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Callipterid peltasperms of the Dunkard Group, Central Appalachian Basin

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ABSTRACT

The Dunkard Group is the youngest late Paleozoic rock unit in the Central Appalachian Basin. Its age, however, remains controversial. In its southern and western two-thirds the Dunkard is comprised largely of red beds, sandstone and siltstone channel deposits and paleosols. In its thickest, most northerly exposures, in southwestern Pennsylvania, northern West Virginia, and east-central Ohio, much of the lower part of the unit is composed of coals, non-marine limestones and gray, often calcareous, paleosols. Age dating is confounded by the non-marine nature of the deposit and by the lack of dateable volcanic ash beds. Dunkard fossils include plants, vertebrates, and both aquatic and terrestrial invertebrates. Most of the fossil groups point to an age very close to, if not including, the Pennsylvanian–Permian boundary, though the exact position of that boundary is uncertain. Callipterids make their first appearance in the Dunkard flora in the middle of the Washington Formation and continue into the Greene Formation, but in different beds from those containing wetland floral elements. Publication of these plants in the "Permian Flora" of Fontaine and White (1880) created an immediate controversy about the age of the unit because *Callipteris conferta* (now *Autunia conferta*) was, at the time, considered to be an index fossil for the base of the Permian. Subsequent collecting has revealed these callipterds to comprise four species: *A. conferta*, *Autunia naumannii*, *Lodevia oxydata* and *Rhachiphyllum schenkii*. Callipterids – and the conifers with which they are sometimes associated – are typically found in seasonally dry equatorial environments and most likely constitute an environmentally controlled biofacies. This biofacies is not well known, resulting in limited biostratigraphic utility.

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1. Introduction

The callipterids are a group of late Paleozoic tropical plants, characterized by foliage formerly classified as *Callipteris*. This genus was split into five genera when the generic name appeared to be illegitimate (Kerp and Haubold, 1988). Reproductive organs revealed that one of the resulting genera, *Autunia*, is a peltasperm (Kerp, 1988). Other callipterids also appear to be peltasperms (e.g., Naugolnykh and Kerp, 1996; Poort and Kerp, 1990) and it can be assumed that this is true for most if not all callipterids. Peltasperms are related to, and possibly descended from, the callistophytalean pteridosperms (Crane, 1985; Hilton and Bateman, 2006). If the callipterids prove to be a natural lineage, they originated during, or prior to, the Middle Pennsylvanian (Pšenička et al., 2011), and later radiated extensively (DiMichele et al., 2005; Kerp, 1988; Naugolnykh, 1999). This radiation appears to have occurred in environments with seasonally distributed moisture (Kerp, 2000), probably under wet-subhumid to dry-subhumid climates (terminology sensu Cecil and Dulong, 2003). Whereas peltasperms in general spread widely throughout Pangean tropical and northern temperate latitudes (see discussion in Naugolnykh and Kerp, 1996), the callipterids formed prominent elements mainly in Permian tropical floras. The near absence of these plants from typical Late Pennsylvanian wetland floras and their occurrences in deposits with or associated with indicators of seasonality (e.g., Feldman et al., 2005), are strong evidence of their preference for seasonally dry settings.

As Kerp (2000) has noted, callipterids occur only occasionally with conifers (Chaney and DiMichele, 2007; Galtier and Broutin, 2008), another group considered to favor seasonally dry habitats. Fossils of the two groups largely are found separately, even within rock sequences from which both groups otherwise are known (e.g., Kerp and Fichter, 1985),

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suggesting different habitat preferences and, unsurprisingly, environmental heterogeneity and complexity in seasonally dry landscapes.

