

Large-leaved *Annularia* species (Equisetopsida) in Pennsylvanian Variscan Euramerica—a Preliminary Review

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ABSTRACT

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Seven fossil-species can be distinguished within the range of late Carboniferous and early Permian equisetopsid (“horsetail”) foliage formerly assigned to *Annularia stellata*. The shoots bearing this foliage also produced distinctive strobili often known as *Calamostachys tuberculata*. These foliage species can be differentiated by leaf and whorl morphology, and each species has a distinct geographical and stratigraphical range. The group first appeared in the intramontane basins of the Variscan Mountains in the late Duckmantian, and then expanded into the lowland paralic coal swamps in the Bolsovian–Asturian. The group continued to flourish in coal swamp refugia during the Stephanian but eventually disappeared during the early Permian.

Key-words—Equisetopsida, Horsetails, *Annularia*, Pennsylvanian, Permian.

INTRODUCTION

AMONG the iconic plant fossils of the Pennsylvanian (late Carboniferous) coal-bearing deposits of Euramerica are star-shaped whorls of leaves. They were some of the first plant fossils of this age to be illustrated, albeit often identified as the extant angiosperm *Galium* L. (Fig. 1). Today they are regarded as foliage of fossil subarborescent equisetopsids and assigned to the fossil-genus *Annularia* Sternberg.

The plants that produced *Annularia* foliage flourished in the Pennsylvanian palaeotropical wetlands often referred to as the coal swamps. The leaf-remains first appear in the Lower Pennsylvanian, and increase significantly in abundance and taxonomic diversity in the Middle Pennsylvanian. This diversification includes a proliferation of distinctive large leaf-whorls, which have traditionally been named *Annularia stellata* (Schlotheim) Wood, and which are associated with and occasionally attached to (e.g., Rößler & Thiele–Bourcier, 1999) strobili known as *Calamostachys tuberculata* (Sternberg) Jongmans. However, the taxonomy

and distribution of the fossils known as *A. stellata* are still poorly understood, and it has been suggested that more than one plant species may be represented.

In order to test this idea, the present paper reviews the illustrated published records of *A. stellata* and its homotypic synonym *Annularia longifolia* Brongniart as listed in the Fossilium Catalogus (Jongmans, 1914; Jongmans & Dijkstra, 1969; Dijkstra & van Amerom, 1995) and in the most important monographs on these fossils (Jongmans, 1911; Jongmans & Kukuk, 1913; Crookall, 1969; Abbott, 1958). These data have been supplemented by evidence from key palaeobotanical collections, including in the Natural History Museum (London), the Kidston Collection (British Geological Survey, Keyworth), Université de Lille (France), Naturalis (Leiden) and the National Museum (Prague, Czech Republic).

Chronostratigraphy uses the Heerlen regional scheme as summarised by Wagner (1974), Wagner and Winkler Prins (2016) and Knight *et al.* (2023) as this gives a better stratigraphical resolution in these terrestrial successions than the IUGS Global Chronostratigraphy (Cohen *et al.*, 2013).

SYSTEMATIC PALAEOONTOLOGY

The higher ranked taxonomy is based on Smith *et al.* (2006), Chase & Reveal (2009) and Elgorriaga *et al.* (2018). The genera and species are regarded as fossil–taxa as defined in the International Code of Nomenclature (ICN–Turland *et al.*, 2018) Art. 1.2 and refer exclusively to the foliage; they may be related to, but are not the same as whole plant taxa (see discussion in Cleal & Thomas, 2010, 2021; Cleal *et al.*, 2021). The distributional data for each fossil–species are summarised in the Supplemental Files.

Class—EQUISETOPSIDA Agardh

Order—EQUISETALES Dumort.

Family—CALAMITACEAE Unger

Remarks—This family is sometimes named Calamostachyaceae S.V. Meyen, which is typified by a fossil–genus of reproductive organs (Meyen, 1978). However, this

is contrary to accepted nomenclatural practice as laid down in the ICN, where the earliest published family name must be used whose type can be included within the family. That name is Calamitaceae (Unger, 1840), whose type (*Calamites suckowii* Brongniart) is generally regarded as belonging to the family (Cleal *et al.*, 2012; Cleal & Shute, 2016). The Calamitaceae differs from the extant Equisetaceae Rich. ex DC. mainly by the strobili having a whorl of sterile bracts between each whorl of sporangiophores (Elgorriaga *et al.*, 2018).

Genus—ANNULARIA Sternberg, 1821

Remarks—*Annularia* comprises relatively large, lanceolate to spatulate leaves arranged in flat whorls oriented at right–angles or obliquely to the stem. *Asterophyllites* Brongniart, the other fossil–genus widely used for equisetopsid foliage in coal swamp macrofloras, has in contrast more slender, linear leaves arranged in cup–like whorls around the stem (Cleal & Thomas, 2018).

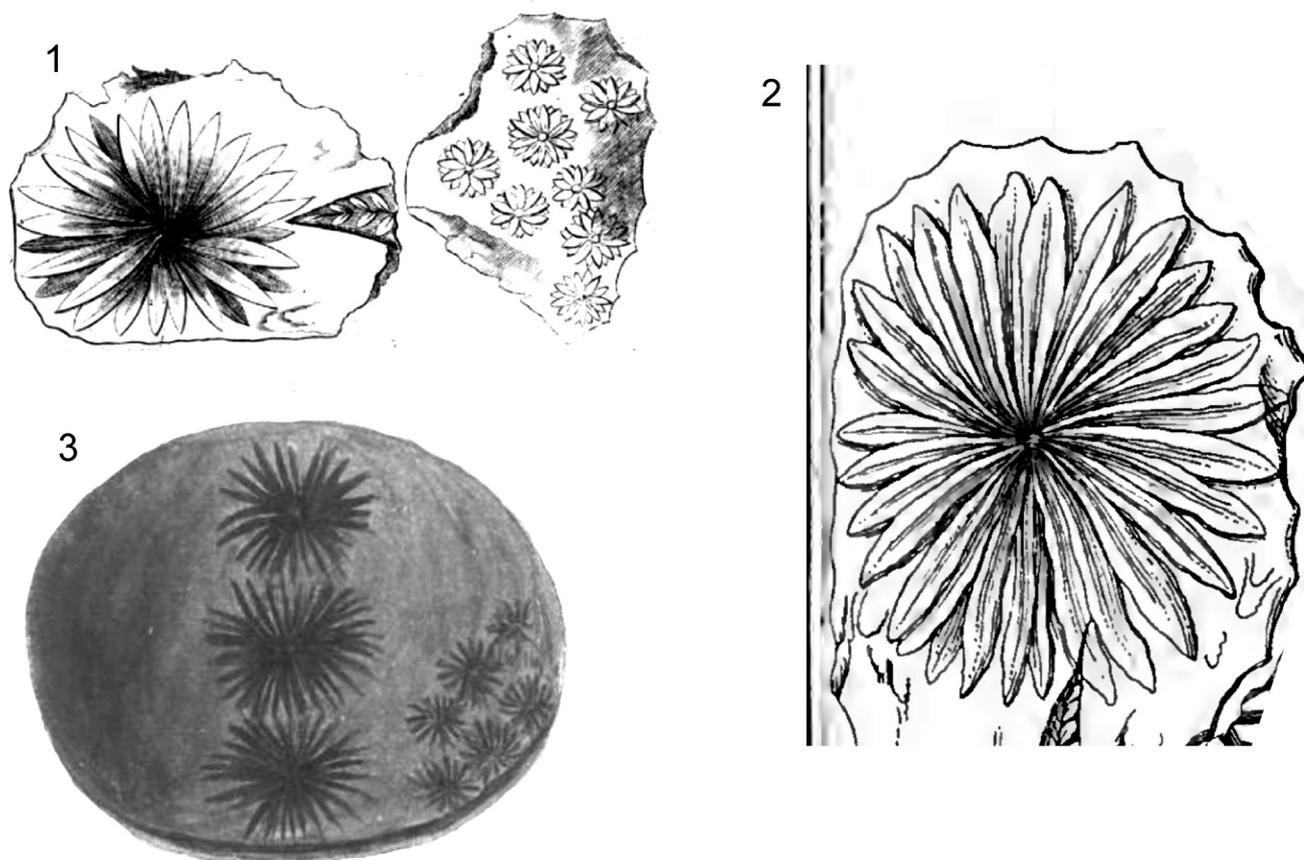


Fig. 1—Early (pre–19th Century) illustrated records of *Annularia* foliage. (1) Lhwyd, 1699, pl. 3, figs 201, 202. (2) Scheuchzer, 1709, pl. 3, fig. 3. (3) Walch, 1771, pl. ω, figs 2, 3.

Table 1—Morphological characters of foliage on ultimate branches in the seven fossil-taxa recognised in the traditional concept of *Annularia stellata*. Whorl shape is designated by the ratio of the shortest: longest leaf length in a whorl.

