavatheca* [70], because of the type of preservation so is not considered in
258 this comparison. *C. bohémica*, comprises one sporangium with lousy preservation and is not taken into
259 account for comparison. Also, *C. caledonica*, recently transferred to the genus *Aberlemnia* was not taken
260 into account because the sporangia characters differ from the genus *Cooksonia* [67].

261

262

Cooksonia cambrensis (Lang, *emend.* Gonez & Gerrienne, 2010)

263

Cooksonia cambrensis (Fig. 3 i, j)

264

Repository: PBSJ 1769

265

Description: The specimen consists of an isolated coalified compression constituted by the last section of a narrow axe and a sporangium in apical position. The complete structure is 2.00 mm in length. The axe is 0.29 mm wide, widening upwards near the junction sporangium-axes. The sporangium-axes contact is narrow, abrupt, and well marked by a black line, probably due to a thick walled-cell zone. The sporangium is more or less circular in outline, measuring 1.02 mm wide, and 0.74 mm high.

270

Remarks: The specimen from the Rinconada Formation displays the majority of the characters elected by [23] to characterize *Cooksonia cambrensis*, such as the circular sporangium shape and a narrow sporangium-axis junction. However, due to the fragmentary nature of Rinconada's Formation specimen, some features, like the type of branching and the circular outline of the sporangium, were not preserved. Our specimen differs with *C. banksii* and *C. hemisphaerica* in the sporangium-axis junction, being transitional in both species and narrow and abrupt in *C. cambrensis* and Rinconada's plant. Also, while *C. cambrensis* sporangium outline is circular, *C. banksii* bears a sunken U-shape sporangial cavity, and *C. hemisphaerica* sporangium outline is globose. *C. pertoni* differs with having a flat-sided trumpet shape sporangium and a gradual transition between the axis and the sporangium. Sporangia preserved in *C. paranensis* [68] (plate or bowl shaped with flat apical surface), *C. bohémica* [22] (ranging from reniform to elliptical) and *C. crassiparietilis* [71, 67] (reniform, bivalvate, with a thick distal dehiscence line) allow to discard the assignment of Rinconada specimen to these species.

282

283

284

Genus: *Salopella* Edwards and Richardson, 1974

285 Type species: *Salopella allenii* Edwards and Richardson, 1974

286 *Salopella marcensis* (Fig. 4 a, b)

287 Repository: PBSJ 1763

288 **Description:** Plant fragment with at least one dichotomy. The principal axe is at least 2.88 mm high, and
289 the secondary axe is 2.92 mm high with two elongated terminal sporangia. Sporangia are elliptic, parallel-
290 sided, isotomously branched, with blunt apices, 0.50 mm wide and 1.40 mm height. The sporangia are
291 attached only at the base. The angle between sporangia is 30°.

292 **Remarks:** This specimen is assigned to *Salopella marcensis* [64] on the base of dichotomously branched
293 axes, which terminate in two large fusiform sporangia. The Rinconada specimen has only one angle
294 preserved between the first and the second order axes of 90°, as reported by [70]. In comparison, *S. allenii*
295 differs from the new material in its sporangial greater size and smaller branching angle. *S. xinjiangensis*
296 from the Pridoli of northwest China is poorly known [72]. Several species of *Salopella*-type have been
297 described from the upper Silurian-Lower Devonian from central Victoria, Australia. *S. australis* has one
298 sporangium per daughter axe. In the Rinconada specimen, there are two sporangia per daughter axe. Also,
299 *S. australis* sporangia size is five times longer and three times wider than Rinconada materials. Compared
300 to *S. caespitosa*, the size of axes and sporangia are greater than *S. marcensis*; also the secondary dichotomy
301 that leads to the sporangia is longer in *S. caespitosa*. Additionally, the sporangia of *S. caespitosa* has a
302 constriction near the apical part that is not present in *S. marcensis*. *S. ladiae* has branching angles acute
303 (15°-50°) whereas *S. marcensis* has branching angles between 35°-90°. Furthermore, sporangia in *S.*
304 *ladiae* are both height and wider than *S. marcensis*.

305 Genus *Steganotheca*

306 Type species: *Steganotheca striata* Edwards, 1970

307 *Steganotheca striata* (Fig. 4 c-e)

308 Repository: PBSJ 1765

309 **Description:** The unique specimen is preserved as a coalified compression. The whole structure comprises
310 the last part of the subtending axe and a terminal sporangium. The complete structure measures 9.83 mm
311 in length. The axe is parallel sided with a central black line, probably due to a thick walled-cell zone. The
312 axe has a constant width (0.37 mm), widening upwards near the sporangium-axe junction. The sporangium
313 measures 6.00 mm in length and gets wider (0.75 mm base; 1.19 middle; 1.20 mm top) towards the apex
314 near the sporangium tip. The transition between the sporangium and the subtending axe is smooth. The
315 tip of the sporangium is truncated and topped by a lens-shaped apical plateau. This structure measures
316 1.62 mm length and 0.25 mm width.

317 **Remarks:** The specimen from the Rinconada Formation displays most of the characteristics of the species
318 *Steganotheca striata*, such as mug-shape sporangia characterized by a smooth axe-sporangia junction,
319 sporangia longer than wide, and sporangia truncated to the apex by a lens-shaped plateau. However, [39]
320 and [63] described an oblique striation on the sporangia surface; this is the only character not preserved
321 in Rinconada's Formation specimen, probably due to taphonomic bias. Despite the lack of striation, we
322 consider that the similarities are sufficient to name the Rinconada Formation specimen as *Steganotheca*
323 *striata*.

324 *Isidrophyton* Edwards *et al.*, (2001)

325 *Isidrophyton* sp. (Fig. 4 f)

326 Repository: PBSJ 1772

327 **Description:** The single specimen consists of a coalified, incomplete compression of 6.21 mm. The
328 specimen comprises a main axis of 0.37 mm wide and a possible ramification near the sporangia. The
329 principal axe ends in two short secondary axes, isotomously branching 0.16 mm wide with two terminal

330 sporangia. The sporangia are in pairs, ellipsoidal 0.42 mm wide and 0.35 mm length, and the angle
331 between the two sporangia is 80°.

