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1 *Lesleya* Lesquereux from the Pennsylvanian of the Iberian Massif: part of a
2 dryland megaflora from the Variscan orogen, northwestern Portugal

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25 **ABSTRACT**

26 The Carboniferous–early Permian plant genus *Lesleya* is a characteristic component of
27 ‘dryland floras’ that occupied a wide range of moisture-stressed, well-drained
28 environments in tropical regions of Euramerica. Fossil records of *Lesleya* are almost
29 exclusively found in basinal lowlands. For example, occurrences in Early
30 Pennsylvanian-age, seasonally-dry, parautochthonous deposits in basinal lowlands of
31 North America (e.g., Illinois Basin, USA), indicate that *Lesleya* lived in that region in
32 low altitude (lowland) paleoenvironments during dry climatic intervals. In this paper,
33 we document the first occurrence of *Lesleya* during the Carboniferous on the Iberian
34 Massif, in lower Gzhelian (Upper Pennsylvanian) strata of the Douro Carboniferous
35 Basin, in northwestern Portugal. This newly discovered occurrence includes a new
36 species, *Lesleya iberiensis* sp. nov., recognized on the basis of natural molds of leaves.
37 The Portuguese *Lesleya* fossils are from upland intramontane deposits and they occur
38 between coal-beds. Their fossil remains are preserved in mica-rich shales which were
39 deposited between sandstone-dominated fluvial and shale-dominated lacustrine
40 deposits, suggesting that this megaflora was deposited near freshwater bodies. These
41 new data provide evidence that this megaflora grew in mountain riparian environments
42 within the Variscan orogen, either in localized, well-drained areas or during drier
43 climatic intervals in the Late Pennsylvanian.

44

45 **Keywords:** *Lesleya*; megaflora; Iberian Massif; Variscan orogen; drylands; riparian
46 environments; intramontane basins.

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48

49

Introduction

Pennsylvanian-age ‘dryland floras’ include a diversity of terrestrial plants that occupied a wide range of moisture-deficient and well-drained environments within the Euramerican Floristic Province (here called Euramerica) (e.g., Falcon-Lang 2003; DiMichele et al. 2009, 2010; Falcon-Lang et al. 2009, 2011*a, b*; Bashforth et al. 2014). These dryland floras flourished wherever favorable climatic and edaphic conditions existed, particularly where habitats became dry enough to support such biomes during dry climate intervals (e.g., DiMichele et al. 2009, 2010; Falcon-Lang et al. 2011*b*; van Hoof et al. 2013; Bashforth et al. 2014). Pennsylvanian-age dryland plant communities are still poorly understood compared to biomes that colonized tropical wetland ecosystems (Falcon-Lang 2003; Falcon-Lang et al. 2011*a*). Fossil records for dryland plant communities are almost exclusively found in basinal lowlands (e.g., Leary and Pfefferkorn 1977; Leary and Trask 1985; DiMichele et al. 2009, 2010; Falcon-Lang et al. 2009; Bashforth et al. 2014).

Lesleya is an enigmatic member of ‘dryland (xerophilous–mesophilous) floras’ (generally xeromorphic) and is one of the indicator taxa used to assess soil dryness conditions in Pennsylvanian-age deposits (e.g., DiMichele et al. 2010; Falcon-Lang et al. 2011*a*; Bashforth et al. 2014). Fossils of *Lesleya* are mainly found in seasonally-dry basinal lowlands (e.g., Leary and Pfefferkorn 1977; Leary and Trask 1985; DiMichele et al. 2008, 2010; Falcon-Lang et al. 2011*a*; Bashforth et al. 2014). In North America, paleoecological studies on Pennsylvanian-age parautochthonous deposits have examined seasonally-dry floral assemblages containing conifers, cordaitaleans, and pteridosperms including foliage of *Lesleya* (e.g., Leary and Pfefferkorn 1977; Leary and Trask 1985; Plotnick et al. 2008, 2009; DiMichele et al. 2010). These floral

75 assemblages occur in basin-margin settings developed on drought-prone limestone
76 substrates in basinal lowlands and are preserved in clastic rocks deposited between coal-
77 beds (e.g., Plotnick et al. 2008, 2009; DiMichele et al. 2008, 2010). *Lesleya* is restricted
78 to the equatorial regions of Euramerica, where it occurs in Carboniferous and lower
79 Permian strata (e.g., Sellards 1908; Leary and Pfefferkorn 1977; Leary 1981; Wagner
80 2004; Leary and Trask 1985; Šimůnek 1996; Cleal and Thomas 2004; DiMichele et al.
81 2008, 2010). The megaf flora containing *Lesleya* is limited to lower Bashkirian (Lower
82 Pennsylvanian) strata in North America (e.g., Illinois Basin, USA), but it has a wider
83 paleogeographical distribution in Carboniferous–lower Permian strata of Europe (e.g.,
84 Leary and Pfefferkorn 1977; Leary and Trask 1985; Šimůnek 1996; DiMichele et al.
85 2008, 2010).

86 In this paper, we document the first occurrence of *Lesleya* in the Iberian Massif, on
87 the basis of leaf fossils recently found in lower Gzhelian (Upper Pennsylvanian) strata
88 of the Douro Carboniferous Basin (DCB), in northwestern Portugal (Fig. 1). The DCB
89 is an intramontane basin located adjacent to the Valongo Anticline in the Central Iberian
90 Zone of the Variscan orogen (e.g., Wagner 1983; Domingos et al. 1983; Correia et al.
91 2013). The development of intramontane basins such as the DCB was common during
92 the Variscan orogen (e.g., Wagner 2004; Cleal 2008; Wagner and Álvarez-Vázquez
93 2010; Bashforth et al. 2011) and such basins are well-documented in the Iberian Massif
94 (e.g., Wagner 1983; Pinto de Jesus 2001). While recognizing that our results do not
95 preclude the occurrence of *Lesleya* in a wide range of moisture-stressed environments,
96 in this paper we provide a better understanding of the ‘dryland floras’ in the Iberian
97 Massif, and we assess its significance for interpreting the paleoclimate, paleoecology
98 and paleoenvironment in that region during the Late Pennsylvanian.