	Whorl shape	Leaves in whorl	Leaf length (mm)	Typical leaf shape	Leaf apex	Leaf rigidity	Basal collar width (mm)
<i>A. stradonicensis</i>	0.5–0.7	35–40	45–65	Linear	Obtuse	Lax	0.5
<i>A. inflata</i>	0.7–0.9	20–30	20–40	Oblanceolate	Obtuse–mucronate	Rigid	0.5
<i>A. sardiniana</i>	0.9–1.0	10–30	15–35	Linear	Acute	±Lax	1.0–1.5
<i>A. carinata</i>	0.5–0.7	20–30	15–30	Lanceolate	Acute	Rigid	1.0–1.5
<i>A. noronhai</i>	0.9–1.0	15–20	25–30	Linear	Caudate	Rigid	2.5–3.5
<i>A. spinulosa</i>	0.9–1.0	25–35	20–40	Linear	Acuminate	Rigid	1.0
<i>A. aff. carinata</i>	0.5–0.7	10–20	20–30	Oblanceolate	Obtuse	Rigid	1.0–1.5

The most useful characters for distinguishing *Annularia* species are the degree of anisophylly of the leaf whorls, and the shape of the individual leaves (oblanceolate, linear or tapered), although the latter can be distorted by the margin becoming enrolled (Walton, 1936). The leaf apex (obtuse, mucronate or acute) is also important, although care must be taken as the leaf tip may be partly buried in the rock matrix (Walton, 1936). Leaf size can be useful but only when dealing with the ultimate shoots; the sizes of large leaves borne on the trunk and the lower-order branches are rarely diagnostic (see Daviero & Lecoustre, 2000, fig. 7). The presence of epidermal hairs has been regarded as taxonomically important (e.g., Stur, 1887; Elias, 1931) but cuticle evidence shows that these “hairs” are in fact the surface expression of elongate epidermal cells (Abbott, 1958). All *Annularia* leaves have a single longitudinal vein in a shallow furrow; this plesiomorphic character is not mentioned in the species diagnostic descriptions.

This study suggests that seven fossil-species can be differentiated within the range of foliage that has historically been included in *A. stellata* (Table 1; Fig. 2). There have been previous attempts to subdivide these fossils taxonomically most notably by Diéguez (1985). However, the classification proposed here seems to be more robust as the recognised taxa are not only recognisable morphologically, but also have distinct distributional ranges. These species are dealt with in approximate stratigraphical order of occurrences.

Annularia stradonicensis Cleal, sp. nov.

(Fig. 3)

Holotype—National Museum, Prague, Sternberg Collection specimen E05747 (Fig. 3.1—Feistmantel, 1874, pl. 16, fig. 1); Radnice Member, Kladno Formation (late Duckmantian—Opluštil *et al.*, 2016), exposed in a ravine

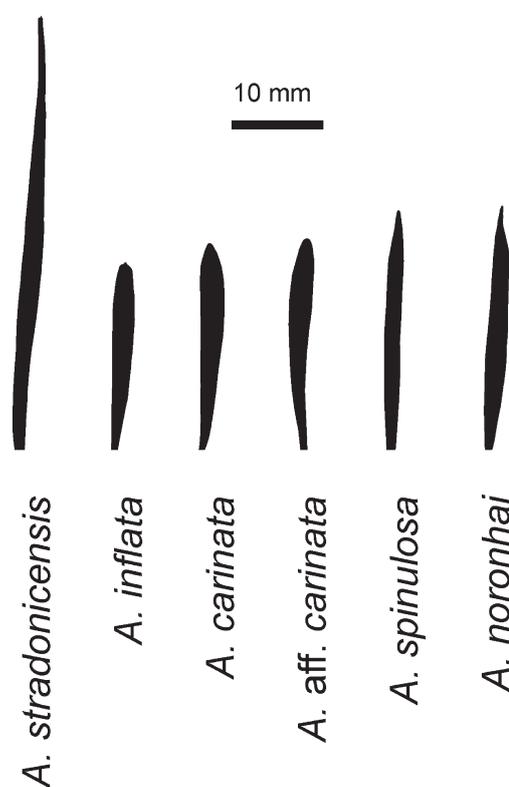


Fig. 2—Outlines of typical pinnules of fossil-species dealt with in this paper. Mostly drawn from specimens photographically figured in this paper, except that for *A. aff. carinata* which was traced from DiMichele *et al.* (2013, fig. 4.3).

between Zdejcina and Stradonke near Beroun (Czech Republic). Specimens E5391 (Fig. 3.2—Feistmantel, 1874, pl. 15, fig. 3), E2648 (Fig. 3.3) and 32927 (Fig. 3.4) are designated as paratypes.

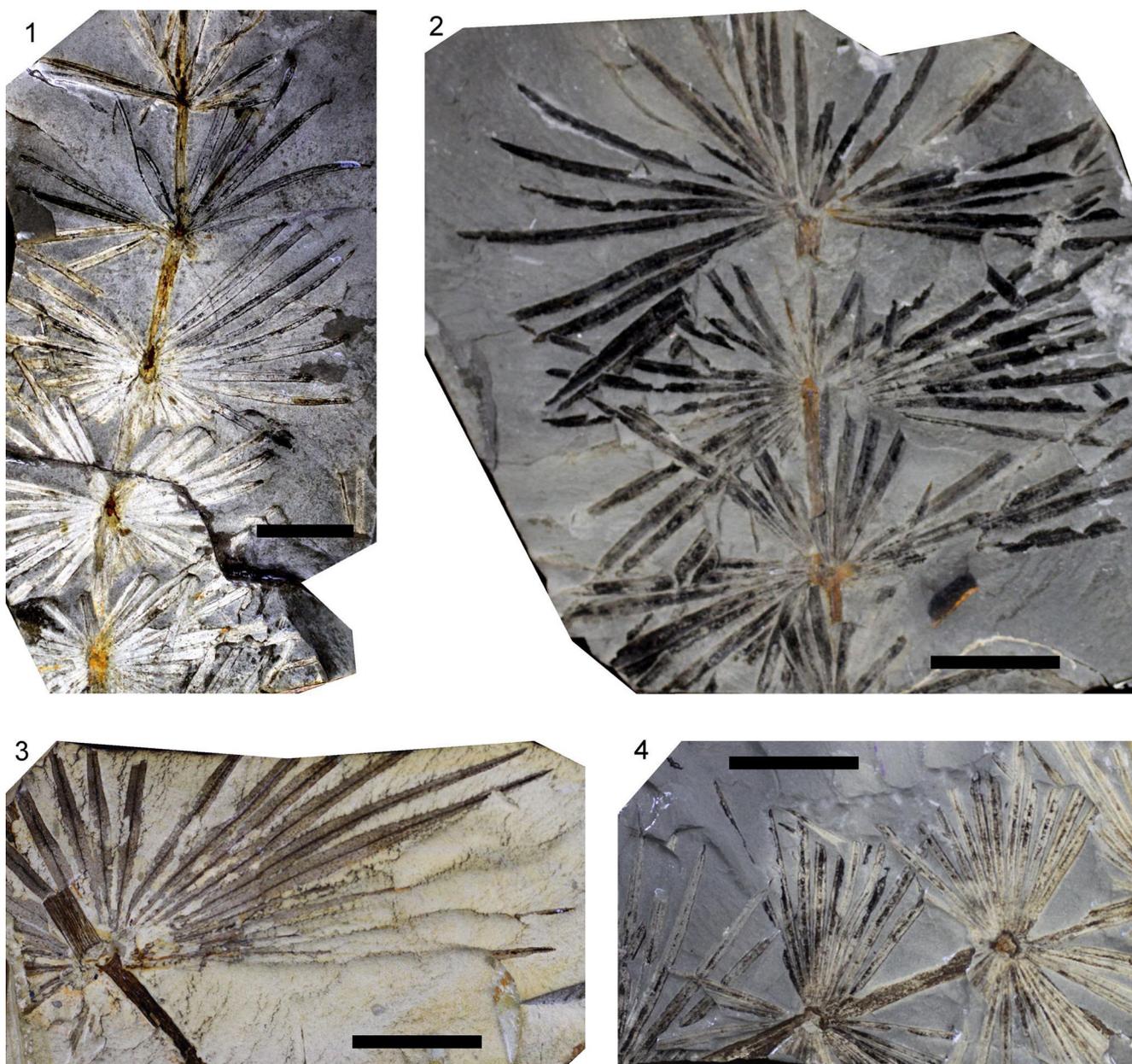


Fig. 3—*Annularia stradonicensis* Cleal, sp. nov., Beroun, near Plzen, Czech Republic; Whetstone Horizon, Kladno Formation (Radnice Member, upper Duckmantian Substage). National Museum, Prague, Sternberg Collection: (1) E05747 (holotype); (2) E5391; (3) E2648; (4) 32927. All scale bars=20 mm.

Diagnostic description—Whorls of 35–40 leaves, anisophyllous (shortest: longest leaf length ratio 0.5–0.7). Leaves lax in appearance, linear, gradually tapered in distal one-fifth to an obtuse tip. Leaves on ultimate branches typically 45–65 mm long, 2–3 mm wide, basally fused to form a narrow (ca. 0.5 mm wide) collar around the stem.

Remarks—Compared with *Annularia inflata*, the species more commonly found in the Westphalian floras of Euramerica, *A. stradonicensis* has consistently larger, less

rigid leaves that are more gradually tapered in their distal part. The types are associated with strobili similar to *C. tuberculata* (Feistmantel, 1874, pl. 16, figs 2, 3) but are smaller, with a slenderer axis, and bracts that were longer and more oblique to the axis. Nemějc (1953) assigned Feistmantel's fossils to a new species, *Calamostachys intermedia* Němejc, but they are clearly in the same general group as *C. tuberculata*.