332 **Remarks:** *Isidrophyton* is a monospecific genus described for the Lower Devonian of Villavicencio
333 Formation [34], defined by having a principal axis that branches isotomously with a single ellipsoidal
334 sporangium in each branch immediately above the dichotomy, features shared by the Rinconada
335 Formation specimen. On the other hand our specimen lacks the fusiform longitudinally structures that
336 cover the axes and is considerably smaller both in vegetative and reproductive traits than the type species
337 *I. ñiñiguezii*, thus we prefer to name the Rinconada Formation specimen as *Isidrophyton* sp., hoping to find
338 more complete specimens for a correct taxonomic approach. Our specimen can be compared also with
339 *Cooksonia*, *Fozzia* and *Renalia*. In *Cooksonia* (Lang, *enmend* Gonez and Gerrienne, 2010), the sporangia
340 are trumpet-shaped, while in *Isidrophyton* sp. are elliptical. *Fozzia minuta* [73], a monospecific taxon from
341 the Emsian of Belgium, has lateral appendages along the axes, both vegetative and fertile. The fertile ones
342 bear a pair of sporangia, semi-circular, semi-oval or fusiform in outline. *Isidrophyton* sp differs from *F.*
343 *minuta* in the shape and size of the sporangia and the lack of lateral appendages. *Renalia hueberi* [74]
344 from the Lower Devonian of Battery Point Formation is a plant characterized by lateral dichotomous
345 branches terminated in rounded to reniform sporangia. The fertile branches bear 1 to 4 sporangia and are
346 scattered may be similar to *Isidrophyton* sp, although they differ in the position and number of sporangia.

347

348 Genus: *Caia* Fanning *et al.* (1990)

349 Type species: *Caia langii* Fanning *et al.* (1990)

350 *Caia langi* (Fig. 5 a-c)

351 Repository: PBSJ 1773

352 **Description:** The only specimen recovered comprises an incomplete coalified compression. The complete
353 specimen is 7.35 mm long. It is composed of a principal axis 0.37 mm wide and bifurcates isotomously

354 once. The axis has smooth and parallel sides. At the bifurcation, the axis increases its width and becomes
355 two secondary axes. One of the secondary axes bears the coalified compression of a sporangium. There is
356 a slight thickening at the base of the subtending axis and the sporangium. The sporangium is elongated,
357 2-3 times longer than wider, 0.54 mm wide and 1.51 mm long, with parallel sides. At the apex of the
358 sporangium, there are four conical emergences. Two emergences are well preserved. The emergences
359 have decurrent bases and are 0.11 mm wide and 0.14 mm long, all concentrated in the apex of the
360 sporangium.

361 **Remarks:** The specimen from the Rinconada Formation presents most of the characters defined by [24]
362 for the monospecific genera *Caia*, such as smooth isotomously branching axes with terminal bifurcating
363 sporangia, longer than wide, bearing conical emergences, as well as the dimensions of the Welsh
364 specimens. Nevertheless, at the Rinconada Formation, only one specimen was preserved with one
365 sporangium after the bifurcation of the subtending axes. In addition, the diagnosis of *C. langii* includes
366 spore characters; in our specimen, we could not recover any spores, nevertheless we name the specimen
367 as *C. langii*. In addition, several Silurian-Devonian genera bear sporangia with emergences. Compared
368 with *Pertonella* [25], its sporangia are plate-shaped and tranvesally disposed; in the Rinconada specimen,
369 the sporangium is elongated. Also, *Pertonella* has two emergences, while in *Caia langii*, there are four
370 emergences. *Dutoita* [75] might have ornamented sporangia with emergences; nevertheless, better
371 specimens are needed to compare. *Horneophyton* has sporangia that are considerably larger than our
372 specimen [76]; it also shows four to five lobes with a columella inside the sporangia, a feature absent in
373 the Rinconada Formation specimen. *Eocooksonia sphaerica* [77] from the Pridoli of China has a border
374 covering the central part of the sporangia, formed by a variable number of emergences (from four to
375 eight), but the general shape of the sporangia is spherical, while in *C. cf langii* the sporangium is elongated,
376 and there is no distinction between the central region and the outlier region with emergences that show
377 *E. sphaerica*. In the same outcrops of the Rinconada Formation, we described another sporangium with

378 emergences on the apical side named Morphotype B. Compared with *C. langii*, Morphotype B sporangium
379 has a conical shape and is smaller than *C. langii*.

380 Genus: *Hostinella* sp. Barrande ex Stur (1882)

381 *Hostinella* sp. (Fig 5 d)

382 Repository: PBSJ 1764

383 **Description:** Specimens consist of incomplete carbonised compressions of smooth sterile axes. Some
384 specimens bifurcate once, while others are just one single axe. Branching is isotomous, widening just
385 before the branching point, and the branching angle varies from 40° to 95°. Principal axes are 0.64 mm
386 wide and 9.80 mm long on average; nevertheless, the longest specimen recorded is 18.24 mm.

387 **Remarks:** Smooth isotomously branching axes are conventionally named *Hostinella* [9]. Coalified
388 preserved axes like the Rinconada Formation specimens have no evidence of cellular preservation and
389 thus may derive either from non-vascular plants or tracheophytes [9]. [68] proposed that naked axes could
390 be assigned to the genus *Tarrantia* [64] based on proximity; however, *Tarrantia* comprises axes as well
391 as reproductive structures [64]. Considering this, solitary axes recovered from the Rinconada Formation
392 are included in the genus *Hostinella*.

393

394 Morphotype A (Fig. 5 e, f)

395 Repository: PBSJ 1775

396 **Description:** The specimen consists of a small fragment with a principal axis of 0.53 mm width and 1.48
397 mm height. The principal axe bifurcates isotomously, finishing at the top in two sporangial-shaped

398 structures. These structures are elliptical, 0.43 mm wide and 0.86 mm long, forming an angle between
399 them of 28°.

400 **Remarks:** The specimen from the Rinconada Formation is fragmentary and lacks particular characters for
401 proper taxonomic identification. The sporangial-shaped structures are identified as reproductive structures
402 based on their apical position and elliptical shape. There are several examples of upper Silurian-Lower
403 Devonian elongate sporangia with similar proportions [63,24,64,9], none of which are similar enough to
404 the Rinconada Formation specimen; a detailed comparison of such incomplete material is premature, so
405 this specimen should remain unnamed.

406

407 Morphotype B (Fig. 5 g, h)

408 Repository: PBSJ 1774

409 **Description:** The single specimen consists of an incomplete coalified compression. The specimen is 4.00
410 mm long. The principal axis is 0.44 mm wide; it bifurcates at the top isotomously into two secondary axes
411 of 0.24 mm wide each. One of the secondary axes ends in a sporangium, and the other is unclear. The
412 sporangium in lateral view has a conical shape. It is 1.00 mm long and 0.50 mm wide; nevertheless, the
413 transition between the secondary axe and the sporangium is smooth and not precise, as is the limit between
414 both structures. The apical end of the sporangium is broad and has four minor emergencies. The
415 emergencies are sharp at the apex, with decurrent bases 0.23 mm high and 0.15 mm wide.

