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Ginkgophytopsis Høeg 1967 emend., a reclassification of enigmatic cuneate leaves of the Euramerican Upper Carboniferous

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ABSTRACT. In Upper Carboniferous Euramerican floras, the generic affinities of enigmatic, cuneate to flabellate "*Ginkgo*-like" leaves remain poorly understood. The species *Cordaites grandifolius* (USA), *Noeggerathia flabellata* (U.K.) and *Ginkgophyllum delvalii* (Western and Central Europe) have been taxonomically studied and compared, but no formal reclassification nor assessment of the North American form in relation to the European specimens has been conducted prior to this study. Reinvestigation of the holotypes and additional material of these species indicates that they do not conform to their current generic assignments on the basis of laminar morphology, axis structure and paleogeographic range. Here, we synonymize the three aforementioned species under the name *Ginkgophytopsis flabellata*, which we also emend. This study summarizes the complex taxonomic history of some of the Late Paleozoic "ginkgophytes," and we also emend the genus *Ginkgophytopsis* on the basis of our morphological reassessment of *G. flabellata*.

KEYWORDS: Pennsylvanian, Silesian, Late Paleozoic, taxonomy, ginkgophytes

INTRODUCTION

Among the known flora of the Pennsylvanian Subperiod (323.2–298.9 Ma), there are plant remains that stand in stark contrast to the commonly occurring dominant taxa, and even are notably different from widely distributed but rare taxa. Among these forms are large, cuneate to flabellate, apetiolate leaves, often apically lobate and possessing open-dichotomous venation: *Ginkgophyllum delvalii* from Western and Central Europe; *Cordaites grandifolius* from the USA; and *Noeggerathia flabellata* from the U.K. Their form is, in some aspects, superficially similar to leaves of the extant genus *Ginkgo*, and they have been considered ginkgophytes by some (White, 1900; Cambier and Renier, 1910; Gothan and Kukuk, 1933; Arnold, 1949; Taylor et al., 2009). Others, however, have assigned these species to the Cordaitales (Lesquereux, 1878, 1880; Seward, 1919; Noé, 1925; Jongmans, 1928, 1932), a Carboniferous seed plant clade considered to be the sister group to the conifer lineages.

The broader affinities of these Paleozoic "ginkgophytes" have never been established, including their affinity with the seed plants or even their evolutionary relationships to

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one another. Here, we investigate the complex taxonomic history of the species *G. delvalii*, *C. grandifolius* and *N. flabellata*, all large, flabellate to cuneate leaves of disputed affinity. As these taxa have been frequently compared historically and possess no consistent morphological dissimilarities or chronostratigraphical separation, we here synonymize them under the name *Ginkgophytopsis flabellata*.

TAXONOMIC BACKGROUND

Ginkgophyllum delvalii (Cambier et Renier 1910) Gothan et Kukuk 1933

Ginkgophyllum Saporta 1875 includes cuneate, twice symmetrically bilobate, apetiolate laminae with parallel, dichotomous, non-anastomosing venation that is especially prominent along the lateral margins of distal lobes (Høeg, 1967; Archangelsky and Cúneo, 1990; Césari and Hünicken, 1992; Taylor et al., 2009; Bauer et al., 2013; Decombeix et al., 2021). *Ginkgophyllum* (*Psygmophyllum*) *delvalii* (Cambier et Renier 1910) Gothan et Kukuk 1933 was first described from the Middle Westphalian A (Silesian, Carboniferous) of the Charleroi Coalfield in Belgium (Table 1, Fig. 1). It is known from cuneate to flabellate, occasionally longitudinally incised laminae up to 35 cm in length with lobed apices, concave lateral margins, and open-dichotomous venation with interveinal striae running parallel to the veins (Fig. 2) (Cambier and Renier, 1910; Kukuk and Gothan, 1932; Høeg, 1942, 1967; Josten, 1991; Josten and Van Amerom, 2003; Taylor et al., 2009). Smaller leaves are typically distinctly cuneate with an arcuate apical margin (Fig. 2A, B, D), but larger specimens often attain a more flabellate form (Fig. 2C) (also see Remy and Remy, 1977: fig. 64). Cambier and Renier (1910) originally placed this species in *Psygmophyllum* Schimper 1870, but recognized that its leaves are much larger than others within that genus. *Pysgmophyllum delvali* was reassigned to *Ginkgophyllum* by Gothan and Kukuk (1933), despite Cambier and Renier (1910) excluding it from this genus due to its lack of thick marginal venation. Høeg (1967) later renamed the species *Ginkgophytopsis delvalii* (see Discussion for notes on this reorganization). We have retained the name *Ginkgophyllum delvalii* for the purposes of the present study in order to avoid confusion, and as there does not seem to be a consensus on the nomenclature.

Several specimens of *G. delvalii* display leaves borne on longitudinally striate, narrow, channeled axes, but these have not been described formally, nor were we able to obtain rights to publish these photographs. Šusta (1932: pl. IV, fig. 1) figured a supposed leafy branch of *G. delvalii* that resembles a cordaitalean axis (*sensu* Bureš et al., 2023), but upon reviewing the specimen, we have determined that the leaf fragments are too incompletely preserved to identify confidently; in fact, the only distinctly distally widening lamina preserved on this slab is situated at a level in the matrix below the branch specimen and its attached leaves. Different forms of seed or pollen sac-like structures ("telangia") have been reported alongside *G. delvalii* specimens (Šusta, 1932: pl. VI, fig. 7; Gothan and Kukuk, 1933: pl. II), but none have been found preserved in connection to the leafy axes of this plant and thus their association is unconfirmed. The known geographic range of *G. delvalii* includes Belgium, the Czech Republic, Germany and Poland (Cambier and Renier, 1910; Šusta, 1925; Kukuk and Gothan, 1932; Stockmans and Willière, 1951, 1952; Josten and van Amerom, 2003; Taylor et al., 2009).

Cordaites grandifolius Lesquereux 1878

Cordaites Unger 1850 encompasses lanceolate to spatulate leaves with semilunate bases, bluntly acute apices, and fine, parallel, occasionally dichotomous venation with longitudinally disposed, fibrous interveinal striae (Unger, 1850; Grand'Eury, 1877; Lesquereux, 1878, 1880; White, 1900; Potonié and Gothan, 1921). An enigmatic plant assigned to this genus, *Cordaites grandifolius* Lesquereux 1878, was described from the Early to Middle Pennsylvanian Pottsville Formation in Pennsylvania, USA (Table 1, Fig. 1). It is known from irregularly incised cuneate to flabellate laminae of a coriaceous texture with fine, open-dichotomous venation with parallel interveinal striae, irregularly lobate distal margins, and an often torn leaf base (Figs 3–6). The holotype (Fig. 3C, D) is the largest specimen ever figured (38 cm laminar length), but Lesquereux (1878) makes mention of larger leaves left unfigured.