Distribution—Intramontane basin of the Bohemia Massif (upper Duckmantian).

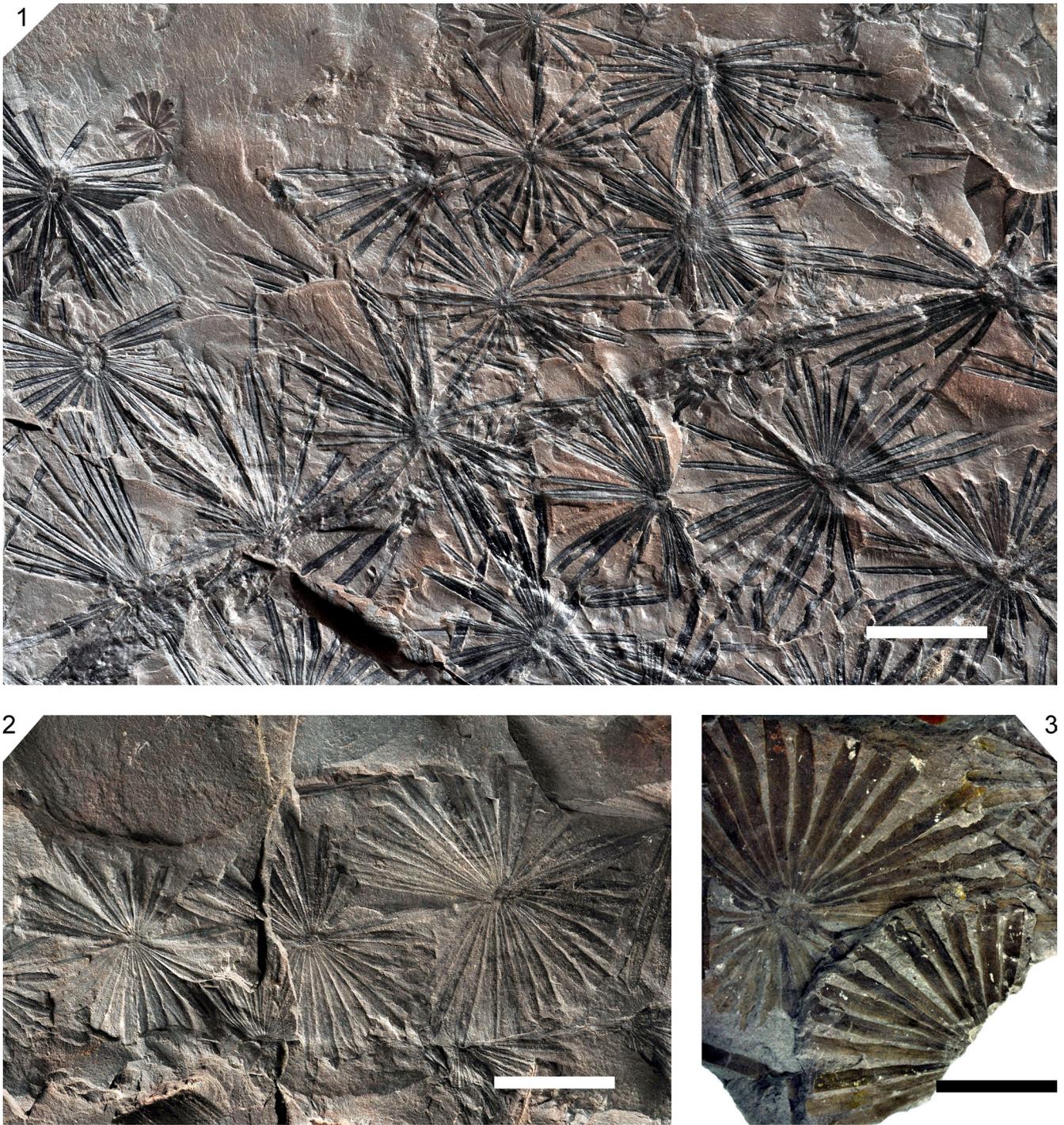


Fig. 4—*Annularia inflata* Lesquereux. (1, 2) Radstock, near Bath, Somerset (UK); Radstock Formation (upper Asturian–lower Cantabrian); British Geological Survey, Keyworth, Kidston Collection; (1) Kidst.6891; (2) Kidst.6892. Reproduced with permission [P7873379, P787374: CP22/039 BGS © UKRI part of the BGS Kidston Collection]. (3) Hostenbach, Lorraine (France); Steinbesch Formation (upper Asturian); University of Lille Collections. All scale bars=20 mm.

Annularia inflata Lesquereux, 1870, p. 423

(Fig. 4)

Lectotype—Illinois State Museum, Worthen Collection specimen ISM 1685 (Lesquereux, 1870, pl. 20, fig. 1; photographically figured Janssen, 1940, pl. 1, fig. 1); Francis Creek Shale (Desmoinesian, lower Cantabrian), Mazon Creek, Illinois. A second syntype was figured by Lesquereux (1870, pl. 20, fig. 2) but its present location is unknown.

Heterotypic synonyms—*Annularia westphalica* Stur, 1887, p. 213; *Annularia geinitzii* Stur, 1887, p. 215; *Carpannularia americana* Elias, 1931, p. 118.

Diagnostic description—Whorls of usually 20–30 leaves, anisophyllous (shortest: longest length ratio 0.7–0.9). Leaves rigid, narrowly oblanceolate with an obtuse tip and small mucro. Leaves on ultimate branches typically 20–40 mm long, 2.5–4.5 mm wide, basally fused to form a narrow, ca. 0.5 mm wide collar around the stem (Adapted from Álvarez-Vázquez & Wagner, 2017).

Remarks—This includes the most abundant and widespread type of foliage formerly included within *A. stellata* found in the Westphalian and lower Stephanian (Atokan to Missourian in the U.S.A. chronostratigraphy). They differ from type *A. stellata* (i.e., *A. spinulosa*—see later) having moderately anisophyllous leaf-whorls, and larger more oblanceolate leaves with an obtuse apex and (where preserved) a small mucro. Álvarez-Vázquez & Wagner (2017) showed that the correct name for this upper Westphalian–lower Stephanian fossil-species is *A. inflata*.

Stur (1887) proposed the name *A. westphalica* for very similar foliage from the upper Asturian of Saarland (Germany), which had been figured previously by Roehl (1869, pl. 4, fig. 6) as *Annularia longifolia*. Unfortunately, this type specimen is lost and at least some of the features regarded by Stur as diagnostic of *A. westphalica* (e.g., the thickened margins of the leaves) are probably the result of taphonomy. Nevertheless, Stur noted that the type of *A. westphalica* had anisophyllous whorls of oblanceolate leaves like those of *A. inflata*. Other leaf whorls from the upper Asturian of Saar-Lorraine seen in the collections of Lille University (e.g., Fig.