99

100 **Geological background**

101

102 **Geographical and geologic setting**

103 The DCB (Fig. 1) occurs within the Douro-Beiras Carboniferous Trough (DBT),
104 which is located within the Central Iberian Zone, in the Iberian Massif of northwestern
105 Portugal. The DBT strikes northwest–southeast, and is 85 km in length with a width of
106 less than 1 km (e.g., Lemos de Sousa and Wagner 1983*a*; Pinto de Jesus 2001, 2003).
107 Within the DBT, there are several outcrops containing well-documented continental
108 Carboniferous strata, with ages ranging from Westphalian (Bolsovian–Asturian,
109 Moscovian, Middle Pennsylvanian) to Stephanian C (early Gzhelian, Late
110 Pennsylvanian). The DBT is generally interpreted as a pull-apart basin with a sinistral
111 strike-slip component (e.g., Pinto de Jesus 2001, 2003).

112 The basal strata of the DCB unconformably overlie lower Cambrian rocks of the
113 Schist-Greywacke Complex. The upper strata of the DCB are cut by a reverse fault that
114 placed lower–middle Paleozoic (Silurian–Devonian) formations of the Valongo
115 Anticline over strata of the DCB (e.g., Domingos et al. 1983; Lemos de Sousa 1984;
116 Wagner et al. 1984; Pinto de Jesus 2001, 2003).

117

118 **Tectono-sedimentary units and depositional environments**

119 The stratigraphic and sedimentological sequence of the DCB is comprised, from the
120 base to the top, of eight tectono-sedimentary units (TSU), some of which are related by
121 lateral facies variations (Fig. 2A). TSU units A2, B2, C2 and D2 represent the lateral
122 facies variations of TSU units A1, B1, C1 and D1, respectively (Pinto de Jesus 2001,
123 2003; Fig. 2A). The following descriptions are summarized from Pinto de Jesus (2001,
124 2003).

125 The basalmost unit, TSU A1, consists of alluvial fan debris characterized by flow-
126 dominated clastic rocks composed of red-brown or dark grey basal breccia deposits.
127 These deposits include interbedded polymictic conglomerates, generally with a massive,
128 matrix-supported texture and, more rarely, with clast-supported texture lacking well-
129 defined internal sedimentary structures. Clasts are angular and range from silt to boulder
130 (up to 2 meters) in size. Clast lithologies are very variable (shale, greywacke, granite,
131 greisen, gneiss, mica-schist, conglomerate and quartzite) and likely resulted from the
132 erosion of adjacent mountainous regions such as the Valongo Anticline and surrounding
133 areas underlain by the Schist-Greywacke Complex. The basal breccia varies from
134 meters to decameters in thickness. The top of the basal breccia is composed of dark grey
135 to black mudstones, with small angular quartz clasts.

136 TSU B1 contains phytogenic and siliciclastic deposits that occur along the base of
137 the DCB, and consist of alternating strata of shale, sandstone and coal beds. The shale
138 strata display parallel lamination, along which the fossil plants occur. The fossiliferous
139 strata preserve a highly diverse macroflora. At the top of the TSU B1 sequence, the
140 phytogenic and siliciclastic strata are overlain by fluvial deposits.

141 TSU C1 is dominated by fluvial deposits with well-defined erosive lower contacts
142 that cut the underlying strata, including the phytogenic and siliciclastic deposits. These
143 deposits represent a fluvial system complex with vertical accretion composed of
144 interbedded conglomerates, sandstones and siltstones, with pelitic layers more prevalent
145 near the top of the sequence.

146 TSU D1 consists of phytogenic and siliciclastic deposits that occur at the top of the
147 DCB sequence. They were deposited above the fluvial sequences of TSU C1, are very
148 fossiliferous, and consist of alternating beds of coal, siltstone, mudstone and
149 conglomerate. The more pelitic lithofacies generally display either a parallel internal

150 lamination or a more massive texture. These sequences may also contain rare lenticular
151 bodies composed of conglomerate or coarse sandstone.

152 TSU A2 is characterized by deposits of intra-Carboniferous breccia that are in fault
153 contact (a reverse fault) with older Carboniferous and Silurian strata within the DCB.
154 Most of the breccia deposits exhibit a clast-supported texture, although a matrix-
155 supported texture is observed locally. The breccia consists of clasts of quartzite, shale,
156 quartz and more rarely sandstone in a silty-clay matrix. Clasts can range up to 30 cm in
157 length and typically are subangular to subrounded. The deposits vary in thickness from
158 a few meters to about 50 meters.

159 TSU B2 consists of phytogenic and siliciclastic deposits of the base of the DCB.
160 Their characteristics are very similar to the observed in the TSU B1.

161 TSU C2 is dominated by fluvial deposits, whose structure and composition are very
162 similar to that of TSU C1.

163 TSU D2 consists of phytogenic and siliciclastic strata that are the youngest deposits
164 preserved in the DCB and have a stratigraphy similar to that of TSU D1.

165

166 **Dryland megafloral assemblages, non-marine faunal associations, and**
167 **stratigraphic age**

168 The DCB strata preserve a diverse fossil megaflora that establishes an early
169 Stephanian C (early Gzhelian) age and indicates a continental intramontane syntectonic
170 environment of deposition (e.g., Wagner 1983; Wagner and Lemos de Sousa 1983;
171 Lemos de Sousa and Wagner 1983*a, b*; Domingos et al. 1983; Pinto de Jesus 2001,
172 2003).