416 **Remarks:** The Rinconada Formation specimen has several characteristics that fit numerous early plant
417 descriptions. Nevertheless, the unique characteristics, such as the sporangium emergencies, are not typical
418 for Silurian-Devonian floras. Compared to *Pertonella* [25], the Rinconada specimen is considerably
419 smaller, both in axis width and sporangium size; also, the emergences in *Pertonella* sporangia are two,

420 rounded, and with a truncated top [68]. [68] also suggest that *Pertonella* from the Devonian of Brazil
421 might have the same emergencies in the axes. This feature was not observed in the Rinconada specimen.
422 The genus *Dutoitia* [75] probably has ornamented axes and sporangia; however, illustrations are not very
423 clear. *Horneophyton* sporangia are considerably larger than our specimen [76], it also shows. four to five
424 lobes, with a columella inside the sporangia, a feature absent in the Rinconada Formation specimen. *Caia*
425 [24] sporangia have a variable number of emergencies at the distal third of the sporangia. These
426 emergencies are three to seven in number and have a blunt apex and decurrent bases. These characteristics
427 are not present in our specimen. Recently, Xue *et al.* [77] described *Eocooksonia sphaerica* from the
428 Pridoli of China, with a border covering the central part of the sporangia, formed by a variable number of
429 emergencies. *E. spahaerica* emergencies are four to eight in number and more prominent on average than
430 Rinconada Formation specimen emergencies. The presence of emergencies in sporangia is a critical
431 generic character in early land plants; nevertheless, the Rinconada Formation specimen is incomplete and
432 only one in number. Despite the differences with the taxa mentioned above, we prefer to keep our
433 specimen unnamed until more complete specimens are discovered.

434

435 **Taphonomic features of the fossil assemblage**

436 Flora remains were found in massive tabular sandstone strata with limited boundaries, grading up to
437 narrow thin sandstone and shale beds, close to olistholite bodies (Figs 6 a-c). The plant specimens are
438 abundant, with moderate state of preservation, mostly fragmentary. Isolated sporangia, connected to axes
439 are randomly disposed all over the bedding planes. The taphonomic features analysis includes: degree of
440 packing and relative orientation of the fossil assemblage, degree of fragmentation of the fossil plant
441 remains, the presence of trace fossils (type) and the relative size of mica [78].

442 Regarding the paleofloristic assemblage of the Rinconada Formation, the fossil plant assemblage
443 is densely to loosely packed with no relative orientation (Fig 6 d). The degree of fragmentation is partial,
444 considering that the vast majority of the plant remains have connections between reproductive structures

445 and subtending axes, and a certain amount of *Hostinella* sp. has several degrees of dichotomies (Fig 6 g).
446 Samples display only horizontal trace fossils of the type classified as *Gordia* isp., and finally the size of
447 mica regarding the fossiliferous planes is under 0.50 mm (Figs 6 g, h).

448 Considering the taphonomic features recognized above, the plant fossil assemblage was subjected to a
449 lower sedimentation rate. The presence of horizontal trace fossils indicate low energy environmental
450 conditions [79]. In addition, the trace fossils identified as *Gordia* isp. are interpreted as feeding or
451 traceborrows which is a sign of higher concentration of organic material (plants) with a low sedimentation
452 rate [80-84]. Finally, the fine grain size of mica (0.18-0.29 μm in average) found in the same facies,
453 represents normal marine deposition in low energy environmental conditions [85,78].

454 On the other hand, the graptolites are scarce and mainly present in two different astogenetic states: juvenile
455 specimens (majority), with sicula and development of three to five thecae at most; and mature specimens
456 (minority), which lack a proximal end preserved (Fig. 6 e, f). It is worth mentioning that some juvenile
457 colonies show a broken or not completely preserved sicula. As well as the associated plant remains, the
458 graptolites are arranged randomly.

459 The mentioned juvenile-graptolite dominance might suggest a stressful paleoenvironmental conditions,
460 which would generally impede that the colonies reach mature astogenetic states. These faunal features in
461 the graptolite assemblages, together with the sedimentary features of the host strata, allow to interpret
462 the sedimentary deposition related to flows of fine grain materials coming in hyperpycnitic currents from
463 the continent [86]. These flows would be loaded with flora remains and would trap planktonic organisms
464 with subsequent deposition by decantation of the suspended load (Fig. 6 i).

465 The fossil association between graptolites and plants remains preserved in the Rinconada Formation,
466 represents a parautochthonous fossil assemblage [*sensu* 87,88]. In a paleogeographic context, the
467 gathering between graptolites and plant remains was relatively close to the source area, allowing the
468 interpretation of the paleogeographic distribution of both fossil groups and the southward dispersion of

469 late Silurian floras. Furthermore, the lack of preferential orientation of the fossil plant could be the result
470 of transportation mechanisms by suspension along the water surface [89,78].

471 The Rinconada Formation is characterised by complex sedimentary features. According to [90] the
472 sedimentary paleoenvironment of the Rinconada Formation mélange corresponds to an inner marine
473 platform, dominated by gravity flows in variable slope zones of the basin. The taphonomic features of the
474 fossil association points to an inner marine platform, not far from the coast, where organic particles could
475 decant in a relatively serene paleoenvironment dominated by gravity flows.

476 The fossil assemblage of the Rinconada Formation (plants and graptolites) is preserved in massive fine
477 sandstone with no preferential orientation, partially fragmented and loosely packed. The sedimentary
478 mechanisms that produce such arrangement are extrabasinal turbidity currents associated with lofting [86].
479 This process allows the direct transfer of organic matter (mainly plant remains) and sediments from the
480 continent to inner basin shelves, mixing in the case of Rinconada Formation matrix, marine and
481 continental fossils in the same facies.

482

483 **Discussion and conclusions**

484 The Pridolian flora of the Rinconada Formation is characterised by a low diversity association of
485 Eutracheophytes. Taxa such as *Aberlemnia* (ex *Cooksonia*) *caledonica*, *Cooksonia pertoni*, and
486 *Hostinella*. sp, have been reported in northern areas as Bolivia and Northwest of Argentina (NOA) [8-
487 9,67,10]. The discovery of this flora in the Rinconada Formation and their similarity with the Bolivian
488 and the Anglo Welsh Basin assemblage makes it possible to extend the geographical scope towards more
489 southern areas of the phytogeographic unit of South Laurussian-Northwest Gondwana [13](Fig 7).

490 The presence of *A. caledonica* and *C. paranensis* in the Pridolian beds of the Rinconada Formation,
491 extends the biocron of these two taxa to the Pridoli, as well as the genus *Isidrophyton* sp, first described
492 for the Lower Devonian of the Villavicencio Formation (Table 1). Considering that the brazilian taxa has

493 now a Pridolian age, this (Table 1) triggers the question: How rhyniophytoids assemblages from South
494 Laurussian-Northwest Gondwana share so many genera when climatic conditions were different and both
495 regions were separated by the Rheic Ocean?