The early development of floras from seasonally dry landscapes is poorly known, however, largely due to hydrological factors related to the preservation of organic matter. The most likely times for fossil formation in basinal lowlands are when conditions for plant preservation favor both short-term and long-term burial (Gastaldo and Demko, 2010). Increasing evidence indicates that during the Pennsylvanian, these favorable periods were during wettest parts of glacial–interglacial cycles, which in equatorial latitudes mainly occurred during the middle and late stages of glacial maxima, when sea levels were at their lowest (Cecil et al., 2003; Horton et al., 2012; Peyser and Poulsen, 2008). This assured both short-term burial of organic matter under rainfall-driven high water tables, and intermediate-term burial under subsequently rising sea levels, during ensuing interglacials (Elrick and Nelson, 2010). Ultimate long-term burial relied on continual basinal subsidence, an assumption made plausible by recent "digital" correlations, indicating that glacial-interglacial cycles can be correlated with high fidelity from the Midcontinent USA, through the eastern North American coal basins, to as far as the Donets Basin of the Ukraine (Eros et al., 2012; Falcon-Lang et al., 2011a; Heckel et al., 2007). There also is evidence indicating that seasonally dry floras occurred in basins regularly during much of the Middle and Late Pennsylvanian (Falcon-Lang et al., 2009, 2011b; Plotnick et al., 2009), but mainly during those intervals of climate and sea-level cycles when climate was seasonally drier — during glacial minima/marine highstand through early glacial maxima/lowstand, thus when the potential for both short-term and intermediate-term burial and preservation were at their lowest. Callipterid and conifer-rich floras did not begin to be preserved regularly, or become the most common floras in lowland basins until the most favorable times for preservation – the wettest times of a given glacial–interglacial cycle – themselves became relatively seasonally dry. This occurred during the later Pennsylvanian and Permian, depending on location within the Pangean tropics (Tabor and Poulsen, 2008).

This digression into callipterid ecological and preservational patterns is important for understanding controversies surrounding their importance in the biostratigraphic zonation of terrestrial sequences and the consequences of this for the debate about the age of the Dunkard Group. The most widespread callipterid species, *Autunia* (formerly *Callipteris*) *conferta* (Kerp, 2000) was long considered an index species for the base of the Permian (see extensive discussions in various papers in Barlow, 1975). Consequently, its discovery in Dunkard rocks, in combination with other unusual elements, led Fontaine and White (1880) to propose that the Dunkard Group was at least partially, if not entirely, of Permian age. David White, of the U.S. Geological Survey, though initially in favor of a partial Permian age (White, 1904), ultimately came to agree (White, 1936) that the entire Dunkard Group was of Permian age, a position long asserted by I.C. White (see discussion in Lyons and Wagner, 1995). Through the 20th century, the age of these rocks continued to attract attention and controversy (e.g., Clendening, 1972; Clendening and Gillespie, 1972; Cross, 1954, 1958; Cross et al., 1950; Darrah, 1975; Bode, recorded in the discussion following the paper by Gillespie et al., 1975; Martin, 1998), with the callipterids playing a major part.

What is clear, however, is that the callipterids, and the peltasperms in general, are facies fossils. Their appearance in a geological section reflects seasonally dry climatic conditions. Callipterids, conifers and a variety of other plants not typically encountered in Pennsylvanian tropical wetland assemblages, nonetheless occur in the Pennsylvanian lowlands and even latest Mississippian, though not mixed with wetland species (e.g., Aizenverg et al., 1975; Augusta, 1937; Bassler, 1916; Boyarina, 2010; Cridland and Morris, 1963; Doubinger, 1979; Doubinger and Langiaux, 1982; Doubinger et al., 1995; Falcon-Lang et al., 2009; Galtier et al., 1992; Havlena, 1958; Hernandez-Castillo et al., 2001; Langiaux, 1984; Lyons and Darrah, 1989; Martino and Blake, 2001; Němejc, 1951; Plotnick et al., 2009; Rothwell et al., 1997, 2005; Šimůnek and Martínek, 2008; Wagner and Lyons, 1997; Winston, 1983; Zhou, 1994). To use these floras for accurate biostratigraphic determinations, one must be dealing with biome-restricted assemblages wherein evolutionary changes can be identified and tracked through time with high precision and accuracy (for discussion see Broutin et al., 1990; DiMichele and Aronson, 1992; DiMichele et al., 2008; Kerp, 1996; Mapes and Gastaldo, 1986). Unfortunately, the seasonally-dry assemblages of the pre-Permian are inadequately known at present for this task. Their sporadic appearances within stratigraphic sequences otherwise dominated by the wetland biome are indications of climate oscillation, shifting species pools and preservational happenstance, but these occurrences are too few for detailed reconstruction of evolutionary changes.