173 In previous studies of the DCB fossil megaflora, Lemos de Sousa and Wagner
174 (1983*b*) emphasized the occurrence of *Pseudomariopteris* cf. *busquetii* (Zeiller) Danzé-

175 Corsin, cf. *Taeniopteris multinervia* Weiss and *Neuropteris ovata* Hoffmann var.
176 *pseudovata* Gothan and Sze. Those author's interpretations of the paleoenvironmental,
177 paleoecological and paleogeographic conditions for the DCB strata were based on the
178 strata being adjacent to mountainous regions, such as Valongo Anticline, and on the
179 occurrence of dryland (xerophilous–mesophilous) floras in the Iberian Massif. Previous
180 descriptions of the DCB dryland floras also identified the conifers *Ernestiodendron*
181 *filiciforme* (Von Schlotheim pars) Florin, cf. *Culmitzschia frondosa* (Renault) var.
182 *zeilleri* (Florin) Clement-Westerhof and *Culmitzschia parvifolia* (Florin) Clement-
183 Westerhof and the cordaitales *Dicranophyllum gallicum* Grand'Eury and
184 *Dicranophyllum lusitanicum* (Heer) Lima (Wagner 1983; Wagner and Lemos de Sousa
185 1983; Domingos et al. 1983).

186 In addition to these floras, paleozoological studies (Eagar 1983) documented
187 occurrences of the non-marine bivalves *Anthraconaia lusitanica* Teixeira and
188 *Anthraconaia* (?) *altissima* Eagar in the DCB. These bivalves indicate freshwater
189 conditions, which are common in intramontane limnic basins (e.g., Eagar 1983, 1987;
190 Eagar and Belt 2003; Pleijel et al. 2004; Racheboeuf et al. 2002, 2008; Charbonnier et
191 al. 2008; Schultze 2009; Tibert et al. 2011).

192

193 **Material and methods**

194

195 The *Lesleya* fossils reported herein are natural molds of leaves collected from
196 recently discovered, early Gzhelian-age (Late Pennsylvanian) outcrops in the DCB,
197 located within the São Pedro da Cova region of northwestern Portugal (Fig. 1; outcrop
198 location: 41°09'42.56''N; 08°30'14.68''W). These outcrops correspond to the upper
199 part of TSU B2 in transition to TSU C2 of the DCB stratigraphy (Fig. 2A). The *Lesleya*

200 fossils occur at various stratigraphic levels, within compressed grey shales that are
 201 interbedded with sandstone deposits of variable thickness (Figs. 2B and 3). The grey
 202 shales are composed of two distinct lithofacies: mica-rich shales that contain abundant
 203 detrital muscovite and clay-rich shales with more pelitic features. Both lithofacies are
 204 reasonably well exposed and contain a variety of fossils: the mica-rich shales contain
 205 various megafloral elements (e.g. *Lesleya* and *Cordaitea*), whereas the clay-rich shales
 206 contain non-marine bivalves (*Anthraconaia*) and insects (blattodeans) (Figs. 2B and 3).

207 The *Lesleya* leaves were found in association with leaves of *Cordaitea*. An associated
 208 flora, consisting of species such as *Neuropteris ovata* ?var. *pseudovata* Gothan and Sze,
 209 *Linopteris neuropteroides* (Gutbier) Potonié, *Dicksonites plukenetii* (Sternberg) Sterzel,
 210 *Pecopteris cyathea* (Von Schlotheim) Brongniart, *Pseudomariopteris cordato-ovata*
 211 (Weiss) Gillespie et al. ex Krings and Kerp, *Sphenophyllum oblongifolium* (Germar and
 212 Kaulfuss) Unger, *Calamites suckowii* Brongniart, *Callipteridium* (*Eucallipteridium*)
 213 *gigas* (Gutbier) Weiss, *Acitheca polymorpha* (Brongniart) Schimper and *Asterophyllites*
 214 *equisetiformis* (Von Schlotheim) Brongniart. This fossil plant assemblage occurs in
 215 association with lacustrine deposits containing non-marine bivalves that are probably
 216 *Anthraconaia lusitanica* Teixeira (Figs. 2B and 3).

217 The associated flora and fauna were previously identified and described by Wagner
 218 (1983, 1984) and Eagar (1983) in lower Gzhelian strata of the Iberian Massif and in the
 219 DCB (Wagner 1983; Eagar 1983; Lemos de Sousa and Wagner 1983a, b, 1985a, b;
 220 Wagner and Lemos de Sousa 1983).

221 Our report of *Lesleya* in the DCB is founded on four natural molds of leaves. The
 222 fossils were carefully cleaned either manually or mechanically with a vibro-tool. To
 223 help interpret its original structure, a latex cast (i.e., a positive replica) was made of the
 224 holotype. In order to preserve the integrity of the original specimen, its surface was

coated with Paraloid B-72 dissolved in a dilute acetone solution before the latex was applied. Before being photographed, the latex cast was coated with magnesium oxide to enhance details. The holotype is stored in the Museum of Natural History and Science of the University of the Porto (UP-MHNFPC), Porto, Portugal. The three paratypes are stored in the Czech Geological Survey (ZS), Prague, Czech Republic.

Systematic paleontology

Division Gymnospermophyta

Class Pteridospermopsida Oliver and Scott, 1904

(or Class Cycadopsida Brongniart, 1843)

Order and Family unknown

Genus *Lesleya* Lesquereux, 1880

Remarks: *Lesleya* is restricted to equatorial regions of Euramerica where it ranges from the Carboniferous to early Permian (Table 1, Fig. 4). The geographic distribution of *Lesleya* is more widespread in Europe, where occurs mainly in Upper Pennsylvanian and lower Permian strata. In North America, *Lesleya* is found mainly in Lower Pennsylvanian strata, but some occurrences in lower Permian deposits have been documented (e.g., Leary and Pfefferkorn 1977; Leary and Trask 1985; Šimůnek 1996; DiMichele et al. 2008, 2010).