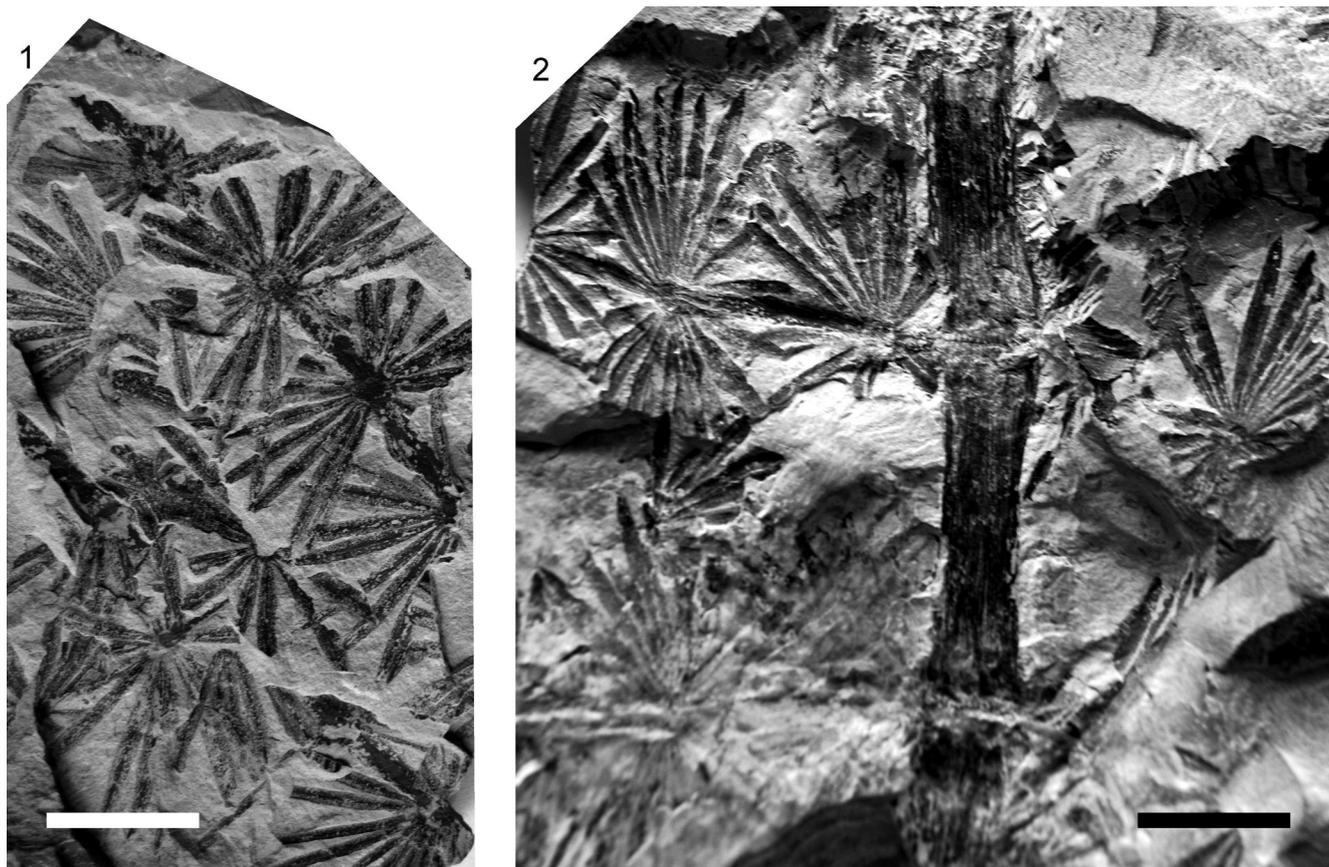


Fig. 5—*Annularia sardiniana* Cleal *et al.*, San Giorgio Formation (Asturian), San Giorgio, near Iglesias, Sardinia (Italy); Pittau-Del Rio Collection, Geological and Palaeontological Museum, Cagliari University, Sardinia (Photos by G. Scanu); (1) MGPDL 17397 (holotype); (2) MGPDL 17410.

4.3) are indistinguishable from the von Roehl specimen and support the synonymy of the two species names.

Annularia geinitzii Stur was typified by specimens from the upper Asturian Zwickau Coalfield, and has whorls of similar-shaped narrowly oblanceolate leaves with an obtuse apex (Geinitz, 1855, pl. 19; Stur, 1887, pl. 16b). Stur (1887) mainly characterised *A. geinitzii* by the leaves apparently having prominent adaxial epidermal hairs, but these are probably just elongate epidermal cells. The leaf and whorl shape are otherwise indistinguishable from *A. inflata*.

Carpannularia americana Elias was based on shoots from the lower Desmoinesian of Clinton, Missouri (USA) with whorls of large, oblanceolate leaves (Elias 1931, pls 12–15), very similar to the Mazon Creek specimens of *A. inflata*. He compared them with *A. westphalica* and *A. geinitzii*, but did not use those names as he regarded them as being inadequately typified. Cridland (1968) and Álvarez-Vázquez & Wagner

(2017) suggested that Elias's specimens were conspecific with *Annularia mucronata* Schenk but that species was based on specimens from the lower Permian Shanxi Formation of Puxian County, Shanxi (China) with significantly more lanceolate leaves (Schenk, 1883, pl. 30, fig. 10). Elias (1931) described “seed-like” structures attached to his *C. americana*, which are probably insect galls (Correia *et al.*, 2020).

Annularia inflata shoots have been found with strobili attached similar to *C. tuberculata* (Röbber & Thiele-Bourcier, 1999) but which are smaller (55 mm long, 13 mm wide) and so more similar to the *C. intermedia* strobili associated with *A. stradonicensis*.

Distribution—Midcontinent North America (Desmoinesian–Missourian); Northern Variscan–Appalachian foreland (Bolsovian–Asturian); southern Variscan Foreland (Asturian–Barruelian); Donets Basin (Asturian); Variscan

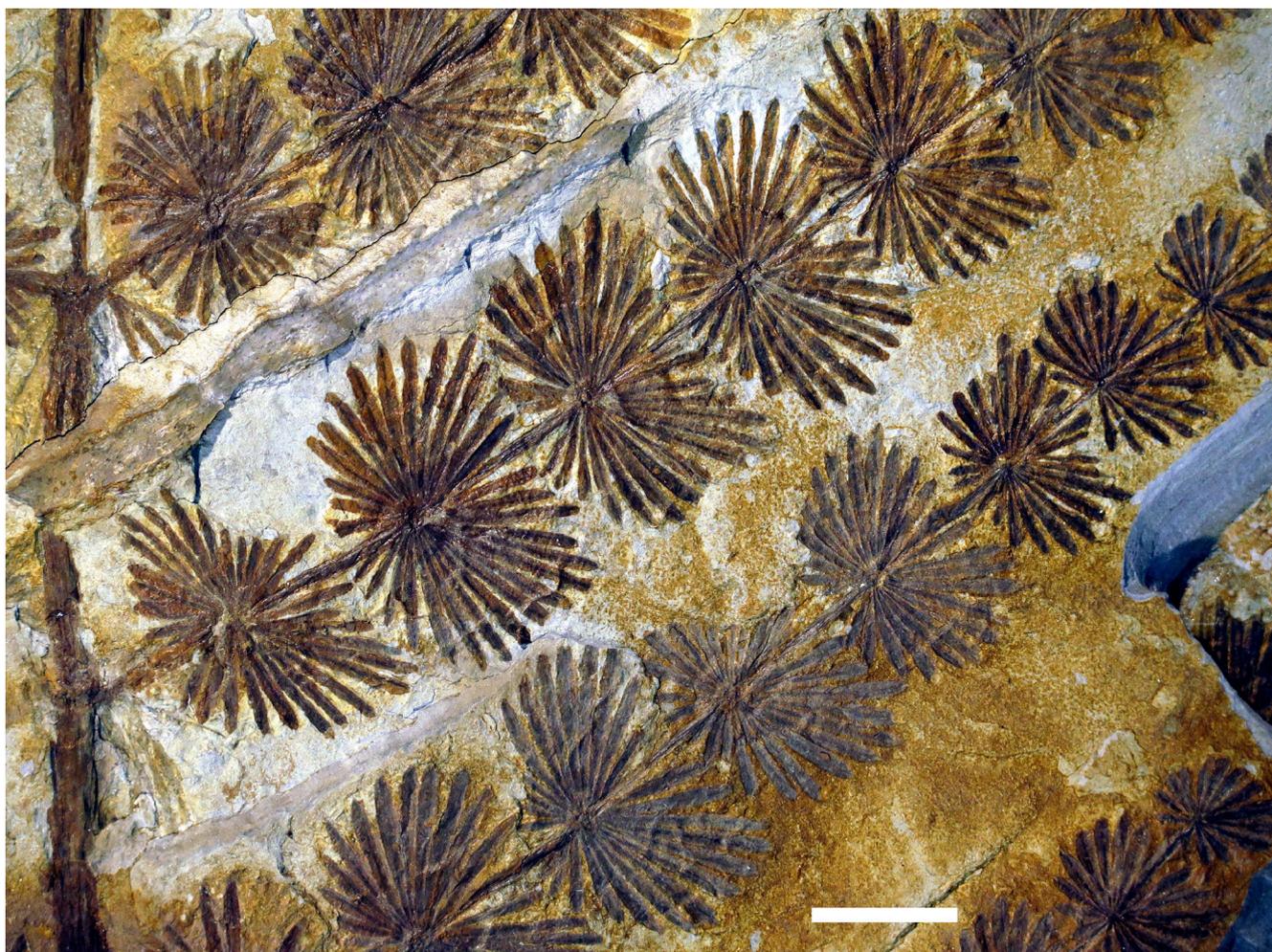


Fig. 6—*Annularia carinata* Gutbier, ‘Frana vecchia’ near Casera Auernig, Pontebba, Carnic Alps (Italy). Museo Friulano di Storia Naturale in Udine (Italy): MFSNgp 985. Scale bar = 20 mm. Photo by S. Opluštil (Charles University, Prague); for image of complete specimen see Opluštil *et al.* (2021, pl. 4).