Little published data exist on axes or reproductive structures associated with these laminae. Lesquereux (1880) describes several

Table 1. Occurrences of specimens of *Cordaites grandifolius*, *Ginkgophyllum delvalii* and *Noeggerathia flabellata* in order of discovery

Classification	Formation and locality	Age	Citation
Noeggerathia flabellata	Bensham Seam, Carboniferous coal measures at Jarrow Colliery, Jarrow, Tyne and Wear, U.K.	Middle Westphalian A, Silesian, Carboniferous	Lindley and Hutton, 1831
Cordaites grandifolius	Interconglomerate coal measures, Pottsville Formation, Campbell's Ledge near Pittston, Pennsylvania, USA	Early or Middle Pennsylvanian, Carboniferous	Lesquereux, 1878, 1880
Ginkgophyllum delvalii	Schist of roof of Duchesse layer, Hamendes Shaft, Charbonnages Réunis, Charleroi Coalfield, Jumet, Belgium	Middle Westphalian A, Silesian, Carboniferous	Cambier and Renier, 1910
Ginkgophyllum delvalii	Duchesse layer, Hamendes Shaft, Charbonnages Réunis, Charleroi Coalfield, Jumet, Belgium	Westphalian B, Silesian, Carboniferous	Renier, 1910
Ginkgophyllum delvalii	Roof of Coal seam 16 (804), Františka Mine (Grube), Karviná Formation, Doubrava Member, Upper Silesian Basin, Karviná, Czech Republic	Westphalian A, Silesian, Carboniferous	Šusta, 1925
Ginkgophyllum delvalii	Rhur District, North Rhine-Westphalia, Germany	Middle Westphalian A, Silesian, Carboniferous	Kukuk and Gothan, 1932
Ginkgophyllum delvalii	Constantin der Große Colliery, Bochum, North Rhine-Westphalia, Germany	Westphalian A, Silesian, Carboniferous	Collected by M. Hirmer in 1932 (Taylor et al., 2009)
Ginkgophyllum delvalii	Lower bituminous coal, hanging wall, Dickebank Seam, Constantin der Große Colliery, Bochum, Arnsberg, North Rhine-Westphalia, Germany	Westphalian A, Silesian, Carboniferous	Gothan and Kukuk, 1933
Ginkgophyllum delvalii	0.50 m above and 1.40 m below 8th vein under the Sainte-Barbe de Ransart vein, Aiseau-Presle coal mine and Sainte-Begge quarry, Middle and Upper Sippenaken Zones, Charleroi Coalfield, Jumet, Belgium	Westphalian B, Silesian, Carboniferous	Stockmans and Willière, 1951, 1952
Ginkgophyllum grandifolium	Undesignated formation below "Cycle A," quarries northwest of Grand Ledge, Eaton County, Michigan, USA	Pennsylvanian, Carboniferous	Arnold, 1949
Ginkgophyllum delvalii	Constantin der Große Colliery VI/VIIb, Bochum, North Rhine-Westphalia, Germany	Westphalian B, Silesian, Carboniferous	Remy and Remy, 1977
Ginkgophyllum delvalii	Ruhr District, North Rhine-Westphalia, Germany	Westphalian, Silesian, Carboniferous	Josten, 1991
Ginkgophyllum delvalii	Hagen-Vorhalle quarry, Hagen, Arnsberg, North Rhine-Westphalia, Germany	Marsdenian, Namurian B, Carboniferous	Josten and Van Amerom, 2003
Ginkgophyllum delvalii	Orzeskie Beds, Upper Silesian Coal Basin, Kopalnia Węgla Kamiennego Szombierki mine, Szombierki, Bytom, Poland	Westphalian B, Silesian, Carboniferous	NA – collected by M. Kania in 2025
Cordaites grandifolius	Youngstown, Mahoning County, Ohio, USA	Carboniferous	NA – unpublished J.S. Newberry manuscript

scattered "nutlets" similar in form to the fertile organs of *Cordaianthus*, as well as a narrow, channeled axis bearing an attached "flowering" raceme, but this specimen was not illustrated and cannot be located; neither the fructifications nor the raceme are suggested by Lesquereux (1880) to have been found in attachment to leafy axes of this species. The known geographic range of *C. grandifolius* is limited to Michigan, Ohio and Pennsylvania, USA (Table 1, Fig. 1). Noé (1925) and Darrah (1969) reported occurrences of this species at Mazon Creek in Illinois, but these specimens are so incomplete that they cannot be reasonably identified as *C. grandifolius*.

Noeggerathia flabellata Lindley et Hutton 1831

Noeggerathia von Sternberg 1821 was described from alternating obovate leaves arranged along a narrow axis. The species *Noeggerathia flabellata* Lindley et Hutton 1831 (Fig. 7) was named for large, flabellate laminae from the Bensham Coal Seam (Middle Westphalian A, Silesian, Carboniferous) at Jarrow Colliery, Jarrow, Tyne and Wear, and the Northumberland and Durham Coalfield, U.K. (Table1, Fig. 1). The holotype (Fig. 7A) is a large, flabellate, coriaceous leaf with an emarginate apex and fine, occasionally imperceptibly open-dichotomous venation (Lindley and Hutton, 1831). The paratype (Fig. 7C) displays multiple smaller laminae attached alternately by long, decurrent bases to a narrow, channeled axis (also see Fig. 7D, E). Lindley and Hutton (1831) classified this plant as a "palm" (*sensu* Brongniart, 1845), but it was later reassigned to the order Paleophyllales alongside *Ginkgophyllum delvalii* by Høeg (1967). This species is known only from northern England (Table 1, Fig. 1), although Asama (1967) and Kon'no (1968)

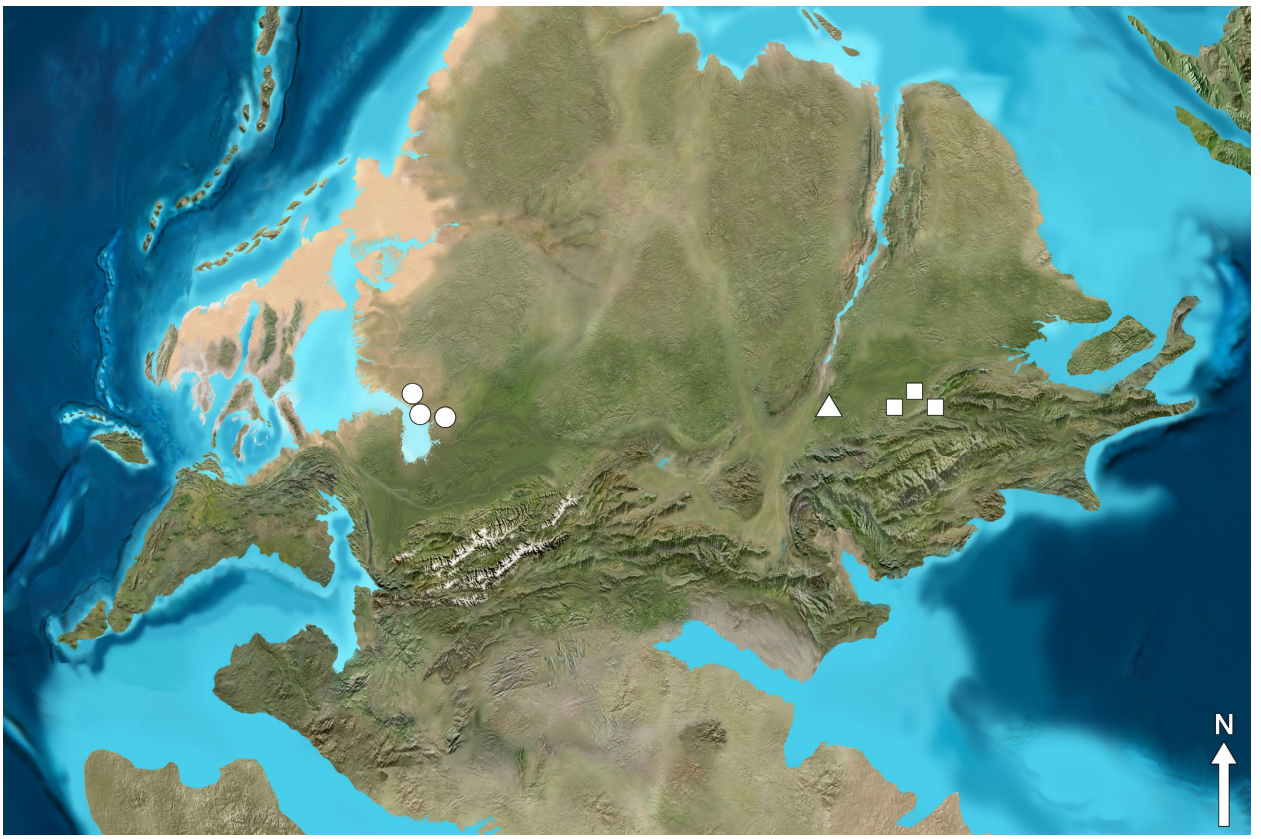

Figure 1. Pennsylvanian/Silesian Mollweide projection map of equatorial Euramerican Pangaea (~300 Ma) with approximate locations of *Cordaites grandifolius* (circles), *Ginkgophyllum delvalii* (squares), and *Noeggerathia flabellata* (triangle) specimens. Source map ©2023 Colorado Plateau Geosystems Inc.