Lesleya contains 11 previously described species (e.g., Šimůnek 1996; Fig. 4, Table 1). Most species were established on the basis of fragmentary material (e.g., Lesquereux 1879 [atlas: pl. 25, figs. 1–3], 1884; Zeiller 1890; Remy and Remy 1975, 1978). Species are differentiated mainly on the basis of leaf characters (see Table 1), such as: leaf shape

including type of apex and base shape; type of margin (e.g., entire or undulate margin); and venation pattern, including type of venation (e.g., simple/pinnate or dichotomous; curved or sinuous), number of lateral veins per cm on margin, and angles between midvein/lateral vein and lateral vein/margin (e.g., Leary and Pfefferkorn 1977; Leary 1980; Šimůnek 1996). Where organically preserved material is available, cuticular features also are useful for differentiating species of *Lesleya* and assessing their phylogenetic relationships (e.g., Florin 1933; Šimůnek 1996). Here, we describe a new species of *Lesleya* recognized on the basis of leaf fossils from lower Gzhelian (Upper Pennsylvanian) deposits in Portugal. The new Portuguese species is most similar to *Lesleya cheimarosa*, a geologically older congener described by Leary and Pfefferkorn (1977) from lower Bashkirian (Lower Pennsylvanian) deposits in the Illinois Basin, USA, and known by very complete leaf specimens, including the holotype (see Leary and Pfefferkorn 1977, pl. 8, figs. 1, 2; Leary and Trask 1985, pl. 1, fig. 2).

The higher level affinities of *Lesleya* are uncertain. Its familial and ordinal affinities are unknown (e.g., Taylor et al. 2009), whereas at the class level *Lesleya* variously has been assigned to, or allied with, both the Cycadopsida and Pteridospermopsida (Remy and Remy 1977, 1978; Leary 1990). A relationship between *Lesleya* and Permian–Mesozoic cycads has been suggested on the basis of their similar foliage (e.g., Florin 1933; Remy and Remy 1978; Leary 1990, 1993, 1998; Wagner 2004; Taylor et al. 2009). *Lesleya* also has been suggested as a probable ancestor to cycads (Remy and Remy 1978; Leary 1990; Taylor et al. 2009). Florin (1933) regarded *Lesleya* as a primitive gymnosperm, however, it is not closely related to Permian seed ferns or Mesozoic gymnosperms based on morphological and epidermal features. In addition, Wagner (2004) proposed *Lesleya* as the tropical ancestor of the south temperate, Permian *Glossopteris* Brongniart. That ancestral affinity seems unlikely considering

275 differences between the two groups in their venation patterns (anastomosed/reticulated
276 venation in *Glossopteris* versus pinnatifid/pinnate venation in *Lesleya*) and reproductive
277 organs (e.g., Leary 1990, 1993, 1998).

278

279 ***Lesleya iberiensis* sp. nov.**

280 (Figs. 5 and 6)

281

282 **Etymology:** The specific epithet refers to the discovery of this species in the Iberian
283 Massif.

284 **Holotype:** Natural mold of a nearly complete, large leaf broken in three pieces
285 (separately numbered as UP-MHNFCEP-094951/-094952/-094954) and preserved in
286 grey shales (Fig. 5).

287 **Paratypes:** The three paratypes also are natural molds of leaves preserved in grey
288 shales (Fig. 6): ZS 507 and ZS 508 are the lower parts of two different leaves,
289 whereas ZS 510 is a nearly complete, but poorly preserved leaf.

290 **Type locality:** Outcrops located in DCB, São Pedro da Cova region, northwestern
291 Portugal (Fig. 1).

292 **Type horizon and age:** Compressed dark grey, mica-rich shale lithofacies; TSU B2
293 (Figs. 2B and 3). Early Gzhelian or Late Pennsylvanian in age.

294 **Diagnosis:** Simple leaves, maximum dimensions about 225 mm long and 50 mm wide;
295 margins strongly arched towards the leaf base; base long and narrow (cuneate); margin
296 entire; midvein broad, 1.0 to 3.0 mm wide; lateral veins fork once or twice; lateral veins
297 oblique, slightly curved (arched) with a 7° to 15° angle at the midvein and 5° to 35°
298 angle on margin; 10–13 veins per cm on margin. See Table 1 for more detailed
299 comparisons with other named congeners.

Description: The holotype (Fig. 5) is a nearly complete leaf missing its tip and an irregular portion midway along its length. The leaf has a maximum width of 50 mm and its preserved length is 225 mm; when intact, its total length would have been about 250 mm. The lateral veins are widely spaced (11–13 veins per cm on margin) and fork once or twice. They are oblique, slightly curved or arched from the midvein to the margin and, as measured along the mid-length of the leaf, form angles of 7° to 15° with the midvein and 30° to 35° with the margin. The midvein is broad (1.0–2.5 mm wide) and bears several longitudinal striations. The paratypes ZS 507a, b (Fig. 6A, B) and ZS 508 (Fig. 6D) are lower parts of two leaves, with preserved dimensions of 100 mm long and 44 mm wide for ZS 507 and 70 mm long and 23 mm wide for ZS 508. In both specimens, the lateral veins are oblique, curved from the midvein to the margin, spaced 10–12 veins per cm on margin and fork once or twice, forming angles of 9° to 14° with the midvein and 5° to 18° with the margin. The midveins are 1–3 mm wide. The third paratype, ZS 510 (Fig. 6C), is a nearly complete, but poorly preserved leaf, >170 mm long and 44 mm wide. The lateral veins are oblique, slightly curved from the midvein to the margin, spaced 10–12 veins per cm on margin and fork once or twice, forming angles of 8°–12° with the midvein, and 16°–27° with the margin. The midveins are 2–3 mm wide.

All four examples of *Lesleya iberiensis* sp. nov. display strongly arched margins with a narrowing at the leaf base (i.e., cuneate-shaped leaf base; see different types of leaf bases in Hickey 1977: appendix fig. 4), a long base, and a broad midvein that increases in width towards the leaf base and is longitudinally striated. Although the apex is missing from all four specimens, we restore it as having a lanceolate outline (see reconstruction drawing of holotype in Fig. 5C).

324 **Remarks and comparisons:** The Portuguese material displays morphological features
325 typical of the genus *Lesleya*. According to the original generic diagnosis from
326 Lesquereux (1880, p. 142), *Lesleya* is characterized by the following combination of
327 features: “Pinnae simple, very entire, sublanceolate, gradually narrowing towards the
328 base, traversed by a thick costa effaced under the apex; veins oblique, curved, equal,
329 repeatedly dichotomous”. Subsequent treatments by Leary and Pfefferkorn (1977) and
330 Leary and Trask (1985) described *Lesleya* foliage as simple, large and wide leaves,
331 generally 10 cm in width and with a length that can exceed 30 cm (although there also
332 are some smaller forms from the Czech Republic; e.g., Šimůnek 1996), having a
333 lanceolate/sublanceolate apex and arched margins with a narrowing at the well-
334 developed leaf base, a broad midvein, and oblique lateral veins that are curved, and
335 equally repeatedly dichotomous.