496 The Ludlow-Pridoli interval is characterised by periods of global cooling denoted by variations in the
497 carbon cycle, a positive excursion of δO^{18} and a fall in sea level [91,12]. This time interval of cold climate
498 is known as the Middle Ludfordian Glaciation [91]. According to [12], the fall in sea level result of the
499 glacial event would have reconfigured the coastlines, leaving a narrower Rheic Ocean between Southern
500 Laurasia and Northwest Gondwana. These conditions provided new emerging areas that would favour
501 the dispersion of spores and would have functioned as suitable substrate (“soils”) with new reserves of
502 nutrients, favouring the spreading habitats, and the consequently expansion of early land plants.
503 Furthermore, the facies of Rinconada Formation fossil assemblage are interpreted as an inner marine
504 platform [90], as well as the Lipeón Formation facies are interpreted as marginal marine environments
505 [92]. Compared with the Pridolian fossil record of South Laurasia [15,70], most of the plant fossil
506 assemblages occur in coastal marine deposits. This could explain the distribution of Pridolian flora
507 between South Laurasia and Northwest Gondwana across the Rheic Ocean. The diversification of the flora
508 during the regressive events would have been accentuated during the Pridoli, where a rapid climate change
509 occurs from the cold conditions of the Ludfordian to super-greenhouse conditions [93]. The warm
510 temperatures have favoured the expansion and diversification of early land plants, denoted by an increase
511 in the diversity of trilete spores producers [12]. Probably, the flora content of the Rinconada Formation
512 results from the expansion towards the southernmost areas during the Pridolian, resulting from the
513 progressive increase of the temperatures in extreme green-house conditions conforming part of the Initial
514 Plant Diversification and Dispersal Event [11]. This paleoclimatic event, together with a wide dispersal
515 capacity of the flora might have allowed it to populate these areas according to [9] and [13].

516

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755

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761 materials. J.A.A., C.K. and A.R.B revised the manuscript. All the authors wrote the manuscript.

762 **Figure legends**

763 **Figure 1.** Map of the distribution of the Rinconada Formation at the Chica de Zonda Range showing its geographical
764 distribution, the upper and lower contacts and the distribution of the olistoliths. Red star shows the place where
765 samples were collected.

766

767 **Figure 2.** Detailed stratigraphic column of the Rinconada Formation where the plant fossils were found, at the
768 Chica de Zonda Range locality. PD, piedmont deposits. Scale in the graphic.

769

770 **Figure 3.** a-c *Aberlemnia caledonica*. a, Specimen PBSJ-1770. c, specimen PBSJ-1771. b, detail drawing of a
771 showing the last section of the subtending axe and the sporangium-axis concave junction (yellow arrow). d, e
772 *Cooksonia paranensis*. d Specimen PBSJ-1766 showing the compression. e, drawing of d, showing the sporangium-
773 axis junction (red arrow) and the sporangial chamber (yellow arrow). f-h *Cooksonia pertoni*. f-g specimens
774 PBSJ1767 and PBSJ-1768 showing a coalified trumpet-shape sporangium. h, drawing of g, showing the sporangial
775 chamber (red arrow) and the operculum (yellow arrow). i, j *Cooksonia cambrensis*. i, specimen PBSJ-1769 showing
776 the junction sporangium-axis (red arrow). j, drawing of the specimen PBSJ-1769 reconstructing the missing section
777 of the sporangium (dotted line). Scale bars: 1 mm.

778

779 **Figure 4.** a-b. *Salopella marcensis*. a, coalified compression of specimen PBSJ-1763. b, detail of sporangia. c-e
780 *Steganotheca striata*. c, general aspect of specimen PBSJ-1765. d, detail of the top of the sporangia. e, drawing of
781 d showing the apical plateau broken (yellow arrow) and two possible striations (red arrow). f, *Isidrophyton* sp.
782 coalified impression of specimen PBSJ-1772 with two terminal sporangia (yellow arrow). Scale bars: 1 mm.

783 **Figure 5.** a-c. *Caia langi*. a, general aspect of the specimen PBSJ-1773 showing the isotomously
784 bifurcation (yellow arrow). b, detail of the sporangium. c, drawing of b, showing the sporangium and four
785 conical emergencies at the apex (yellow arrows). d, *Hostinella* sp. specimen PBSJ-1764, notice the
786 isostomously branching axes (yellow arrow). e-f, Morphotype A. e, coalified compression of specimen
787 PBSJ-1775. f, drawing of e, showing the two sporangial-shaped structures (yellow arrows). g-h,
788 Morphotype B. g, coalified compression of specimen PBSJ-1774. h, drawing of g, showing the bifurcation
789 (red arrow) and the conical emergence at the apex of the sporangium (yellow arrow).

790 **Figure 6.** a. General view of the Rinconada Formation outcrops, showing the matrix (red arrow) and the
791 olistoliths (white arrows). b. detail of a, showing the bearing fossil strata (yellow scheme) and the olistolith
792 over the matrix (red arrow). c, detail of syndimentary deformation (red arrow). d, orientation of the
793 fossil plants (yellow arrows). e-f, *Skalograptus parultimus* found in the same strata of the fossil plants. g,
794 detail of the degree of fragmentation of the plant fossil assemblage and mica size (yellow arrows). h, trace
795 fossils found in the same facies of the fossil plant strata, classified as *Gordia* isp. i, interpretation of the
796 process that preserved together plants fossil and graptolites.

797 **Figure 7.** Palaeogeographic reconstruction of the continents during the interval Ludlow-Pridoli. Map
 798 showing the distribution during, Ludlow (red star) and Pridoli (blue star), fossil assemblages and the
 799 Rinconada Formation fossil plants strata. NL = North Laurussian unit; K = Kazakhstan unit; NEG =
 800 Northeast Gondwana unit; SL-NWG = South Laurasia-Northwest Gondwana unit. Modified from [94]
 801 and [12].

802 **Table 1.** First appearance of each taxa described in this work.