assigned superficially similar leaves from Japan and China respectively to *N. flabellata*; these specimens, however, do not possess the overall flabellate form of this species, and we instead refer those described by Kon'no (1968) to *Rhipidopsis* Schmalhausen 1879.

MATERIALS AND METHODS

Ginkgophyllum delvalii specimens

We studied photographs of IRSNB a 10068 (holotype – Cambier and Renier, 1910) (Fig. 2A) and 6645 (Renier, 1910) (Fig. 2B) from the Institute of Natural Sciences in Belgium (IRSNB), as well as an additional *Ginkgophyllum delvalii* (no catalogue number – Taylor et al., 2009) (Fig. 2C) from the Bavarian State Natural Science Collections for Paleontology and Geology in Germany. IRSNB a 10068 and 6645 were collected from near the Duchesse layer of the Hamendes Shaft of the Charbonnages Réunis in the Charleroi Coalfield, Belgium (Table 1). The *G. delvalii* previously figured by Taylor et al. (2009) was collected from the Constantin der Große Colliery in Bochum, North Rhine-Westphalia, Germany (Table 1).

We also included in our analysis PP 63656 (Fig. 2D, E) from the Field Museum of Natural History (FMNH) in Chicago, Illinois. This specimen was collected from the Orzeskie Beds of the Upper Silesian Coal Basin at the closed Kopalnia Węgla Kamiennego Szombierki mine in Szombierki, Bytom, Poland (Table 1).

Cordaites grandifolius specimens

We examined USNM P19105 (holotype – Lesquereux, 1878) (Fig. 3C, D) and USNM P19103 (paratype – Lesquereux, 1878) (Fig. 3A, B) from the Smithsonian National Museum of Natural History (USNM) in Washington, D.C., as well as UP 2525 (Fig. 4B, C, E), UP 2529 (Fig. 4D), and P 22203 from FMNH. All of these specimens occur in gray siltstone from the Pottsville Formation at Campbell's Ledge, approximately 4 km north of Pittston, Luzerne County, Pennsylvania, USA (Table 1).

Photographs were investigated of the *Ginkgophyllum* (*Cordaites*) *grandifolium* holotype 25042 (Arnold, 1949) (Fig. 5A) from the Saginaw Formation in Grand Ledge, Eaton County, Michigan, USA (Table 1). This specimen is housed at the University of Michigan Paleontology Museum in Ann Arbor, Michigan. From the FMNH collections, we also studied PP 62538, PP 62539, PP 62540, PP 62541, PP 62542, PP 62543, PP 62544 (Fig. 5B), PP 62545 (Fig. 5C), 62546, and 62548, all preserved in gray siltstone from the North Quarry of Grand Ledge.

From the Yale Peabody Museum of Natural History (YPM), we examined photographs of YPM PB 023709 (Fig. 6A) and YPM PB 23332 (Fig. 6B, C), the former of which is from Youngstown, Mahoning County, Ohio, USA, and Carboniferous in age (Table 1) – the

latter has no locality information. The label of YPM PB 023709 does not report a formation, but mentions an unpublished manuscript by J.S. Newberry that we were unable to locate.

Noeggerathia flabellata specimens

We studied photographs of NEWHM G72.46 (holotype – Lindley and Hutton, 1831) (Fig. 7A), NEWHM G74.15 (paratype – Lindley and Hutton, 1831) (Fig. 7C), and NEWHM G26.60 (Fig. 7B) from the Bensham Seam of the Carboniferous coal measures at Jarrow Colliery, Jarrow, Tyne and Wear, U.K. (Table 1), as well as NEWHM G28.10 (Fig. 7D, E) from the Carboniferous coal measures of the Northumberland and Durham Coalfield, U.K. (Table 1). These specimens are housed at the Great North Museum: Hancock (NEWHM) in Newcastle upon Tyne, U.K.

CUTICLE EXTRACTION

We unsuccessfully attempted to extract cuticle from the specimens UP 2525, UP 2529, P 22203, PP 62538, PP 62544 and PP 62545; to our knowledge, no cuticle has ever been obtained from *Ginkgophyllum delvalii*, *Noeggerathia flabellata*, or other specimens/taxa with similar gross morphology.

PHOTOGRAPHY AND IMAGE PROCESSING

We photographed specimens housed at FMNH with a Nikon Z 7II camera and NIKKOR Z 35 mm f/1.8 S and NIKKOR Z MC 105 mm f/2.8 VR S lenses. We used Adobe Photoshop 2025 to produce composite images from photographs with different fields of focus and Camera Raw Editor to adjust contrast, white balance, exposure, etc. for complete images.

SYSTEMATICS

Here we emend the diagnoses of *Ginkgophytopsis* Høeg 1967 and *Ginkgophytopsis flabellata* Høeg 1967 to include an accurate description of the apetiolate, decurrent leaf bases, alternate foliar arrangement, and channeled axes present on the holotype of the type species. We also synonymize the species *Ginkgophyllum delvalii*, *Cordaites grandifolius*, and *Noeggerathia flabellata* under the name *Ginkgophytopsis* (*Noeggerathia*) *flabellata* (Lindley et Hutton 1831) Høeg 1967, the lattermost epitheton having priority.

Ginkgophytopsis (Høeg 1967) emend. Pratt et al.

Diagnosis. Large flabellate to cuneate laminae of coriaceous texture without a midrib, often irregularly distally incised or lobate but rarely symmetrically bifurcate. Venation fine, dense, often imperceptibly open-dichotomous with thin, occasionally anastomosing striae between veins. Leaves apetiolate with decurrent bases, alternately arranged on narrow, channeled axes. Reproductive structures unknown.

Ginkgophytopsis flabellata (Lindley et Hutton 1831) Høeg 1967 emend. Pratt et al.

Figs 2–7

Synonymies and selected references. (For a complete list of name references, see Supplementary File 1[1]).