336 The Portuguese material also is comparable to *Megalopteris* (Dawson) Andrews,
337 1875. This is due to the fact that *Megalopteris* and *Lesleya* foliage look very similar,
338 especially when preserved in a fragmentary state. Lesquereux (1880, p. 142) stated:
339 “This genus [*Lesleya*] is related by some of its characters to *Neuropteris* and by its
340 nervation of its fine species especially to *Megalopteris*”. *Megalopteris* and *Lesleya* both
341 have large and wide foliage, lanceolate/sublanceolate apexes and arched margins, a
342 broad midvein, and oblique lateral veins that are curved and equally repeatedly
343 dichotomous. Upper pinnules of *Megalopteris* fronds can display arched margins with a
344 narrowing at the pinnule base (e.g., Zeiller 1900, fig. 85) reminiscent of leaf bases in
345 *Lesleya*. Leary (1980, p. 30) characterized *Megalopteris* as follows: “Frond rugose,
346 rachis thick, striated, broadly winged, pinnae alternate, very oblique, acute at apex,
347 often an inch wide and six inches long, margin undulate; midrib disappearing before
348 reaching apex, veins numerous, very oblique, curved, forking thrice very obliquely”.

349 According to Leary (1980), *Lesleya* differs from *Megalopteris* in that *Lesleya* foliage
350 consists of simple leaves, whereas *Megalopteris* is a compound leaf or pinnae
351 comprised of three or more lobes or pinnules (see Leary and Pfefferkorn 1977, fig. 8;
352 pls. 6–8; Leary and Trask 1985, pl. 1; see also additional descriptions by Leary and
353 Pfefferkorn 1977 and Cross et al. 2005). Leary (1980, p. 30) also stated, “...when a
354 complete leaf or frond is preserved, or even a fragment sufficient to observe the division
355 into two or more lobes, generic separation is quite simple”. The Iberian leaf fossils
356 reported herein are sufficiently intact to demonstrate the absence of any *Megalopteris*-
357 like division; that supports our assignment of these specimens to *Lesleya*. Florin (1933)
358 was able to distinguish stomata of two genera based on cuticular material. Cuticular
359 features are uninformative for establishing the generic identity of *Lesleya iberiensis* sp.
360 nov., because no organically preserved (cuticular) material is available.

361 Among the 11 previously described species in the genus, *Lesleya cheimarosa* Leary
362 and Pfefferkorn 1977 from the early Bashkirian (Early Pennsylvanian) of the Illinois
363 Basin, USA (see Leary and Pfefferkorn 1977, pl. 8, figs. 1, 2; Leary and Trask 1985, pl.
364 1, fig. 2) is most similar to *Lesleya iberiensis* sp. nov. Both species are known by very
365 complete leaves that have entire margins, are similar in size and shape (i.e., large and
366 wide leaves, have strongly arched margins that narrow towards a cuneate-shaped base)
367 and have dichotomous venation. The holotype leaf of *L. cheimarosa* was described by
368 Leary and Pfefferkorn (1977, p. 25) as follows: “Simple leaf of considerable size, about
369 20 cm long and 4 cm wide, lanceolate with acute to attenuate tip. Base long and narrow
370 (acuminate). Margin entire, venation pinnate, midrib thick, 0.7 to 2.0 mm wide; lateral
371 veins fork once or twice; lateral veins S-shaped with a 10° to 20° angle at the midvein,
372 30° to 70° angle in center, and 40° to 70° angle on margin; 24 to 36 veins per cm on
373 margin”. Based on that description, *L. iberiensis* sp. nov. differs from *L. cheimarosa* in

374 details of the lateral veins. Specifically, *L. cheimarosa* displays S-shaped (sinuous) and
375 numerous (24–36) lateral veins (see Leary and Pfefferkorn 1977, fig. 8C, F, pp. 22, 23;
376 pl. 6, fig. 5; pl. 8, figs. 1, 2; see also description of Leary 1980), whereas *L. iberiensis*
377 sp. nov. has lateral veins that are slightly curved and fewer in number (10–13) and more
378 widely spaced (see Table 1). More detailed comparisons among all 12 congeners are
379 presented in Table 1.

380

381 Discussion

382

383 Living habitat, deposition and preservation of *Lesleya* in intramontane basins from 384 the Iberia Massif

385 In Lower Pennsylvanian rocks in the Illinois Basin, USA, *Lesleya* occurs in
386 parautochthonous deposits in seasonally-dry, basinal lowlands (e.g., Plotnick et al.
387 2008, 2009; DiMichele et al. 2008, 2010). In that region, *Lesleya* lived in low altitude
388 environments during intervals of relatively dry climate (e.g., DiMichele et al. 2008,
389 2009, 2010). In the Iberian Massif, the Late Pennsylvanian-age *Lesleya* described herein
390 is preserved in immature shales that are in gradational contact with sandstone deposits
391 (Figs. 2B and 3). These DCB strata represent deposition at more upland elevations and
392 occur in areas adjacent to mountainous regions, such as the Valongo Anticline located
393 in the Central Iberian of the Variscan orogen (e.g., Wagner 1983; Domingos et al. 1983;
394 Correia et al. 2013). These strata previously have been shown to be syntectonic,
395 siliciclastic, intramontane deposits resulting from the erosion of surrounding areas (e.g.,
396 Wagner 1983; Domingos et al. 1983; Pinto de Jesus 2001; Figs. 1 and 7). Moreover, the
397 frequent and cyclic occurrence of sandstone deposits in the DCB (described as TSU
398 C1/C2), including those occurring between the *Lesleya* deposits within TSU B2 (Figs. 2

399 and 3), indicate that this megaflora was associated with fluvial-dominated environments
400 (Figs. 1 and 7). This evidence indicates that *Lesleya* grew in riparian environments in
401 mountainous regions within the Variscan orogen during the Late Pennsylvanian.