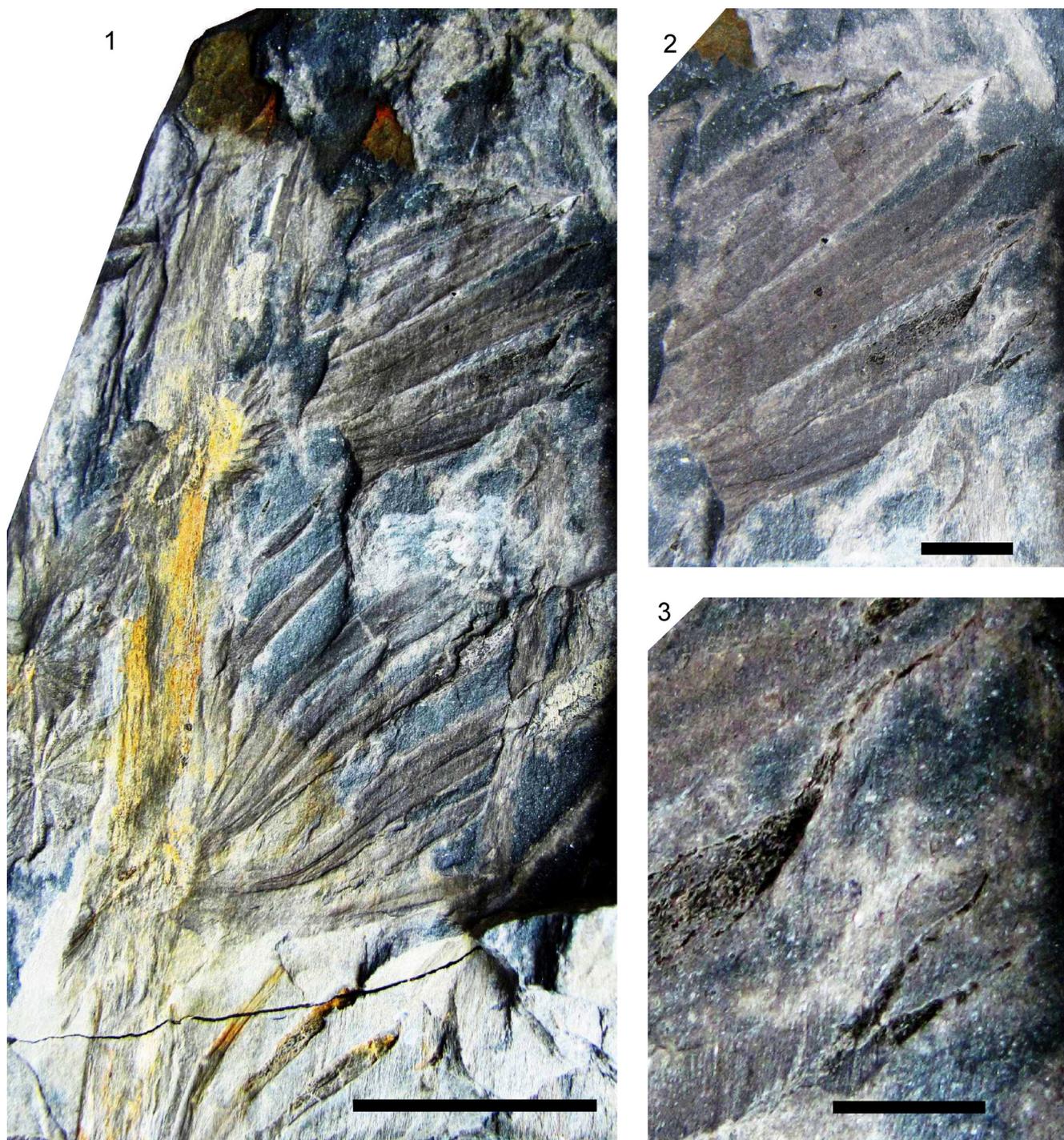


Fig. 7—*Annularia noronhai* Correia *et al.* (holotype), Stephanian C, São Pedro da Cova, Douro Basin (Portugal); Portugal Museum of Natural History and Science, University of Porto (Specimen UP–MHNFCP–154065; Photo by P. Correia); (1) whole specimen; (2, 3) spinose tips of leaves. Scale bar = 20 mm (Fig. 1), 5 mm (Figs 2, 3).

intramontane basins (upper Asturian–Barruelian, rarely down to upper Bolsovian and up to Saberian).

Annularia sardiniana Cleal *et al.*, 2016, p. 1157

(Fig. 5)

Holotype—Geological and Palaeontological Museum, Cagliari University (Sardinia, Italy), Del Rio Collection specimen MGPD L 17397 (Fig. 5.1–Cleal *et al.*, 2016, fig. 3a); San Giorgio Formation (Asturian) San Giorgio, Sardinia (Italy).

Diagnostic description—Mainly isophyllous whorls of 10–30 (typically 20) leaves. Leaves on ultimate branches typically 18 mm long (sometimes up to 35 mm), 2.0–2.5 mm wide, linear–lanceolate, rather lax with acute to bluntly acute apex. Leaves basally fused to form a 1.0–1.5 mm wide collar around stem (Adapted from Cleal *et al.*, 2016).

Remarks—This species is only known from the San Giorgio Formation in Sardinia. It is closest to *A. carinata* in having leaves with an acute but not mucronate apex. However, *A. sardiniana* has generally larger and more linear leaves, and the leaf whorls are more consistently isophyllous. The leaves of *A. sardiniana* also have a distinctively thin limb, giving them a somewhat lax appearance, rather different from most other species in the group discussed here.

Distribution—Variscan intramontane basin, Sardinia (Asturian).

Annularia carinata Gutbier, 1849, p. 9

(Fig. 6)

Syntypes—Gutbier (1849, p. 2, figs 4–8) figured five syntypes but one (his fig. 8) is a *Calamostachys tuberculata* strobilus. Lőcse *et al.* (2020, fig. 12A) figured another of the syntypes (Gutbier’s fig. 7) but this has less swollen leaves than the other specimens and so has not been designated as lectotype. A formal choice of lectotype must await further study of the syntypes. According to Lőcse *et al.* (2019, 2020) Gutbier’s specimens originated from the Grüna Tuff of the Asselian lower Planitz Formation at Reinsdorf in the Chemnitz Basin, Saxony (Germany).

Diagnostic description—Whorls of usually 20–25 leaves (rarely up to 30 leaves low in shoot), strongly anisophyllous (shortest: longest length ratio 0.5–0.7. Leaves on ultimate shoots up to 25 mm long, 3 mm wide, lanceolate to slightly oblanceolate, with acute to bluntly acuminate tip but lacking a distal mucro. Leaves basally fused to form a 1.0–1.5 mm wide collar around stem (Modified from Barthel, 1976).

Remarks—The interpretation of this species is largely based on Barthel (1976), who recognised that the large-whorled *Annularia* specimens from the Chemnitz Basin differed from the types of *A. spinulosa* (“*stellata*”). Barthel’s Chemnitz specimens have strongly anisophyllous whorls of leaves that were generally shorter, narrower and more oblanceolate, and are more similar to Gutbier’s types of *A. carinata*, which also came from the Chemnitz Basin.

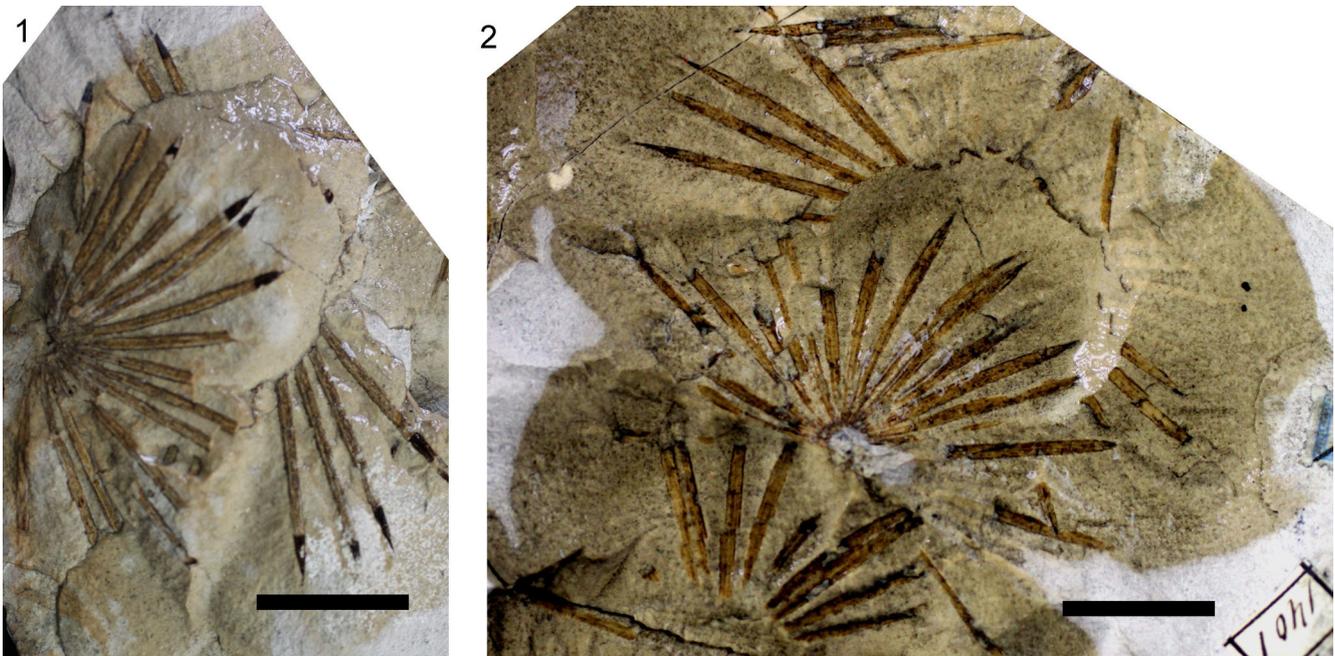


Fig. 8—*Annularia spinulosa* Sternberg (types), Döhlener Formation (Autunian), Saxony, Germany; National Museum, Prague, Sternberg Collection (Photos by L. Váchova and J. Sklenář); (1) E39 (holotype); (2) E1989. All scale bars=20 mm.

Annularia inflata differs in having less strongly anisophyllous whorls, larger, more oblanceolate leaves with an obtuse apex, and often with a mucronate tip.