1831 *Noeggerathia flabellata* Lindley et Hutton, pp. 89–90, pl. XXVIII and XXIX.
1870 *Psygmophyllum flabellatum* Schimper, p. 193.
1878 *Cordaites grandifolius* Lesquereux, pp. 318–319.
1879 *Cordaites grandifolius* Lesquereux, pl. LXXVII, figs 1–2a.
1878a *Ginkgophyllum flabellatum* Saporta, p. 873.
1910 *Psygmophyllum delvali* Cambier et Renier, pl. VI, fig. 1.
1910 *Psygmophyllum delvali* Renier, pl. CXVIII.
1912 *Psygmophyllum flabellatum* Arber, pp. 392, 394–395, 397–404, pl. XLII, figs 2 and 3, pl. XLIII, fig. 7, pl. XLIV, figs 8, 10, and 11.
1919 *Psygmophyllum flabellatum* Seward, pp. 80–81, 84–85, 87–88, figs 665 and 666.
1925 *Psygmophyllum purkyněi* Šusta, figs 1 and 2.
1932 *Cordaites delvali* Jongmans, fig. 42.
1932 *Psygmophyllum delvali* Kukuk et Gothan, pp. 725, 727, figs 1–3.
1933 *Ginkgophyllum delvali* Gothan et Kukuk, pp. 66–73, pl. A.
1933 *Ginkgophyllum purkyněi* Gothan et Kukuk, p. 73.
1938 *Ginkgophyllum delvali* Kukuk, pp. 175–176, figs 188 and 208.
1942 *Ginkgophyton delvali* Høeg, pp. 110, 112.
1949 *Ginkgophyllum grandifolium* Arnold, pp. 224–225, pl. XXXI, fig. 3.
1951 *Ginkgophyton delvali* Stockmans et Willière, pp. 16–17, pl. A, figs 1 and 2.
1952 *Ginkgophyton delvali* Stockmans et Willière, pp. 32, 47–48, 76, 300, pl. XXVII, figs 1–3.
1967 *Ginkgophytopsis delvalii* Høeg, p. 378.
1967 *Ginkgophytopsis flabellata* Høeg, p. 376, fig. 296.
1977 *Ginkgophytopsis delvalii* Remy et Remy, figs 63 and 64.
1991 *Ginkgophyllum delvali* Josten, p. 352, pl. CCXIV.
2003 *Ginkgophyllum delvali* Josten et Van Amerom, pp. 59, 65, pl. CXV.
2009 *Ginkgophytopsis delvalii* Taylor et al., p. 664, fig. 16.30.

[1] Supplementary File 1: Complete list of Ginkgophytopsis flabellata synonymies

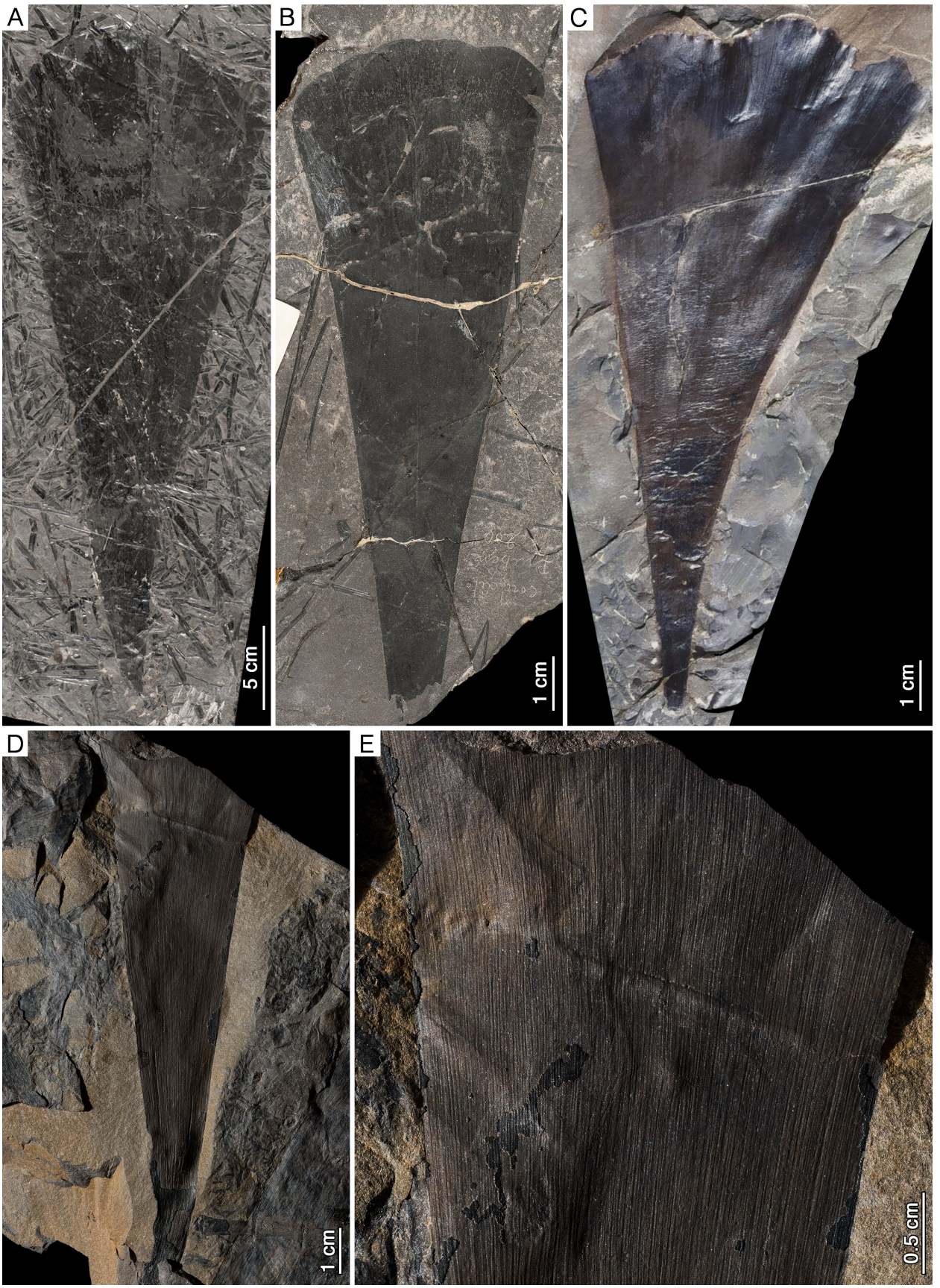

Figure 2. *Ginkgophytopsis flabellata* specimens (previously assigned to *Ginkgophyllum delvalii*) from the Charleroi Coalfield, Belgium (**A** and **B**), and Bochum, Germany (**C**). **A**. Holotype – IRSNB a 10068 (Cambier and Renier, 1910); **B**. 6645 (Renier, 1910); **C**. Specimen without catalogue number (Taylor et al., 2009); **D**. PP 63656; **E**. Closeup of venation near the distal margin of PP 63656. Photographs by J. Lalanne and T. Hubin (IRSNB) (**A** and **B**) and M. Krings (Bavarian State Natural Science Collections for Paleontology and Geology) (**C**), and the authors (**D** and **E**)

Figure 3. *Ginkgophytopsis flabellata* specimens (previously assigned to *Cordaites grandifolius*) from near Pittston, Pennsylvania, USA. **A**. Closeup of USNM 19103 leaf base. Arrow indicates vein dichotomy; **B**. Paratype – USNM 19103 (Lesquereux, 1878, 1879, 1880); **C**. Closeup of laminar incision on USNM 19105; **D**. Holotype – USNM 19105 (Lesquereux, 1878, 1879, 1880). Photographs by J. Nakano and J. Wingerath (USNM)

Excluded specimens.

1925 *Cordaites grandifolius* Noé, p. 15, pl. XLV, fig. 2.
1928 *Cordaites delvali* Jongmans, p. 46, pl. V, fig. 2.
1932 *Psygmophyllum delvali* Šusta, pp. 153–156, 158–163, pl. IV, figs 1, 2.
1967 *Psygmophyllum flabellatum* Asama, pp. 148–151, pl. II, fig. 1, pl. III, fig. 1.
1968 *Psygmophyllum flabellatum* Kon'no, pp. 164, 198, pl. XXIV, fig. 3, pl. XXV, fig. 1.
1969 *Cordaites grandifolius* Darrah, p. 185, pl. XLVIII, fig. 3.

Holotype. NEWHM G72.46 (Great North Museum: Hancock, U.K.) (Fig. 7A) Lindley and Hutton, pp. 89–90, pl. XXIX.