The Dunkard flora has been widely collected and many of its common elements have been illustrated. However, there are few illustrations of the callipterids. The original Fontaine and White (1880, Plate XI, Figs. 1–4) figures were engravings, and lack fine detail. Photographic illustrations of callipterid specimens appear in Darrah (1975, Figs. 1–3), Gillespie et al. (1975, Plate I A and Plate VIII A; refigured in Blake et al., 2002, Plate XXXV, Figs. 1–2, 6) and Gillespie and Pfefferkorn (1979, Plate 3, Figs. 6–8; refigured in Blake et al., 2002, Plate XXXV, Figs. 5, 7). Consequently, the main objective of this paper is to describe and illustrate the Dunkard Group callipterids and detail their stratigraphic distribution. Some of these specimens come from previously unillustrated collections made by David White in 1902, and T.E. Williard in 1903 (housed at the National Museum of Natural History), and by Aureal T. Cross (housed at the Field Museum of Natural History), who worked extensively in the Dunkard in the late 1940s and early 1950s. In addition, we illustrate a specimen of *A. conferta* from the collections of R.D. Lacoe, which he acquired in the late 1800s and sent to the National Museum of Natural History as part of the transfer of his collection to the Smithsonian in the mid-1890s; this specimen is of significance because it may be the oldest surviving Dunkard callipterid specimen "in captivity".

Based on this study, three callipterid genera and four species occur in rocks of the Dunkard Group: *Autunia conferta* (Sternberg) Kerp, *A. naumannii* (Gutbier) Kerp, *Lodevia oxydata* (Goeppert) Kerp and Haubold, and *Rhachiphyllum schenkii* Kerp.

2. Geology of the Dunkard Group

2.1. Stratigraphy

In this study, we follow the terminology used by the Fedorko and Skema (2013), which divides the Dunkard into the Washington and Greene Formations (Fig. 1). Martin (1998) summarizes the history of Dunkard stratigraphic nomenclature. The Washington Formation, at the base of the Dunkard, encompasses those rocks from the top of the Waynesburg coal to the base of the top of the Upper Washington Limestone. The Greene Formation encompasses all rocks above the top of the Upper Washington Limestone, and is thicker than Washington formation.

The Dunkard Group is an erosional remnant that crops out in southwestern Pennsylvania, eastern Ohio, central and western West Virginia, and possibly in small outliers in western Maryland. It reaches a maximum thickness in the Pittsburgh–Huntington Synclinorium of approximately 340 m in Greene County, Pennsylvania, and adjacent parts of Wetzel County, West Virginia. The Dunkard consists of cyclic successions of sandstone, shale and mudrocks, and limestone with minor coal (Beerbower, 1961), the latter particularly in the thicker lithological section, to the north and east. Here the clastic strata are largely buff and gray in color in the Washington formation, with minor red beds, which become more conspicuous higher in the section, in conjunction with decreased abundances of coal (Fedorko and Skema, 2013). Toward the south and southwest, the Dunkard section becomes increasingly red and is mostly a sequence of stacked paleosols interbedded with