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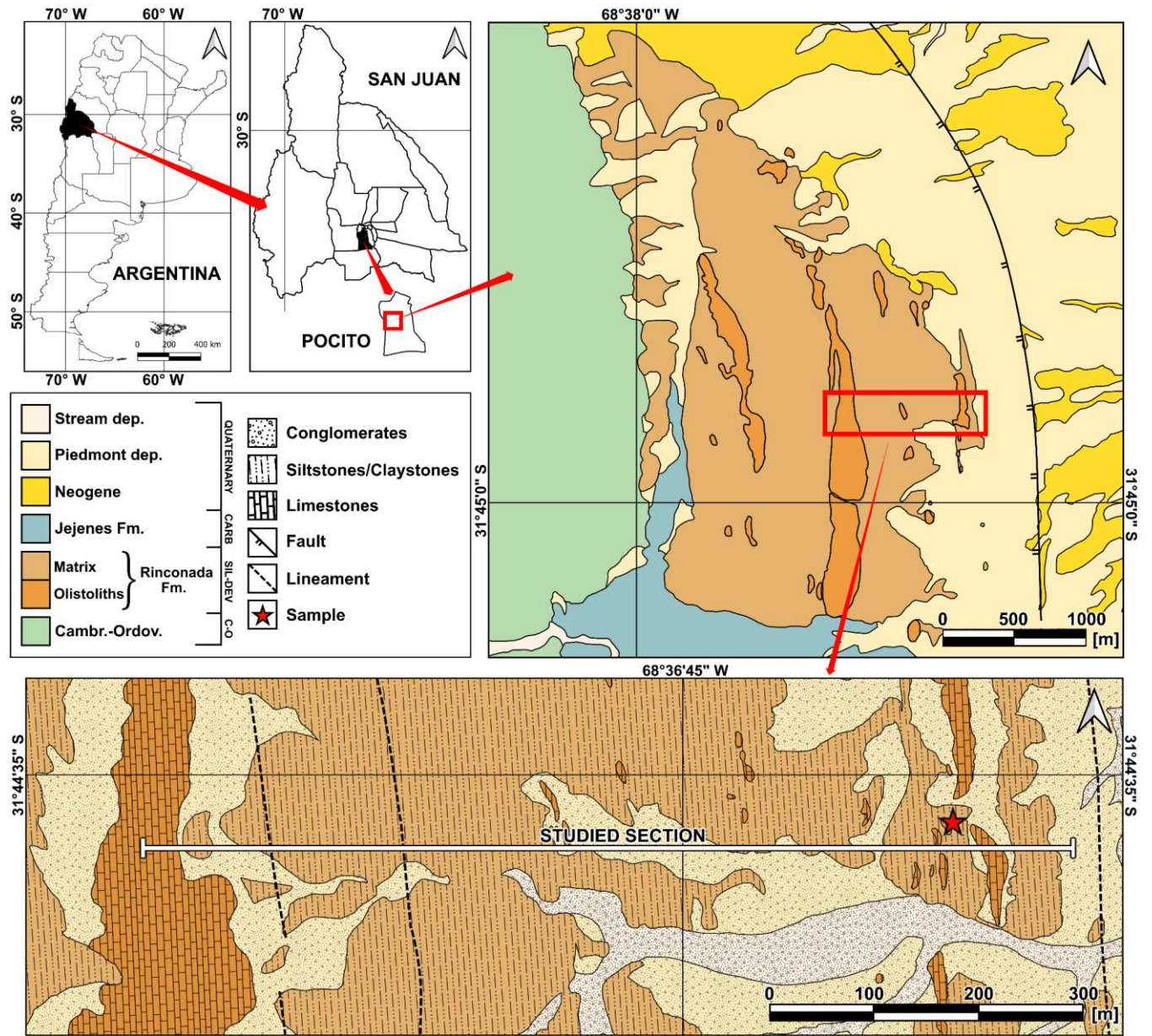
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Species	Age	Locality/Formation	Reference
<i>Aberlemnia caledonica</i>	early Lochkovian	Paraná Basin	Gonez & Gerrienne. [65]
<i>Cooksonia paranensis</i>	early Lochkovian	Ponta Grossa Formation/ Paraná Basin	Gerrienne et al. [68]
<i>Cooksonia pertoni</i>	Pridoli	Anglo-Welsh Basin (Ludford Corner, Ludlow)	Rogerson et al. [26]
<i>Cooksonia cambrensis</i>	Pridoli	Anglo-Welsh Basin (Freshwater East, Pembrokeshire)	Edwards. [23]
<i>Salopella marcensis</i>	Pridoli	Anglo-Welsh Basin (Perton Lane, Hereford)	Fanning & Edwards. [64]
<i>Steganoteca striata</i>	Pridoli	Anglo-Welsh Basin (Capel Horeb, Powys)	Edward & Rogerson. [63]
<i>Caia langi</i>	Pridoli	Rushall Beds/Downton Castle Sandstone Formation	Fanning et al. [24]
<i>Isidrophyton</i> sp	mid-Lochkovian-latest Pragian	Villavencio Formation	Edwards et al., [34]
<i>Hostinella</i> sp	Ludlow-Pridoli	Lipeón Formation	Edwards & Rogerson. [63]

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810 **Competing interests:** The author(s) declare no competing interests.