Geographic distribution. Belgium, the Czech Republic, Germany, the Netherlands, Poland, U.K., USA.

Stratigraphic occurrences. Namurian B–Westphalian B, Silesian, or Early–Middle Pennsylvanian, Carboniferous.

Diagnosis. Cuneate to flabellate, coriaceous, entire or distally emarginate or lobate but rarely symmetrically bilobate laminae attached by long, decurrent, apetiolate bases to narrow, channeled, longitudinally striate axes. Distal margin arcuate, lateral margins concave. Venation fine and often imperceptibly open-dichotomous with occasionally anastomosing interveinal striae running parallel to veins.

Description. Smaller laminae cuneate to spatulate (Figs 3B, 4B), assuming more flabellate form in larger specimens (Figs 3D, 5A–C, 7A, B). Laminae widen linearly from a basal angle of 10–37° and range from 10–52 cm long by 7–20 cm wide at widest point. Distal margin arcuate to linear and lobately incised in larger specimens (Figs 4E, 7B). Lateral margins concave. Leaf bases often torn, but apetiolate and decurrent when preserved in attachment to axes. Laminar surface coriaceous with fine, often imperceptibly open-dichotomous venation and occasionally anastomosing, parallel interveinal striae. Vein and interveinal stria concentration of 10–20 per cm basally and 20–50 per cm near apex. Some specimens preserved attached to a narrow, channeled axis that is longitudinally striate and possibly lignified (7C–E – also see note in Introduction about photographs). Reproductive structures unknown.

DISCUSSION

GENERIC COMPARISONS

There are similarities in the descriptions of *Cordaites grandifolius*, *Ginkgophyllum delvalii*, and *Noeggerathia flabellata* that have been previously investigated. Seward (1917) suggested that *C. grandifolius* and *G. delvalii* may be identical, and subsequently renamed the latter *Cordaites delvali* (Seward, 1919). Arnold (1949) reclassified *C. grandifolius* from the Saginaw Formation in Michigan, USA, as *Ginkgophyllum grandifolium*, recognizing its affinity with European "ginkgophytes." White (1900) also mentioned a possible ginkgoalean affinity in his description of *C. grandifolius*, and Jongmans (1928, 1932) later described Dutch specimens as *Cordaites delvali*. *Noeggerathia flabellata* and *G. delvalii* were grouped into *Ginkgophyton* (Høeg, 1942) and then *Ginkgophytopsis* (Høeg, 1967), and Arber (1912) investigated similarities between *N. flabellata* and *G. delvalii* (but referred the latter instead to a large *Cordaites* leaf).

Kukuk and Gothan (1932) and Josten (1991) both excluded *Ginkgophyllum delvalii* from *Cordaites* due to its dichotomous venation, but this is contradictory to the well-established presence of this feature in *Cordaites* (Grand'Eury, 1877; Lesquereux, 1878, 1880; White, 1900; Potonié and Gothan, 1921). Gothan and Kukuk (1933) sustained the exclusion of *G. delvalii* from *Cordaites* because of its cuneate form, but suggested a possible affinity with other cordaitaleans. Additionally, Cambier and Renier (1910) compared the longitudinal incisions in *G. delvalii* leaves to those commonly seen in cordaitaleans; they did not, however, consider these laminar incisions to be a true anatomical feature, but rather taphonomic damage or tears from wind exposure during life, an interpretation echoed by Høeg (1967) and Taylor et al. (2009). This represents a major morphological difference between *G. delvalii* and the *Ginkgophyllum* holotype, *G. grassetii* Saporta 1875, as the latter possesses a distinct bilobate pattern of laminar incision (Høeg, 1942, 1967; Retallack, 1980; Decombeix et al., 2021). Additionally, *Ginkgophyllum* laminae are characterized by prominent marginal venation, a feature not seen in *G. delvalii* (Fig. 2) (Cambier and Renier, 1910; Césari and Hünicken, 1992; Escapa and Cúneo, 2003; Decombeix et al., 2021).

Figure 4. Additional *Ginkgophytopsis flabellata* specimens (previously assigned to *Cordaites grandifolius*) from near Pittston, Pennsylvania, USA. **A**. UP 2529; **B**. UP 2525; **C**. Closeup of base of UP 2525; **D**. Closeup of leaf overlap in UP 2529. Top arrow indicates interveinal stria anastomosis, bottom arrow indicates vein dichotomy; **E**. Closeup of distal margin of UP 2525

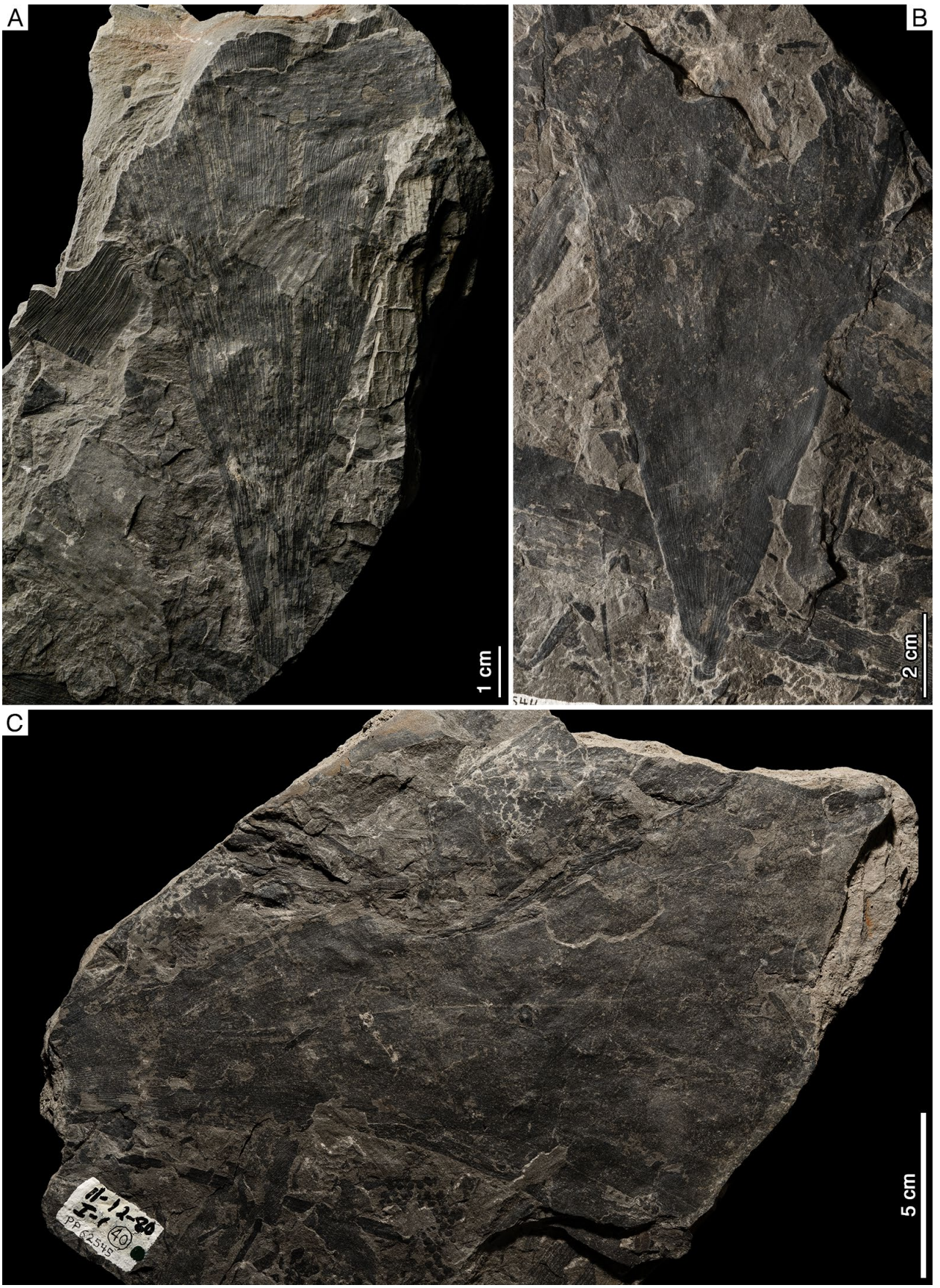

Figure 5. *Ginkgophytopsis flabellata* specimens (previously assigned to *Ginkgophyllum grandifolium*) from Grand Ledge, Michigan, USA. **A**. *Ginkgophyllum grandifolium* holotype – University of Michigan 25042 (Arnold 1949); **B**. FMNH PP 62544; **C**. FMNH PP 62545