Prior to Barthel's analysis, the taxonomic status of *A. carinata* was uncertain. Gutbier (1849) had distinguished it from *A. longifolia* (= *A. spinulosa*) by the presence of glands on the stem, and the smaller and thicker-limbed leaves with thicker veins. However, the so-called glands have been reinterpreted as spirorbid tubes (Kidston, 1886), and the difference in leaf size and veining are not clearly shown by the syntypes. Most subsequent authors (e.g., Zeiller, 1906) regarded it as conspecific with *A. stellata* (= *A. spinulosa*) but largely because there had been few verifiable records of *A. carinata* other than the types (see comments by Jongmans, 1911, 1914). Jongmans & Kukuk (1913) compared *A. carinata* with *Annularia pseudostellata* Potonié (Potonié, 1899, p. 201) but the types of the latter have slenderer, linear leaves, are stratigraphically much older, and are associated with a quite different type of strobilus (*Cingularia typica* Weiss-Laveine 1989, p. 59).

The best documented examples of *A. carinata* are from the Carnic Alps in Italy (Opluštil *et al.*, 2021, pl. 3, figs 5–8; pl. 4, figs 1–3), where they are associated with strobili similar to *C. tuberculata* but intermediate in size between the strobili associated with *A. inflata* and with *A. spinulosa*. Kerp (1984) suggested a correlation between *A. carinata* and much smaller strobili known as *Calamostachys dumasii* Zeiller, but this was based on stratigraphically younger (Autunian) specimens showing smaller whorls with fewer, thinner-limbed leaves than the species interpreted here as *A. carinata*.

Distribution—Variscan intramontane basins (Saberian, rarely to Stephanian C); southern Variscan foreland (Saberian, rarely to Stephanian C); Donets Basin (Stephanian C).

Annularia noronhai Correia, Šimůnek, Cleal & Sá in
Correia *et al.*, 2021, p. 261

(Fig. 7)

Holotype—Museum of Natural History and Science, University of Porto, Specimen UP-MHNFCP-154065 (Fig. 7—Correia *et al.*, 2021, figs 3, 4); provenance Stephanian C (Gzhelian) shales (horizon H6), São Pedro da Cova, Douro Basin, Portugal.

Diagnostic description—Mainly isophyllous whorls of usually 15–20 leaves. Leaves 25–30 mm long, 2–3 mm wide, linear for most of length, terminating distally in a caudate apex with a prominent 3–5 mm long slender apical prolongation. Leaves basally-fused to form a distinct, 2.5–3.5 mm wide collar that forms a well-developed sheaf around the stem. (Adapted from Correia *et al.*, 2021).

Remarks—This species is like *A. spinulosa* but the leaves have a more pronounced acuminate to caudate apex. There

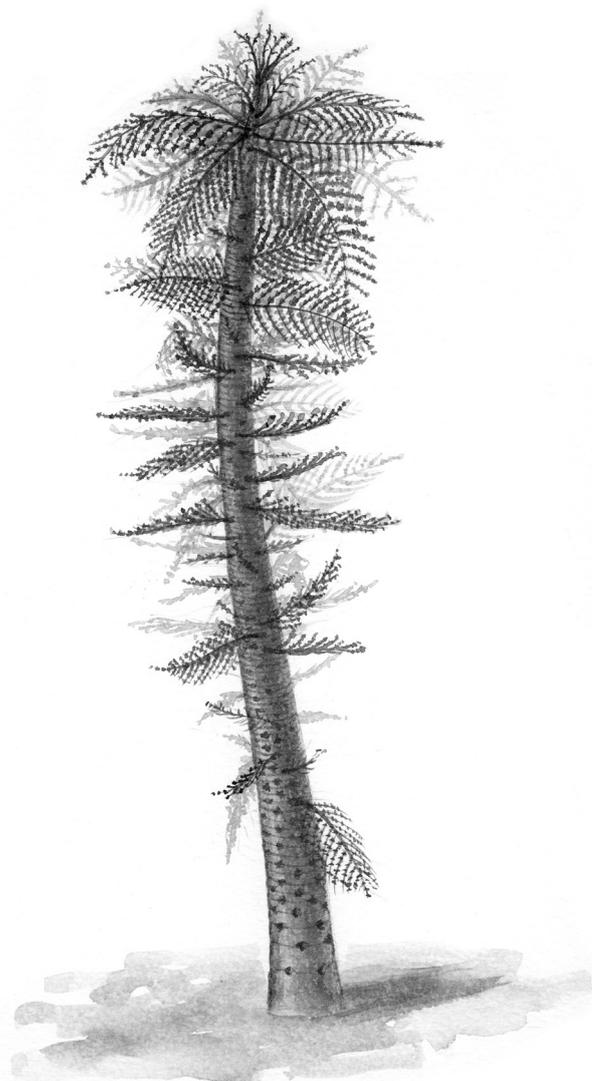


Fig. 9—Reconstruction of subarborescent equisetopsid that produced *Annularia spinulosa* foliage. Refined from Rößler & Noll (2007a, b).

also appear to be fewer leaves in each whorl and the basal collar is more developed. It was found associated with strobili similar to *Calamostachys tuberculata* (Correia *et al.* 2018).

Distribution—Variscan intramontane basin, Portugal (Stephanian C); far western palaeotropical Euramerica (Autunian).

Annularia spinulosa Sternberg, 1821, p. 22

(Fig. 8)

Holotype—National Museum, Prague, Sternberg Collection, specimen E39 (Fig. 8.1—Sternberg, 1821, pl. 19,

fig. 4; photographically refigured Correia *et al.*, 2021, fig. 5; Kvaček *et al.*, 2021, pl. 51, fig. 4); counterpart E1989; provenance Plauenscher Grund, Dresden (Germany), Döhlen Formation (Autunian).

Heterotypic synonyms—*Casuarinites stellatus* Schlotheim, 1820, p. 397, nom. inval.; *Annularia longifolia* Brongniart, 1828, p. 156.

Diagnostic description—Mainly isophyllous whorls of usually 25–35 leaves (as few as 13 per whorl in distal parts of shoot). Leaves linear or slightly oblanceolate with acuminate tip. Leaves on ultimate shoots c. 2 mm wide, up to 40 mm long, basally–fused to form a 1 mm wide collar around the stem; in penultimate branches this basal collar widens to form a sheaf around the stem. (Adapted from Barthel, 1976, 2016).

Remarks—This fossil–species was first described as *Casuarinites stellatus* Schlotheim from the Autunian Halle Formation, Wettin, Saxony (Schlotheim, 1804, pl. 1, fig. 4; 1820), but that species name is invalid (ICN, Art. 13.1). Sternberg (1821) later published the name *A. spinulosa* based on types of similar stratigraphical age from Autunian deposits in Dresden. Sternberg (1825) subsequently regarded *A. spinulosa* to be synonymous with *Casuarinites stellatus* but, as Schlotheim’s species epithet is invalid, Sternberg’s epithet takes precedence (Barthel, 1976, 2000, 2004, 2016). *Annularia longifolia* was illegitimately introduced by Brongniart (1828) to replace *Casuarinites stellatus* and so is also a heterotypic synonym of *A. spinulosa*.

Annularia spinulosa differs from most of the species in this group by having isophyllous whorls of leaves with an acuminate rather than obtuse or acute apex. The nearest comparison is with *A. noronhai*, whose leaves have an even more elongate, caudate apex.

The plant that bore *A. spinulosa* foliage has been reconstructed as an essentially monoaxial plant about 2 m tall (Fig. 9). The main trunk (known as *Calamites multiramis* (Weiss) Kidston & Jongmans) bore numerous scars along its length suggesting the branches were progressively abscised as the plant grew. Much of the foliage was formed as a loose distal crown on the trunk, together with large *C. tuberculata* strobili up to 200 mm long.

Distribution—Variscan intramontane basins (Stephanian C–Sakmarian); southern Variscan foreland (Stephanian C).

Annularia aff. *carinata* Gutbier

Diagnostic description—Strongly anisophyllous whorls of up to 25 leaves. Leaves up to c. 25 mm long, 3 mm wide, strongly oblanceolate with an obtuse apex lacking a distal mucronate tip. Leaves basally fused to form a 1.0–1.5 m wide collar around stem.

Remarks—These specimens from New Mexico and Texas (USA) were originally identified as *A. carinata* and have similar anisophyllous leaf whorls (DiMichele *et al.*, 2010, 2013, 2021; Xu *et al.*, 2018). However, they differ from

both *A. carinata* and *A. spinulosa* in having more bulbously oblanceolate leaves with an obtuse apex. As I have not seen the fossils themselves, I have refrained at this stage from formally giving them a new species name.

Distribution—Far western palaeotropical Euramerica (Autunian).

DISCUSSION

Distribution

Being based mainly on a literature review, the data summarised here on the distribution of the *A. stellata* auct. fossil foliage are unlikely to be complete. There are, for instance, records of *A. stellata* from Upper Silesia (Zdanowski & Żakowa, 1995) and north–western Africa (Jongmans, 1950, 1952) that are unillustrated and so difficult to judge in the context of the taxonomy proposed here. Nevertheless, these preliminary results suggest that at least seven distinct morphological forms (Fig. 3; Table 1) probably merit taxonomic recognition and which unlike previously recognised taxa (e.g., as in Diéguez 1985) have different stratigraphical and palaeogeographical distributions (Figs 10, 11).