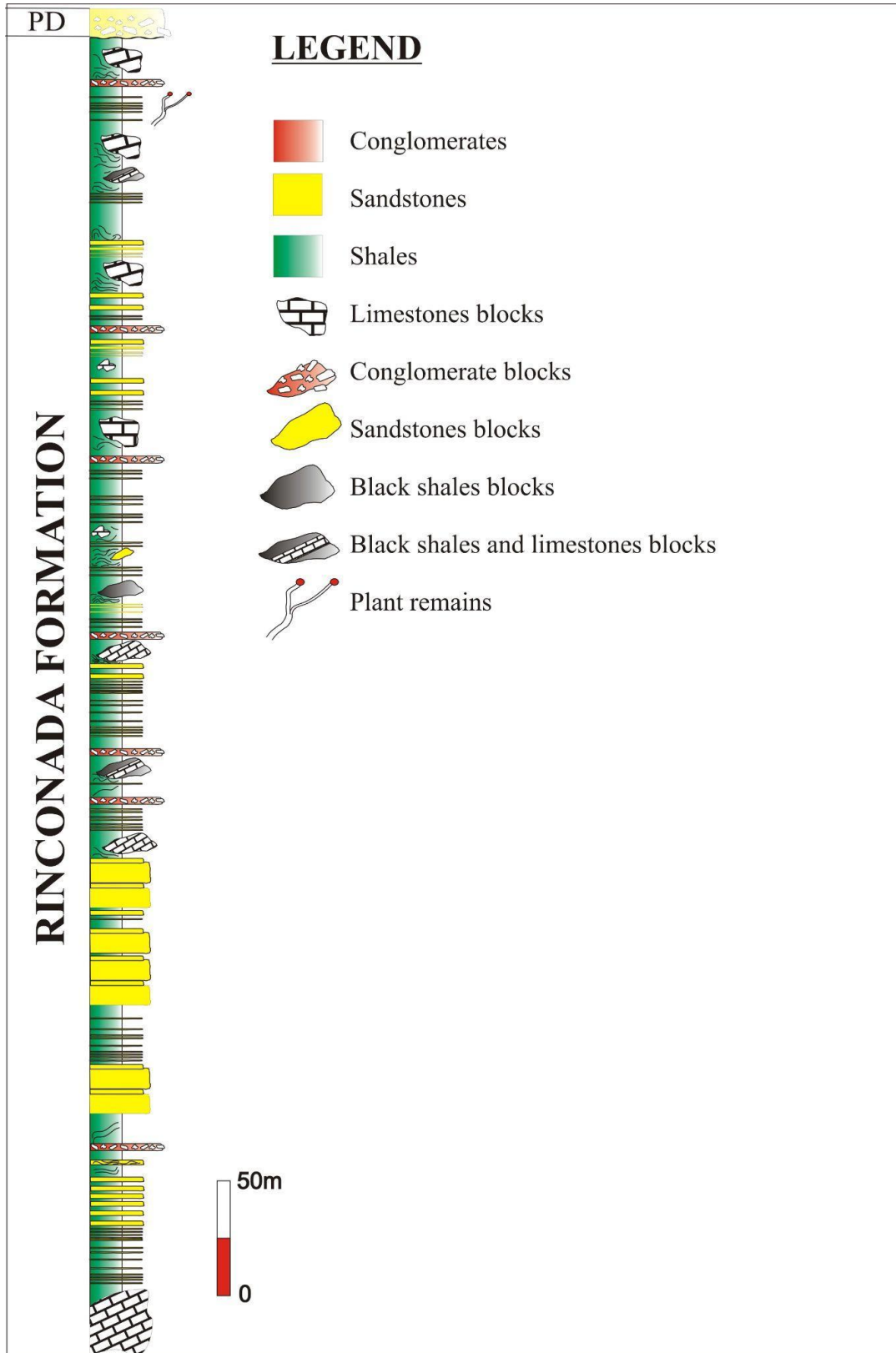
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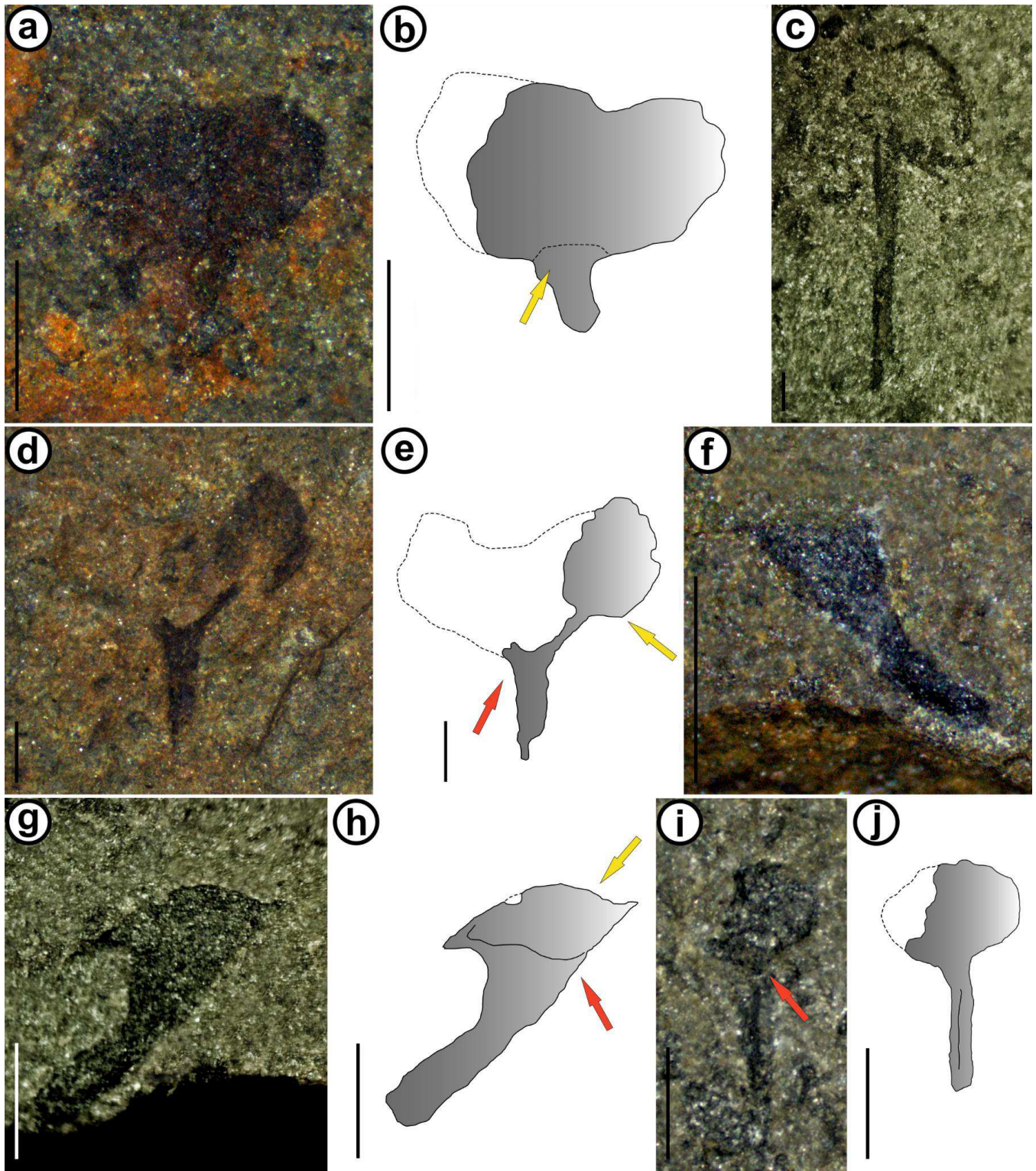
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816 Fig. 2