402

403 **Interpretation of the climate, vegetation ecology and lacustrine depositional**
404 **environments in DCB**

405 In lower Bashkirian (Lower Pennsylvanian) strata of North America, *Lesleya* has
406 been interpreted as part of a seasonally-dry (= dryland) flora (e.g., DiMichele et al.
407 2010; Falcon-Lang et al. 2011a; Bashforth et al. 2014). The Portuguese *Lesleya*
408 outcrops occur between coal-bed strata in TSU B2 (Fig. 2A). The presence of *Lesleya* in
409 discrete horizons in the Iberian Massif may indicate those plants were growing in
410 localized, drier or well-drained conditions. An alternative interpretation to this scenario
411 is that deposition and preservation of *Lesleya* and possibly other components of the
412 associated flora in the DCB occurred during intervals of drier and less humid climate
413 within the region.

414 In the Portuguese outcrops that contain *Lesleya*, the abundance of
415 pteridosperms/ferns (the most common genera are *Pecopteris*, *Sphenopteris* and
416 *Callipteridium*) and coniferopsids (e.g., *Cordaite*s) indicates that the latter taxonomic
417 groups dominated the resident floral assemblages. Other groups, such as sphenopsids
418 (e.g., *Sphenophyllum*, *Calamites* and *Asterophyllites*) occur less frequently, although
419 they are locally common in the DCB strata, whereas lycopsids and *Lesleya* are very
420 rare. The conifers *Ernestiodendron* and *Culmitzschia* and the cordaitale *Dicranophyllum*
421 have not been documented in the new *Lesleya* outcrops, but they occur commonly in the
422 DCB, in particularly in São Pedro da Cova region.

423 The *Lesleya* deposits are interlayered with lacustrine deposits rich in *Anthraconaia*-
424 like non-marine (limnic) bivalves, which suggests the associated megaflora grew in or
425 adjacent to marginal lacustrine environments.

426

427 **Conclusions**

428

429 In this paper, we document the first occurrence of *Lesleya* within the Iberian Massif
430 of northwestern Portugal. We also describe a new Late Pennsylvanian species, *Lesleya*
431 *iberiensis* sp. nov., on the basis of leaf impressions. Similarities in leaf structures noted
432 for *L. iberiensis* sp. nov. and *L. cheimarosa* (Early Pennsylvanian, USA) may indicate a
433 close relationship between the two congeners, perhaps with the younger *L. iberiensis* sp.
434 nov. having descended from the older *L. cheimarosa* lineage. Although a possible
435 relationship between those congeners is intriguing, it remains conjecture pending a
436 rigorous analysis of relationships within the genus.

437 The discovery of *Lesleya* within the Iberian Massif offers the opportunity to examine
438 relationships among its megaflora, environmental and climatic conditions, and
439 geological-tectonic setting (Fig. 7). The context for the interpreting the
440 paleoenvironmental and paleoecological conditions of *Lesleya* as part of the ‘dryland
441 flora’ in intramontane basins within the Variscan orogen is based on stratigraphic,
442 sedimentological, lithological and geological-tectonic evidence previously presented for
443 the DCB as well as on paleontological data provided by its associated flora and fauna.

444 Previous studies have demonstrated that *Lesleya* preferred seasonally-dry (=dryland)
445 and well-drained environments within Euramerica. In North America, the occurrence of
446 *Lesleya* in Lower Pennsylvanian parautochthonous deposits in seasonally-dry basinal
447 lowlands of the Illinois Basin, USA, indicates *Lesleya* grew there in low altitude

(lowland) environments during dry climatic intervals (see e.g., DiMichele et al. 2008, 2009, 2010). Our report of *Lesleya* in an intramontane basin within the Iberian Massif is an example of this genus also living at higher elevations, where its preferred growing conditions (i.e., seasonally dry and well drained) were present. Those conditions within the Iberian Massif may have been localized or the result of longer term and more widespread, dry climatic intervals in the region during the Late Pennsylvanian.

454

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456

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471

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- 681

682 Figure captions

- 683 Fig. 1. Map showing regional geological setting of the Upper Pennsylvanian (lower
684 Gzhelian) Douro Carboniferous Basin in northwestern Portugal and the detailed
685 geology and location of the *Lesleya* outcrop in the São Pedro da Cova region. Modified
686 from Correia et al. (2013, fig. 1).
- 687 Fig. 2. (A) Generalized stratigraphic and sedimentologic column for the Douro
688 Carboniferous Basin, northwestern Portugal, showing the eight tectono-sedimentary
689 units (TSU) recognized in the sequence (adapted from Pinto de Jesus 2001, fig. 1.3) and
690 the position of the *Lesleya* outcrop. Key for lithologies: a, breccias; b, conglomerates
691 and sandstones; c, siltstones and shales; d, coal beds. (B) Detailed stratigraphic and

692 sedimentologic column for the *Lesleya* outcrop, in the São Pedro da Cova region,
693 showing positions of fossiliferous layers.

694 Fig. 3. Photographs of the *Lesleya* outcrop in the São Pedro da Cova region,
695 northwestern Portugal. (A) View of fossiliferous portion of outcrop, consisting of
696 siliciclastic deposits (mica-rich shale lithofacies) containing *Lesleya* and associated
697 flora (e.g., *Cordaite*s) interlayered with pelitic deposits (clay-rich shale lithofacies) rich
698 in non-marine bivalves (*Anthraconaia*) and some insects. (B and C) Closer views of the
699 upper (B) and lower (C) parts of the fossiliferous sequence showing interlayered shale
700 and sandstone strata.