The stratigraphically earliest examples are the whorls of large, relatively lax leaves of *A. stradonicensis*, from uppermost Duckmantian intramontane deposits of the Bohemian Massif. Although its large leaves look rather different from the other species in this group, its association with strobili similar to *Calamostachys tuberculata* indicates that it was foliage from the same general group of plants.

This is succeeded by the widespread *A. inflata*. The stratigraphically earliest occurrences are from near the base of the Bolsovian in the paralic deposits of Nord–Pas–de–Calais (France), the Ruhr (Germany), Dobrudzha (Bulgaria) and Upper Silesian (Poland). In South Wales, it appears somewhat higher (upper Bolsovian), a delay interpreted by Cleal (2007) as being due to the persistence of marine flooding in this basin (Dusar *et al.*, 2001). In the paralic basins where marine influence was even more persistent during the late Westphalian such as the Midcontinent and Appalachian basins (USA) and the Donets (Ukraine), *A. inflata* tends to be rare until the uppermost Asturian and Cantabrian. The range of these plants therefore seems to have been partly controlled by the extent of marine flooding in an area, which may have affected substrate conditions (see also comments Tenchov & Thomas, 2015, p. 5–6).

Annularia inflata is rarer in the Westphalian of the intramontane basins of the Variscan Mountains. In Saar–Lorraine it does not appear until the upper Sulzbach Formation (upper Bolsovian) and then only relatively rarely, and does not become abundant until the upper Asturian. In Central and Western Bohemia, it does not occur until the Nýřany Member (upper Asturian–lower Cantabrian). This proliferation in

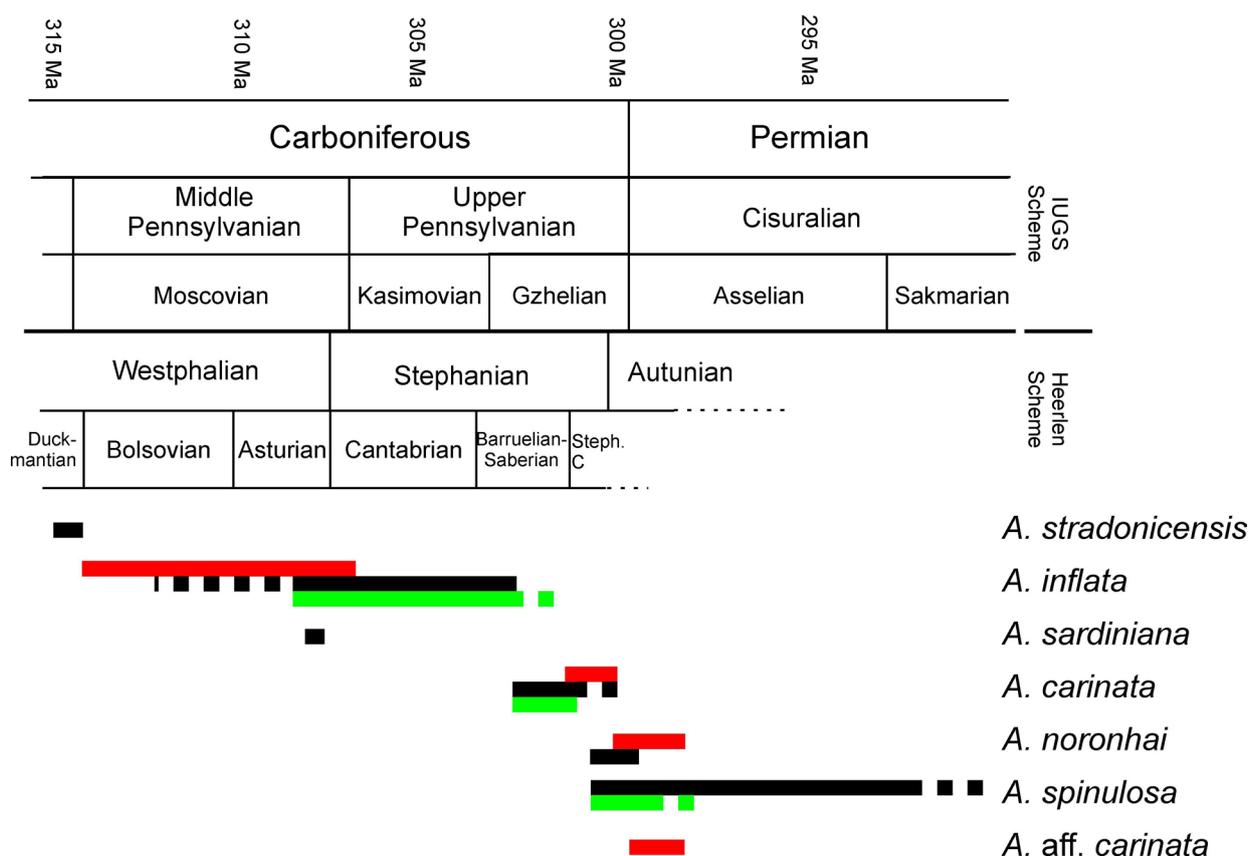


Fig. 10—Summary of chronostratigraphical distribution of the seven fossil-taxa previously assigned to *Annularia stellata*, plotted against the IUGS Global Chronostratigraphical Scheme (Cohen *et al.* 2013), based on stratotypes in marine sequences, and the Heerlen Regional Chronostratigraphy (Wagner 1974; Wagner & Winkler Prins 2016; Knight *et al.* 2023) based on coal-bearing sequences in Euramerica. First three columns show the system, series and stages of the IUGS scheme, the fourth and fifth columns show the stages and substages of the Heerlen scheme.

the upland wetlands therefore seems coincident with the major change in the coal swamp vegetation that occurred in the late Asturian, with the expansion of somewhat better-drained substrates supporting a marattialean–medullosalean dominated vegetation (e.g., Cleal *et al.*, 2007, 2009).

Annularia inflata foliage is at its most widespread in the upper Asturian and lower Cantabrian, occurring across (1) the paralic basins north of the Central Pangaeen Mountains from northern Venezuela and the USA in the west to the Ukraine and Turkey in the east, (2) the southern Variscan Foreland in Spain, and (3) the Variscan intramontane basins (Saar–Lorraine, Bohemian Massif). However, the habitat that supported these plants contracted dramatically during the middle Cantabrian following landscape disruption caused by uplift of the Central

Pangaeen Mountains and climate change with the onset of the Late Pennsylvanian Interglacial (Opluštil & Cleal 2007; Cleal *et al.* 2007, 2009). During middle Cantabrian to Barruelian times coal swamps became restricted mainly to the southern foreland of the Variscan Orogen (notably in the Iberian Peninsula) and intermittently in the Variscan intermontane basins (notably in central and southern France), although the plants producing *A. inflata* continued to flourish here.

The coal swamps underwent a partial recovery in Saberian times, with coal-bearing deposits of this age occurring notably in the Appalachians, the Massif Centrale of France, Saar–Lorraine and the Bohemia Massif, as well as over the southern Variscan Foreland (the Iberian Peninsula, the Carnic Alps and the Balkans). Remnant populations of *A.*