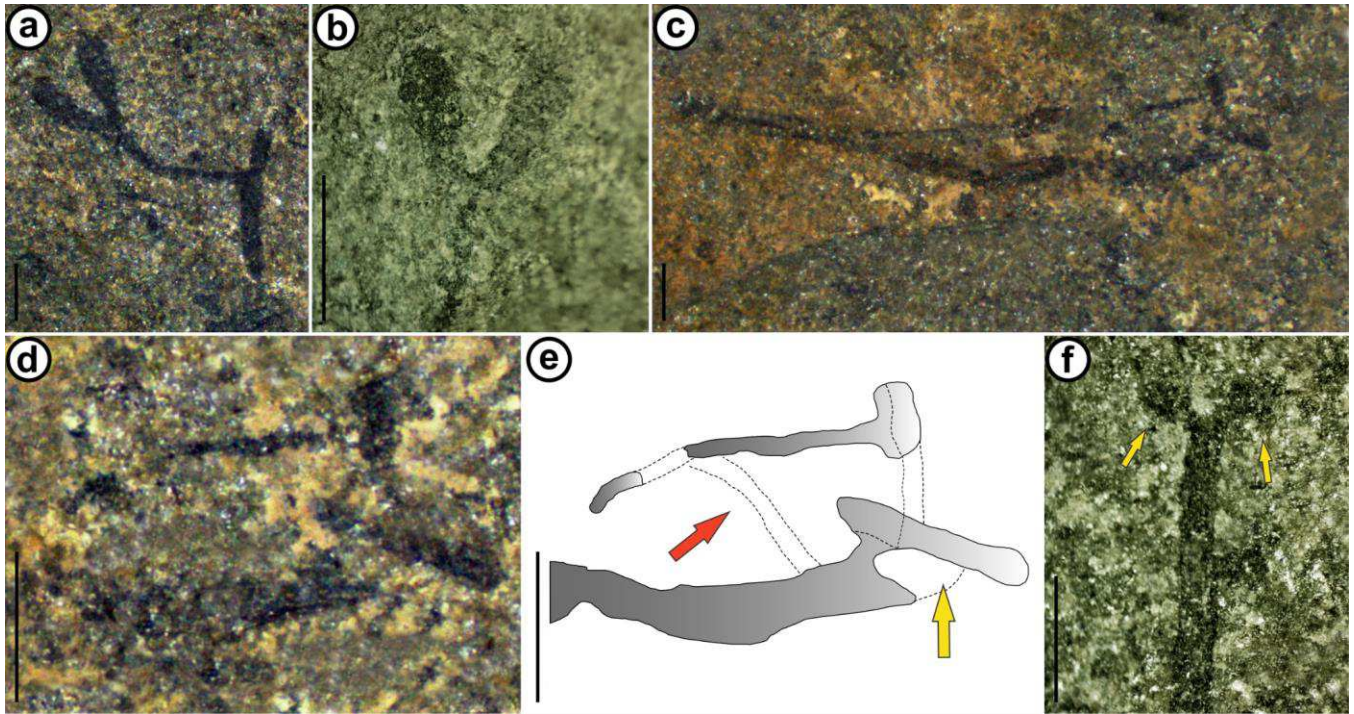


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818 Fig. 3

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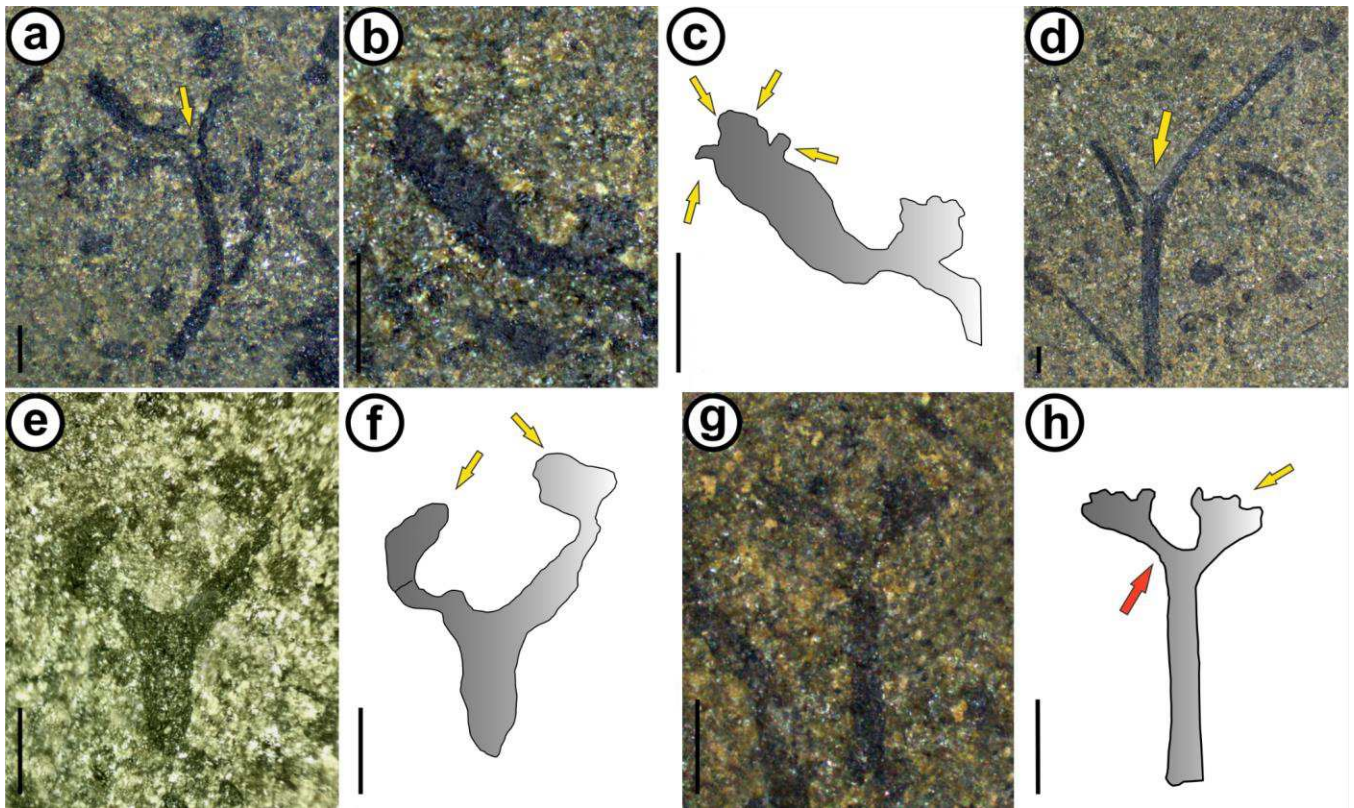
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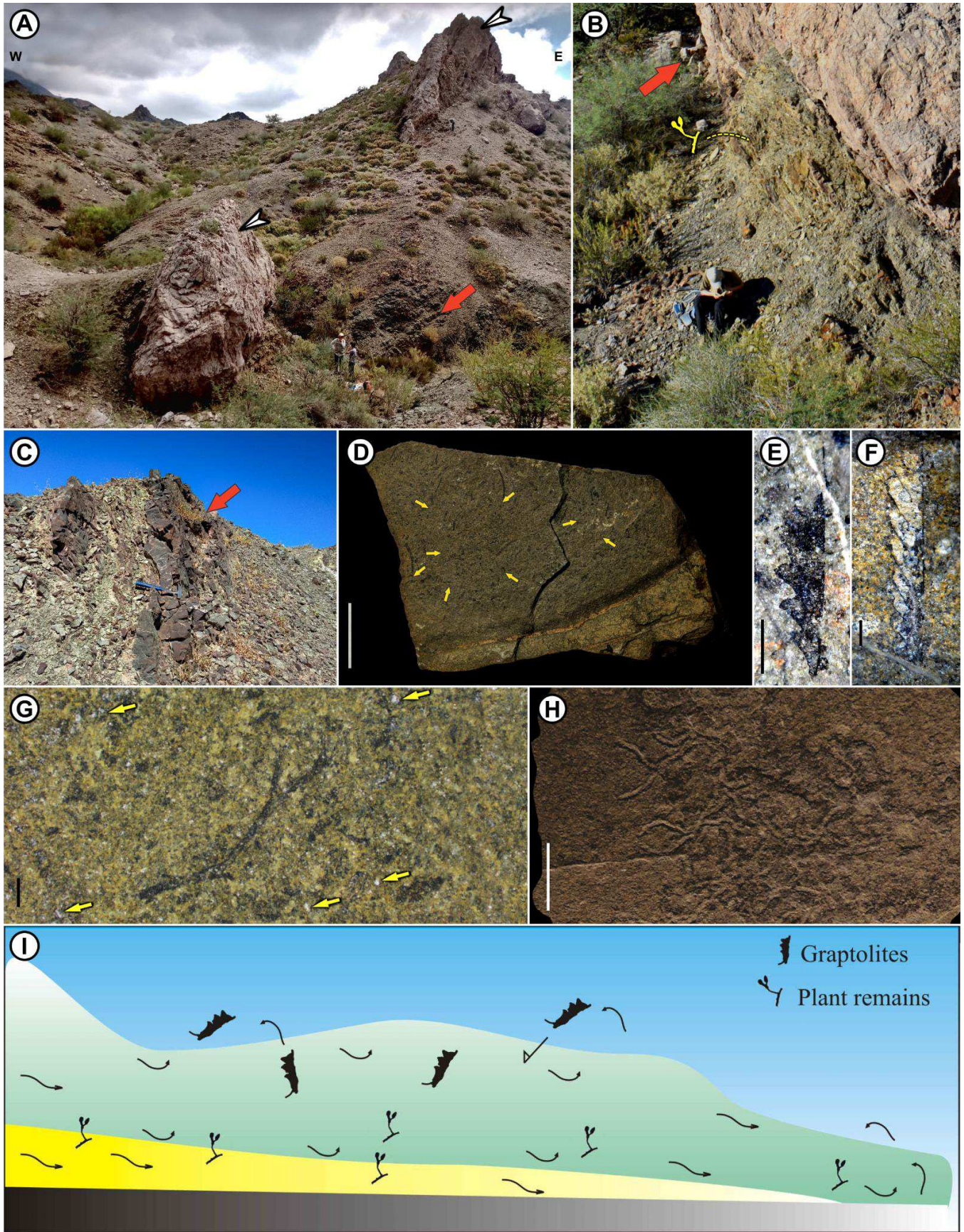
822 Fig 4