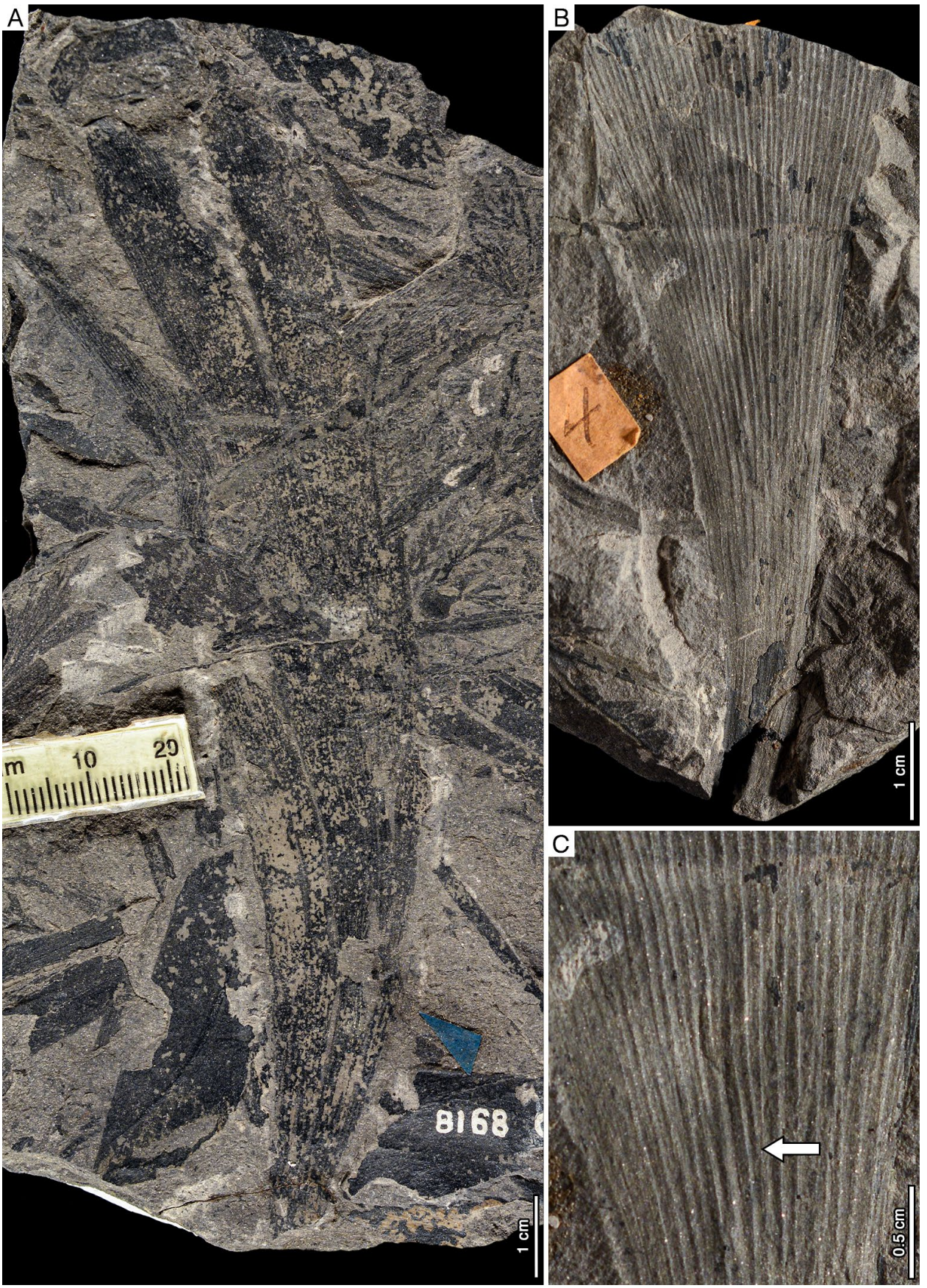

Figure 6. *Ginkgophytopsis flabellata* specimens (previously assigned to *Cordaites grandifolius*) from Youngstown, Mahoning County, Ohio, U.S.A (**A**) and an unknown locality (**B** and **C**). **A**. YPM PB 023709 (unpublished J.S. Newberry manuscript); **B**. YPM PB 23332; **C**. Closeup of YPM PB 23332. Arrow indicates vein dichotomy. Photographs by S. Hu (YPM)