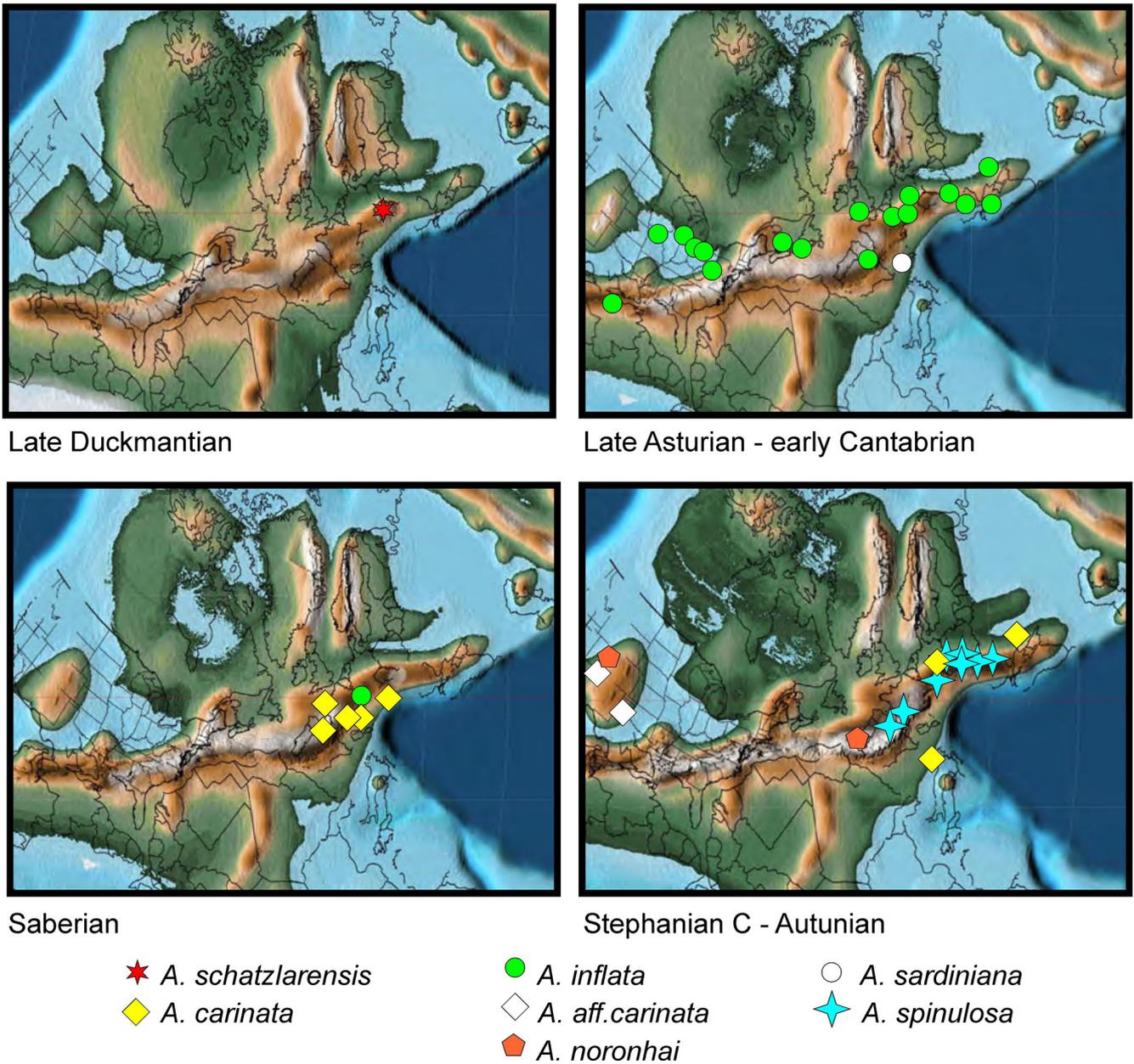


Fig. 11—Documented occurrences of large-leaved *Annularia* foliage previously assigned to *Annularia stellata*, plotted on palaeogeographical maps for the late Duckmantian (late Bashkirian), late Asturian–early Cantabrian (late Moscovian), Saberian (late Kasimovian) and Stephanian C–Autunian (late Gzhelian). Base maps based on Scotese (2014), showing the Central Pangaeian Mountains (in brown) and the foreland areas to the north and south (in green).

inflata bearing plants occurred in the uplands of the Bohemian Massif. However, in most other areas the leaf whorls became more anisophyllous and somewhat smaller, and the individual leaves more distally tapered—forms differentiated as *Annularia carinata*.

Variscan orogenesis and climate change caused further habitat fragmentation of the coal swamps during the latest

Stephanian and early Permian. Nevertheless remnant “wet-spots” (sensu DiMichele *et al.*, 2006) in otherwise well-drained areas remained widespread through the early Permian, including in new areas such as the far west of palaeotropical Euramerica (Texas and New Mexico). There is an increase in taxonomic diversity of these large-whorled forms of *Annularia* at this time, perhaps due to speciation triggered

by the habitat partitioning. *Annularia carinata* continues to occur in lowland paralic areas such as in the Donets and the southern Variscan foreland, whereas in the more upland wetland habitats there are isophyllous whorls of apically more tapered to spinose leaves of *A. spinulosa* and *A. noronhai*, and yet another, unnamed species (*A. aff. carinata*) occurs in the far west of Euramerica. Despite this diversification, however, these distinctive equisetopsids eventually disappear during the early Permian, with the stratigraphically youngest occurrences being in the Sakmarian of New Mexico and central Germany (and possibly the Artinskian in New Mexico, although the species identity of these specimens remains uncertain—DiMichele & Lucas, 2017).

These large-leafed *Annularia* species were clearly major elements of the clastic substrate vegetation on levees and floodplains in the coal swamps, and at their most widespread during the late Asturian–early Cantabrian ranged over nearly one million km² of palaeotropical Euramerica (areas estimates based on Cleal & Thomas, 2005). This presumably reflects the wide dispersal potential of such spore-bearing plants and their success in adapting to the clastic substrates. There is little evidence of these equisetopsids in the Westphalian–age coal–ball floras (e.g., Phillips, 1980), suggesting the earlier species (notably *A. inflata*) were not adapted to the peat substrate habitats. However, remains of the plant that produced *A. spinulosa* preserved in situ in Saxony (Germany) suggest the later forms may have also become adapted to growing in localised areas of peat accumulation (Schneider *et al.*, 2008).

Taxonomy

Distinguishing these seven fossil–taxa can be difficult, especially when dealing with isolated or poorly–preserved specimens, and this raises the question as to the taxonomic rank at which they should be recognised; would differentiating them as varieties or even forma be preferable? It was decided here to recognise them as full fossil–species, partly to avoid the cumbersome trinomial nomenclature that is inherent with taxonomic ranks below species. Moreover, each of the fossil–species seems to have a distinct stratigraphical and palaeogeographical distribution (Figs 10, 11), suggesting that they do not merely represent morphological intra–species variation; this is also supported by the fact that the two end members of the range (the Duckmantian *A. stradonicensis* and the early Permian *A. spinulosa*) are quite distinct from one another. The decision is obviously subjective, but distinguishing them as fossil–species seems to be the more practical and informative option.

In view of the attempts to reconstruct these plants (Hirmer, 1927; Remy & Remy, 1978; Daviero & Lecoustre, 2000; Rößler & Noll, 2007a, b), should we be looking to recognise whole–plant taxa? The problems that arise when trying formally to name whole–plant taxa from the fossil record has been extensively discussed (Chaloner, 1986; Crane,

1984; Bomfleur *et al.*, 2013; Cleal & Thomas, 2021) and it is evident that it usually causes more problems than it solves; it is better to merely use an informal nomenclature for such reconstructions such as in this case “the *Annularia*–plant”. But what about combining the fossil–taxa for the foliage and strobili, as these distinctive large–leafed *Annularia* species seem to be regularly associated with similar strobili? If a reasonably consistent correlation could be demonstrated between these types of foliage and strobili, then this might prove to be taxonomically useful, but this correlation needs to be more firmly demonstrated before it becomes a prudent route to take. Also, it would be necessary to consider the consequence for the stability of the general taxonomy. After all, *A. spinulosa* is the nomenclatural type of *Annularia* so, if the circumscription of *A. spinulosa* is changed to include the *C. tuberculata* strobili, what happens to a fossil–species such as *Annularia pseudostellata* which also has relatively large whorls of leaves but is associated with quite different, *Cingularia* strobili? Eventually, these problems might be solvable, but much more work will be needed on the correlations of the different types of foliage and strobili. At least for the time being, the fossil–taxa of the foliage and strobili are best kept separate.

CONCLUSIONS

Fossil foliage historically referred to as *Annularia stellata* (or its homotypic synonym *Annularia longifolia*) is consistently associated with distinctive strobili often known as *Calamostachys tuberculata*. They are the foliage of a taxonomically coherent (“natural”) group of plants but within which at least seven distinct fossil–species can be recognised, each with its own geographical and stratigraphical range. The group of plants originated in the upland intramontane coal swamps of the Variscan Mountains during Duckmantian times and then during the Bolsovian invaded lowland paralic areas of the Variscan Foreland, as part of a major reconfiguration of the coal swamp vegetation also seen with the medullosalean pteridosperms and herbaceous lycopsids (Thomas, 1997; Falcon–Lang, 2004; Thomas & Cleal, 2017; Cleal & Cascales–Miñana, 2019; Šimůnek & Cleal, 2020). This was part of a major reconfiguration of the coal swamp biotas known as the Morganian–Ammanian transition in the middle Bolsovian (e.g., Trueman, 1946) and coincided with global climatic cooling (the onset of the Late Palaeozoic Ice Age Glaciation Phase C4–Fielding *et al.*, 2008, 2023) causing a drop in sea levels and so less–frequent marine flooding of the paralic basins, and enhanced substrate drainage as the Central Pangaeon Mountains expanded northwards (e.g., Jones, 1991, 1989; Gayer *et al.*, 1993).

The coal swamp biome underwent further significant disruption during the Stephanian due to orogenic habitat fragmentation and climate change, but these large–leafed equisetopsids continued to flourish in the remnant refugial

areas. During this time there was a trend towards smaller whorls of more tapered and eventually more apically-acuminate to caudate leaves, and larger strobili. Leaves with an acuminate-caudate apex invite comparison with drip-tips found in plants growing under conditions of high precipitation (e.g., Malhado *et al.*, 2012) but is unlikely in this case; the Stephanian saw relatively low precipitation in palaeotropical Euramerica, at least compared with Westphalian times (e.g., Besly, 1986; Tabor & Poulsen, 2008).

These large-leaved equisetopsids disappeared from Euramerica in the early Permian, at about the same time as a similar coal swamp biome was developing in Cathaysia (Hilton & Cleal, 2007). There is some evidence of large *Annularia* whorls in these Cathaysian floras (e.g., Halle, 1927) but they are not accompanied by strobili similar to *Calamostachys tuberculata*, suggesting this was adaptive convergence of foliage morphology rather than indicating phylogenetic relationship. It would seem, therefore, that these large-leaved equisetopsids were a major, characteristic component of the Euramerican coal swamps during the second half of its history, from Moscovian to Sakmarian times.

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