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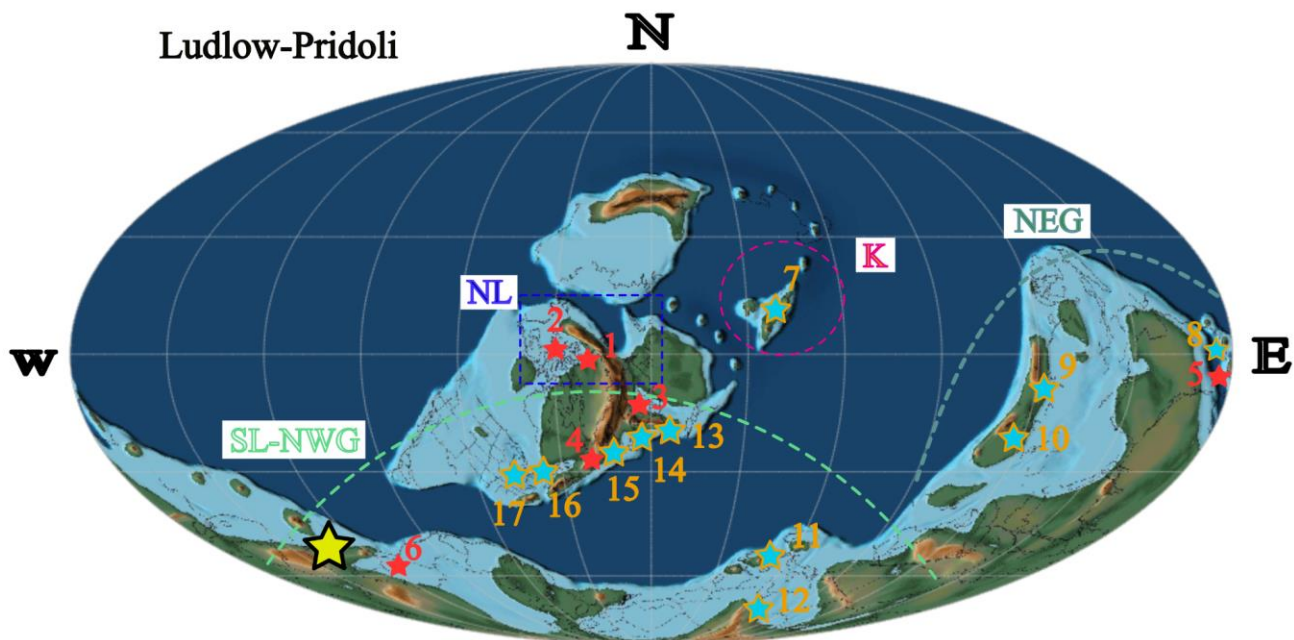
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825 Fig. 5



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827 Fig 6



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|---|---|
| <ul style="list-style-type: none"> ★ Ludlow Plant Data 1-Greenland 2-Canada (Bathurst Island) 3-Sweden 4-Welsh Basin 5-Australia (Victoria) 6-Bolivia ★ Pridoli Plant Data 7-Kazakhstan 8-Australia (Victoria) | <ul style="list-style-type: none"> 9-China (Xinjiang) 10-Vietnam 11-Czechia 12-Lybia 13-Ukraine 14-Poland 15-United Kingdom 16-Canada (Ontario) 17-United States (New York) ★ Rinconada Formation (Argentina) |
|---|---|