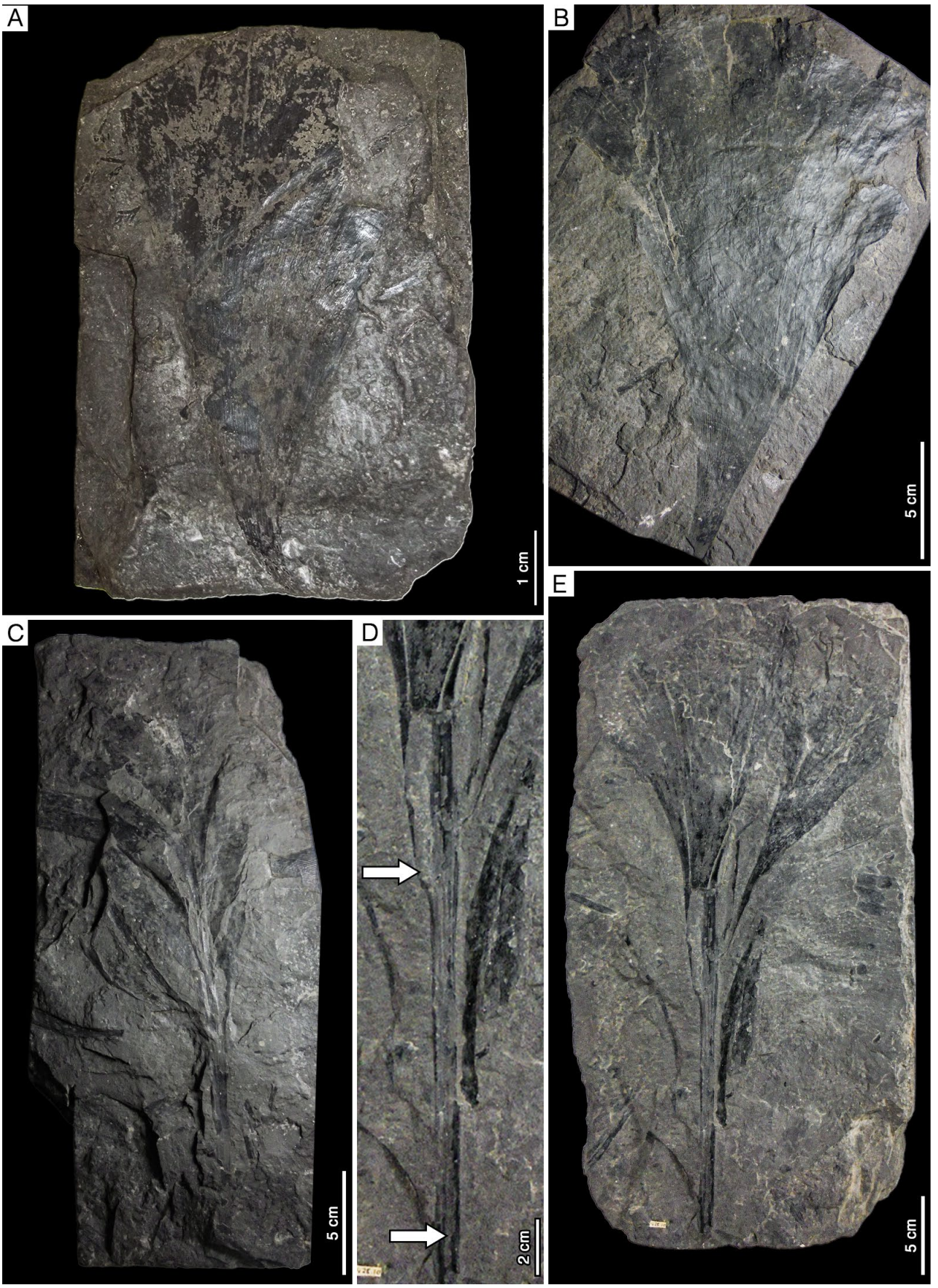

Figure 7. *Ginkgophytopsis flabellata* specimens (previously assigned to *Noeggerathia flabellata*) from Jarrow Colliery, Jarrow, Tyne and Wear, U.K. (**A–C**) and the Northumberland and Durham Coalfield, U.K. (**D** and **E**) **A**. Holotype – NEWHM G72.46 (Lindley and Hutton, 1831); **B**. NEWHM G26.60; **C**. Paratype – NEWHM G74.15 (Lindley and Hutton, 1831); **D**. NEWHM G28.10 closeup depicting axis and leaf attachment. Upper arrow indicates decurrent leaf base, lower arrow indicates channeled axis; **E**. NEWHM G28.10. Photographs by S. Humphrey and R. Metcalfe (NEWHM)

TAXONOMIC HISTORY

Both *Cordaites grandifolius* and *Ginkgophyllum delvalii* have been referred to *Noeggerathia* generally (Lesquereux, 1878, 1880; Kukuk and Gothan, 1932; Gothan and Kukuk, 1933), and have been specifically compared to *Noeggerathia flabellata* (Cambier and Renier, 1910; Šusta, 1932; Høeg, 1942, 1967), *N. obliqua* Göppert 1841 from Sweden, and *N. beinertiana* Göppert 1841 from Poland (Lesquereux, 1878). The inclusion of *N. obliqua* in this grouping is questionable as it is known only from the Devonian – in fact, Schimper (1870) suggested that it may instead be a *Macropterigium* leaflet. *Noeggerathia flabellata* and *N. beinertiana*, however, are known from the Carboniferous and appear quite similar to *C. grandifolius* and *G. delvalii*. Although there are no significant differences in the descriptions of *N. beinertiana* and *G. delvalii*, we have excluded the former from our study as we were unable to locate the holotype specimen figured by Göppert (1841). *Noeggerathia flabellata* and *G. delvalii* have been compared by Høeg (1942, 1967) and Arber (1912), and Gothan and Kukuk (1933) suggested grouping *N. flabellata* with *G. delvalii* to distinguish them from the genus *Psygmophyllum*. Høeg (1967) supported this comparison, placing both in *Ginkgophytopsis*.

The genus *Psygmophyllum* Schimper 1870 (to which *G. delvalii* was originally assigned) was created to separate the species *Noeggerathia flabellata*, *N.* (*Sphenopteris*) *cuneifolia* (Kutorga 1838) Brongniart 1845, *N. expansa* Brongniart 1845, and *N. ctenoides* Göppert 1864 from the type species *N. foliosa* von Sternberg 1821, to which they bear little resemblance (Renault, 1881; Cambier and Renier, 1910; Arber, 1912; Zalessky, 1912, 1918, 1929; Gothan and Kukuk, 1933; Burago, 1967; Høeg, 1967; Stone, 1973). *Psygmophyllum* (*Noeggerathia*) *flabellatum* was designated as the type species of *Psygmophyllum* by Arber (1912), Seward (1919), and Leclerq and Béllière (1928). Saporta (1878b) later reassigned *P. flabellatum* to his new genus *Ginkgophyllum*, splitting it from the Russian forms *P. cuneifolium* and *P. expansum* due to the geographical divide and the presence of a pronounced midrib in the latter two taxa (Zalessky, 1918, 1929; Gothan and Kukuk, 1933; Burago, 1967). Zalessky (1912) had also proposed the name *Palamophyllum* to separate the aforementioned Russian forms (introducing *Palamophyllum mongolicum* as well) from *N. flabellata*, but would later accept the synonymy of the genus with *Psygmophyllum* (Zalessky, 1918; Høeg, 1967).

Zalessky (1918) then erected *Ginkgophyton* to support the exclusion of *Noeggerathia flabellata* from *Gingkophyllum* by Arber (1912), also including in his new genus *Cyclopteris browniana* Dawson 1861, *Noeggerathia obtusa* Lesquereux 1854, *Psygmophyllum kidstoni* Seward 1903, *Psygmophyllum majus* Arber 1912, and *Psygmophyllum williamsoni* Nathorst 1894 (Høeg, 1942; Burago, 1967). Høeg (1942) excluded *N. obtusa*, *C. browniana*, *P. majus*, and *P. williamsoni* from *Ginkgophyton*, assigning the latter three instead to *Platyphyllum* Dawson 1882 (Høeg, 1967; Stone, 1973). *Ginkgophyton*, however, was already in use by Matthew (1910) for unrelated specimens from Canada, and Høeg (1967) later proposed the name *Ginkgophytopsis* for European and South African flabellate, occasionally distally sinuous leaves with dense, bifurcating venation attached to slender axes by long, decurrent petioles. He designated *Ginkgophytopsis* (*Noeggerathia*) *flabellata* as the type species and included *G. delvalii* in this genus as well. *Ginkgophytopsis* is, however, quite heterogenous, and *G. delvalii* and *G. flabellata* bear little resemblance to the other currently accepted forms: *Ginkgophytopsis belgica* Stockmans 1968 and *Ginkgophytopsis* (*Psygmophyllum*) *gilkinetti* (Leclerq et Béllière 1928) Høeg 1967 from Belgium; *Ginkgophytopsis* (*Ginkgophyton*) *giganteum* (Burago 1967) Burago 1977 from Russia (cf. *Saportaea* Fontaine et White 1880); and *Ginkgophytopsis* (*Psygmophyllum*) *kidstonii* (Seward 1903) Høeg 1967 from South Africa.