701 Fig. 4. Stratigraphic ranges and geographic distributions of *Lesleya* species in
702 Euramerica. Adapted from Šimůnek (1996, table 1). Abbreviations: Ca., Cantabrian;
703 Guadalup., Guadalupian; Gzheli., Gzhelian; Kasim., Kasimovian; M., Middle; Saxoni.,
704 Saxonian; Serpukh., Serpukhovian; Stephan., Stephanian; Vi., Viséan; WERS, Western
705 Europe Regional Scale; Zechst., Zechstein.

706 Fig. 5. Holotype leaf (UP-MHNFCP-094951/-094952/-094954) of *Lesleya iberiensis* sp.
707 nov., from the Late Pennsylvanian (early Gzhelian) of the Douro Carboniferous Basin,
708 Sao Pedro da Cova region, northwestern Portugal. (A) Photograph of original specimen,
709 preserved as a natural mold in grey shale, missing its tip, base, and a small piece
710 midway along leaf, and broken in three pieces. (B) Latex cast of original specimen,
711 showing positive relief. (C) Interpretive drawing of original specimen, showing
712 reconstructed leaf margins (dotted lines) based, in part, on paratypes and comparisons
713 with other congeners. Images at different magnifications; scale bars = 20 mm.

714 Fig. 6. Paratype leaves of *Lesleya iberiensis* sp. nov., from the Late Pennsylvanian
715 (early Gzhelian) of the Douro Carboniferous Basin, Sao Pedro da Cova region,

northwestern Portugal. All are photographs of uncoated, original specimens preserved as natural molds in grey shale. (A and B) Paratype ZS 507, lower part of leaf; part (A) and counterpart (B) slabs. (C) Paratype ZS 510, nearly complete, but poorly preserved leaf. (D) Paratype ZS 508, lower part of leaf. Images at different magnifications; scale bars = 20 mm.

Fig. 7. Proposed interpretive model of the living habitat of *Lesleya* and associated flora in riparian environments during the Late Pennsylvanian within the intramontane basin Douro Carboniferous Basin, Variscan orogen, northwestern Portugal. Adapted from Pinto de Jesus (2001) and Einsele (1992). Abbreviations: DCB, Douro Carboniferous Basin; DBT, Douro-Beiras Carboniferous Trough. No vertical or lateral scales implied.

Table caption

Table 1. Comparison of leaf features among *Lesleya iberiensis* sp. nov. and the other 11 named species in the genus. Data compiled from descriptions and figures in papers cited in “Authors” column.

Fig. 1. Map showing regional geological setting of the Upper Pennsylvanian (lower Gzhelian) Douro Carboniferous Basin in northwestern Portugal and the detailed geology and location of the Lesleya outcrop in the São Pedro da Cova region. Modified from Correia et al. (2013, fig. 1).
107x83mm (300 x 300 DPI)

Fig. 2. (A) Generalized stratigraphic and sedimentologic column for the Douro Carboniferous Basin, northwestern Portugal, showing the eight tectono-sedimentary units (TSU) recognized in the sequence (adapted from Pinto de Jesus 2001, fig. 1.3) and the position of the *Lesleya* outcrop. Key for lithologies: a, breccias; b, conglomerates and sandstones; c, siltstones and shales; d, coal beds. (B) Detailed stratigraphic and sedimentological column for the *Lesleya* outcrop, in the São Pedro da Cova region, showing positions of fossiliferous layers.

196x232mm (300 x 300 DPI)

Fig. 3. Photographs of the Lesleya outcrop in the São Pedro da Cova region, northwestern Portugal. (A) View of fossiliferous portion of outcrop, consisting of siliciclastic deposits (mica-rich shale lithofacies) containing Lesleya and associated flora (e.g., Cordaites) interlayered with pelitic deposits (clay-rich shale lithofacies) rich in non-marine bivalves (*Anthraconaia*) and some insects. (B and C) Closer views of the upper (B) and lower (C) parts of the fossiliferous sequence showing interlayered shale and sandstone strata.

183x212mm (300 x 300 DPI)

Fig. 4. Stratigraphic ranges and geographic distributions of *Lesleya* species in Euramerica. Adapted from Šimůnek (1996, table 1). Abbreviations: Ca., Cantabrian; Guadalup., Guadalupian; Gzheli., Gzhelian; Kasim., Kasimovian; M., Middle; Saxoni., Saxonian; Serpukh., Serpukhovian; Stephan., Stephanian; Vi., Viséan; WERS, Western Europe Regional Scale; Zechst., Zechstein.

135x124mm (300 x 300 DPI)

Fig. 5. Holotype leaf (UP-MHNFCP-094951/-094952/-094954) of *Lesleya iberiensis* sp. nov., from the Late Pennsylvanian (early Gzhelian) of the Douro Carboniferous Basin, Sao Pedro da Cova region, northwestern Portugal. (A) Photograph of original specimen, preserved as a natural mold in grey shale, missing its tip, base, and a small piece midway along leaf, and broken in three pieces. (B) Latex cast of original specimen, showing positive relief. (C) Interpretive drawing of original specimen, showing reconstructed leaf margins (dotted lines) based, in part, on paratypes and comparisons with other congeners. Images at different magnifications; scale bars = 20 mm.
184x178mm (299 x 299 DPI)

Fig. 6. Paratype leaves of *Lesleya iberiensis* sp. nov., from the Late Pennsylvanian (early Gzhelian) of the Douro Carboniferous Basin, Sao Pedro da Cova region, northwestern Portugal. All are photographs of uncoated, original specimens preserved as natural molds in grey shale. (A and B) Paratype ZS 507, lower part of leaf; part (A) and counterpart (B) slabs. (C) Paratype ZS 510, nearly complete, but poorly preserved leaf. (D) Paratype ZS 508, lower part of leaf. Images at different magnifications; scale bars = 20 mm. 134x150mm (300 x 300 DPI)

Fig. 7. Proposed interpretive model of the living habitat of *Lesleya* and associated flora in riparian environments during the Late Pennsylvanian within the intramontane basin Douro Carboniferous Basin, Variscan orogen, northwestern Portugal. Adapted from Pinto de Jesus (2001) and Einsele (1992). Abbreviations: DCB, Douro Carboniferous Basin; DBT, Douro-Beiras Carboniferous Trough. No vertical or lateral scales implied.
205x149mm (300 x 300 DPI)

<i>Lesleya</i> species	Authors	Pinna (leaf shape)	Width [mm]	Length [mm]
<i>delafondii</i>	Zeiller 1890	lanceolate	70	>200
<i>grandis</i>	Lesquereux 1880	lanceolate	80	200
<i>cheimarosa</i>	Leary and Pfefferkorn 1977	lanceolate	40	200
<i>angusta</i>	Grand'Eury 1877	lanceolate	17	170
<i>cocchii</i> *	De Stéfani 1901	?lanceolate	16	?
<i>ensis</i>	Zeiller 1888	lanceolate	40	>115
<i>gimmii</i>	Remy and Remy 1978	narrow-elliptical	30–40	>200
<i>microphylla</i> **	Lesquereux 1884	oval-oblong	16	40
<i>simplicinervis</i>	Grand'Eury 1890	?spatulate	27	110
<i>weilerbachensis</i>	Remy and Remy 1975	lanceolate	65	>250
<i>eckardtii</i> ***	Kurtze 1839	lanceolate	23–30	>200
<i>iberiensis</i> sp. nov. in this paper		lanceolate	50	>225

*According Zeiller (1906);

**According to the description;

***This species still be assigned to genus *Taeniopteris* Brongniart by some authors - *Taeniopteris eck*

<i>Lesleya</i> species	Authors	Pinna (leaf shape)	Width [mm]	Length [mm]	Leaf base	Leaf apex	Midvein width [mm]	Margin shape	Venation	N° bifurcations of lateral veins	Angle between lateral vein/ margin	Angle betw lateral ve midvei
<i>delafondii</i>	Zeiller 1890	lanceolate	70	>200	?	obtuse	?	denticulate? to entire	slightly curved	3–74	30°–32°	26°
<i>grandis</i>	Lesquereux 1880	lanceolate	80	220	?cuneate	obtuse	strong	entire to lobate/lanceolate	some sinusoidal effect	3–4	20°–82°	56°–60°
<i>cheimarosa</i>	Leary and Pfefferkorn 1977	lanceolate	40	200	long and narrow (cuneate)	sublanceolate to acute	broad 0.7–2	entire	S-shaped (sinuous)	1–2	40°–70°	10°–70°
<i>angusta</i>	Grand'Eury 1877	lanceolate	17	170	obtuse	blunt	?	entire	slightly curved to margin	0–1	45°–55°	±35°
<i>cocchii</i> *	De Stéfani 1901	?lanceolate	16	?	?	?	2	entire	curved to margin	1–2 near base	±50°	±45°
<i>ensis</i>	Zeiller 1888	lanceolate	40	>115	?	?blunt	1	entire	slightly curved	2–3	35°–40°	10°–12°
<i>gimmii</i>	Remy and Remy 1978	narrow-elliptical	30–40	>200	acute	?	6 at base	entire	slightly S-shaped	2–3	28°–53°	06°
<i>microphylla</i> **	Lesquereux 1884	oval-oblong	16	40	decurent, shortly auriculate	obtuse	?	entire	?	?	50°	very acute
<i>simplicinervis</i>	Grand'Eury 1890	?spatulate	27	110	rounded	rounded	?	entire	slightly curved to margin	0 (simple veins)	±35°	15°–20°
<i>weilerbachensis</i>	Remy and Remy 1975	lanceolate	65	>250	cuneate	acute	1.5–2	dentate	slightly curved	3–74	09°–10°	13°–14°
<i>eckardtii</i> ***	Kurtze 1839	lanceolate	23–30	>200	acute	blunt	2	entire to ?lobate	straight	0 (simple veins)	±60°	60°
<i>iberiensis</i> sp. nov. in this paper		lanceolate	50	>225	long and narrow (cuneate)	?lanceolate	broad 1–3	entire	slightly curved (arched)	1–2	05°–35°	07°–15°

*According Zeiller (1906);

** According to the description;

***This species still be assigned to genus *Taeniopteris* Brongniart by some authors - *Taeniopteris eckardtii* Kurtze 1839 (see Halle 2014).

Leaf base	Leaf apex	Midvein width [mm]	
?	obtuse	?	
?cuneate	obtuse	strong	
long and narrow (cuneate)	sub/lanceolate to acute	broad 0.7–2	
obtuse	blunt	?	
?	?		2
?	?blunt		1
acute	?	6 at base	
decurent, shortly auriculate	obtuse	?	
rounded	rounded	?	
cuneate	acute	1.5–2	
acute	blunt		2
long and narrow (cuneate)	?lanceolate	broad 1–3	

ardtii Kurtze 1839 (see Halle 2014).

vein	N ^o veins per cm/1 in	1 cm on the leaf margin
	8–12	
'	25–30	
'	24–36	
	#10	
	#20	
'	8–12	
	10–13	
te	40	
'	8–10	
'	12–20	
	8–9	
'	10–13	

Margin shape	Venation	Nº bifurcations of lateral veins
denticulate? to entire	slightly curved	3–?4
entire to lobate/lanceolate	some sinusoidal effect	3–4
entire	S-shaped (sinuous)	1–2
entire	slightly curved to margin	0–1
entire	curved to margin	1–2 near base
entire	slightly curved	2–3
entire	slightly S-shaped	2–3
entire	?	?
entire	slightly curved to margin	0 (simple veins?)
dentate	slightly curved	3–?4
entire to ?lobate	straight	0 (simple veins)
entire	slightly curved (arched)	1–2

Draft

Angle between lateral vein/margin	Angle between lateral vein/midvein
30°–32°	26°
20°–82°	56°–60°
40°–70°	10°–70°
45°–55°	± 35°
± 50°	± 15°
35°–40°	10°–12°
28°–53°	06°
50°	very acute
± 35°	15°–20°
09°–10°	13°–14°
± 60°	60°
05°–35°	07°–15°

Draft

Nº veins per 1 cm on the leaf margin

8–12

25–30

24–36

± 10

± 20

8–12

10–13

40

8–10

12–20

8–9

10–13

Draft