Ginkgophytopsis (*Ginkgophyllum*) *delvalii* was removed from this genus as part of Retallack's (1980) emendation, which encompassed cuneate leaves with long, decurrent bases, divided or frayed at the apex with anastomosing and dichotomous venation obscured by woody interveinal striae. He retained *Ginkgophytopsis* (*Noeggerathia*) *flabellata* as the type species and included in this grouping *Cyclopteris cuneata* Carruthers 1872 from Australia, Chile, and South Africa, *Ginkgophyllum scoticum* Høeg 1942 from Scotland, *Ginkgophytopsis kidstonii*, *Chiropteris lacerata* Arber 1913

from Argentina, Australia, Chile, New Zealand, and South Africa, and *Chiropteris tasmanica* Walkom 1925 from Argentina, Australia, and Tasmania. Retallack (1980) considered anastomosing venation to be a more important diagnostic feature than the longitudinal incisions of the laminae (*sensu* Høeg, 1967), as he deemed it too difficult to distinguish between taphonomic damage and true anatomical features; this, however, does not consider the pattern of symmetrical bilobation (including in the species introduced to the genus by Retallack [1980]) in the leaves of *Ginkgophytopsis* species other than *G. flabellata* and *G. delvalii*. Additionally, all of the newly included species, apart from *G. scoticum*, are Triassic in age and quite geographically distant from the known range of *G. flabellata*.

PALEOGEOGRAPHIC DISTRIBUTION AND CHRONOSTRATIGRAPHY

Despite the stark geographic divide in the modern distribution of the specimens now referred to *Ginkgophytopsis flabellata* (Table 1), a paleogeographic map (Fig. 1) demonstrates the proximity of what are now the Northeastern USA and Western and Central Europe and, thus, the location of these species on the same side of the Euramerican Variscan-Appalachian divide. These taxa also occupy nearly identical chronostratigraphic positions (Table 1), suggesting that they existed simultaneously: *Ginkgophyllum delvalii* from the Namurian B and Westphalian A–B, Silesian, Carboniferous; *Cordaites grandifolius* from the Early to Middle Pennsylvanian, Carboniferous; and *Noeggerathia flabellata* from the Westphalian A, Silesian, Carboniferous.

SYNONYMIZATION AND TAXONOMIC CONSIDERATIONS

We have synonymized *Cordaites grandifolius*, *Ginkgophyllum delvalii*, and *Noeggerathia flabellata* (the last of which is the senior synonym based on date of publication) under the name *Ginkgophytopsis flabellata* (Lindley et Hutton 1831) Høeg 1967 emend. Pratt et al. on the basis of their identical morphology (Figs 2–7) and chronostratigraphic placement (Table 1). Despite the still significant paleogeographic gap between the North American and European specimens (Fig. 1), we currently cannot identify any consistent morphological differences that would suggest these forms represent separate species; as such, we maintain their synonymy on the basis of morphology alone, but cuticular evidence or reproductive structures may reveal further insights into their potential differences. Furthermore, the apparent paleogeographic divide may be addressed by future reassessments of Canadian fossil floras that lie between these clusters of specimens.

We have rejected the separation of *G. delvalii* and *N. flabellata* by Høeg (1967), as we have not been able to identify any consistent distinguishing morphological features between them. Høeg (1967) differentiated the two species on the basis of size, overall form, and venation, but did not offer an explanation for the dissimilarities noted in the latter two characteristics. He also used a sample size of only six *G. delvalii* specimens from the type location to determine the size constraints of *G. delvalii*, but more recent specimens have expanded the lower end of this size range to comfortably include *N. flabellata*, which Høeg (1967) noted as being smaller than *G. delvalii*.

It is possible that there is a species-level distinction between *G. delvalii*, *C. grandifolius* and *N. flabellata*, but the lack of cuticular data and the paucity of specimens of the latter two make this affinity difficult to assess. For example, the *C. grandifolius* paratype (Fig. 3A, B) appears to possess significantly coarser venation than most of the other specimens considered here. The morphological differences seen across the leaf specimens examined and synonymized here likely represent natural variation reflective of position within the crown of the plant, whether they were borne on reproductive versus vegetative shoots, or whether they were borne on early developmental stages of the plant; alternatively, these differences could simply be explained taphonomically. There is, however, significant overlap and gradation between the more cuneate and flabellate forms in specimens assigned to *G. delvalii*, *C. grandifolius* and *N. flabellata*, and it is therefore impossible to assign any one of these species to a specific leaf morphology within *Ginkgophytopsis flabellata*. Until a much greater sample size of specimens in North America and the U.K. is obtained, it is difficult to draw any clear, consistent lines between these forms.

We have emended the diagnosis for *Ginkgophytopsis*, as that provided by Høeg (1967)

describes petioles and spiral leaf attachment that are not present in the type species *G. flabellata*. We do not support the retention of the name *Ginkgophytopsis* for *G. belgica*, *G. gilkinetti* and *G. kidstonii*, which exhibit more broadly-angled symmetrical bifurcation of the laminae that is contradictory to the generic diagnosis and not seen in the type species *G. flabellata*; we also reject Retallack's (1980) inclusion of *G. scoticum* and Triassic specimens from the Southern Hemisphere as discussed above. The splitting of a genus as heterogenous as *Ginkgophytopsis*, however, is beyond the scope of the present paper, and we have elected to retain the symmetrically bifurcate forms until such time as a more comprehensive generic review can be performed.

Despite the superficial similarities with and previous assignment of these leaves to the ginkgophytes (White, 1900; Cambier and Renier, 1910; Gothan and Kukuk, 1933; Arnold, 1949; Taylor et al., 2009), *Ginkgophytopsis flabellata* specimens lack the distinctive petiolate and symmetrically bifurcate laminae of *Ginkgo* and related taxa. Due to the absence of cuticular data and organically attached reproductive structures for this genus, however, we cannot confidently place it within any higher taxonomic category at this time. Further study of the seeds and "telangia" described by Gothan and Kukuk (1933) may suggest a ginkgophyte rather than cordaitalean affinity, but these structures have not been found at other localities with *Ginkgophytopsis* leaves (the seed or pollen organ figured by Šusta [1932] does not possess the same acute tips), and never in attachment to an axis with leaves that can be confidently assigned to *G. flabellata*. The broader evolutionary relationships of this species and genus will require further investigation, and may also necessitate cuticular evidence should these data become available.

HABITAT AND ENVIRONMENTAL CONTEXT

Ginkgophytopsis flabellata specimens occur in shales, siltstones and sandstones, and lack association with coal beds in much of Euramerica. This suggests that these plants may have been, under the model of alternating climate regimes in the Pennsylvanian Subperiod, drought-tolerant and prolific under seasonally dry climatic conditions (Cecil, 2003; Cecil et al., 2014; DiMichele, 2014; Bashforth et al., 2016; DiMichele et al., 2020, 2025). Indeed, Arnold (1949) noted the presence of *Megalopteris* specimens among his collection of "*Ginkgophyllum grandifolium*" from Grand Ledge, Michigan, and in the Field Museum of Natural History's A.T. Cross collection from the same area, *Ginkgophytopsis flabellata* is similarly found alongside *Megalopteris*. The latter is often associated with drought-tolerant floras, appearing most frequently in shales, siltstones, and sandstones that evidence seasonal, flashy discharge (Leary and Pfefferkorn, 1977; Bashforth et al., 2021). The abundance of *G. flabellata* under more humid regimes is as yet unknown, and the size of their laminae may prevent them from being accurately identified in coal-ball assemblages.

CONCLUSIONS

The complex history of the plants now synonymized under the name *Ginkgophytopsis flabellata* highlights the difficulties associated with taxonomic studies of the drought-tolerant floras of the Carboniferous, and this reorganization is a step toward better understanding the generic-level affinities of the so-called "ginkgophytes" of the Late Paleozoic. Our reassessment also calls attention to the gulf in communication between North American and European researchers, as the American specimens of *G. flabellata* were historically largely unknown to those studying European representatives of this species. We hope that this study will encourage greater collaboration among European and North American researchers attempting to study the distribution and taxonomy of enigmatic Paleozoic plant forms.

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ADDITIONAL INFORMATION

CONFLICT OF INTEREST. The authors have no conflicts of interest to declare.

ETHICAL STATEMENT. The authors have no ethical statement to make.

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