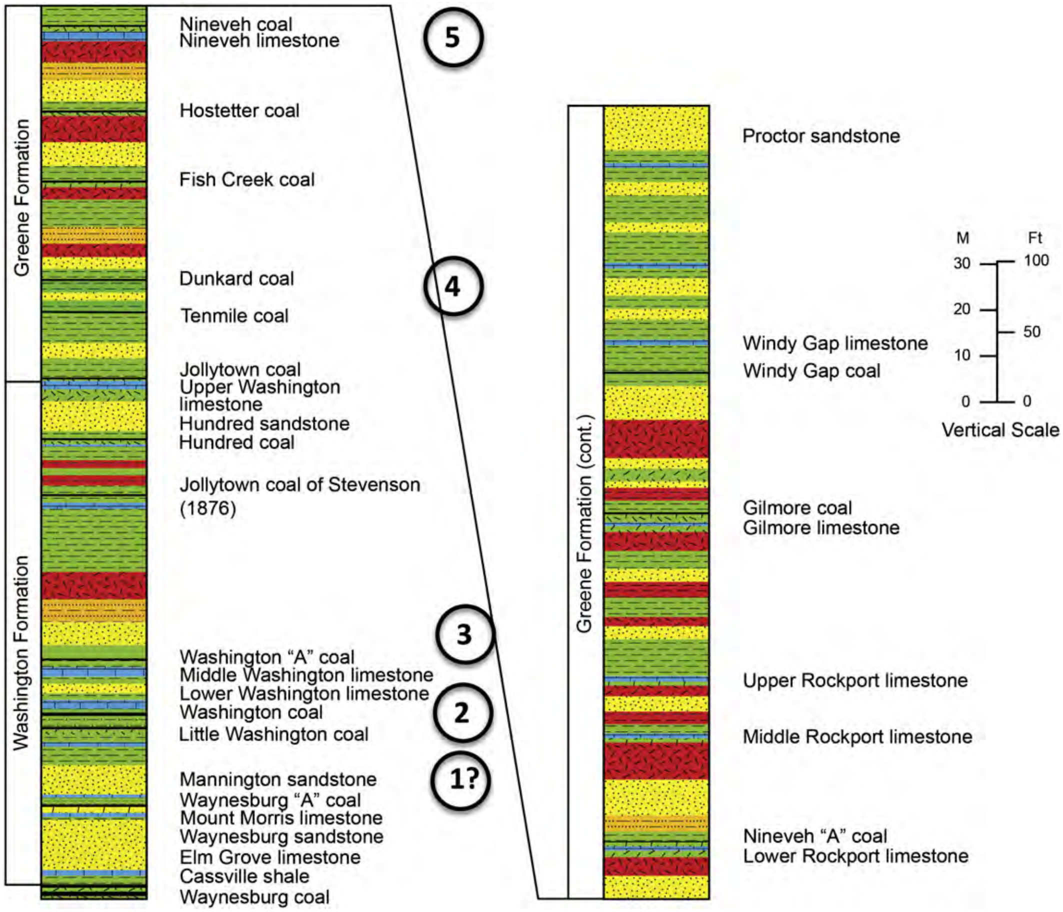

Fig. 1. Dunkard Stratigraphy, after Fedorko and Skema (2013). Numbers indicate horizons from which callipterids have been identified. 1. Between the Waynesburg A and Washington coals. 2. Within or above the Washington coal zone. 3. Within or proximate to the Lower and Middle Washington limestones. 4. In the interval from the Jollytown coal to the Dunkard coal. 5. Near the Nineveh coal.

channel-form sandstone bodies (Berryhill, 1963; Fedorko and Skema, 2013; Martin, 1998).

It is near the "Washington coal complex", in the middle of the Washington Formation (Skema, 2011), from which the first Appalachian basin callipterids are confidently reported. The base of the Washington coal complex is placed at the base of the Little Washington coal (Hennen, 1911), below which is a regionally extensive paleosol (Fedorko and Skema, 2013). The Washington coal complex consists of two to four coal beds separated by shale and/or sandstone. In the northwestern part of the Dunkard outcrop area (Belmont County, Ohio and Marshall County, West Virginia) the complex consists of two coal beds separated by >2 m of gray shale, deposited under brackish conditions. The shale bed contains a brackish fauna, including linguloid brachiopods and myalinid pelecypods (Berryhill, 1963; Cross and Schemel, 1956; Fedorko and Skema, 2013). This fauna is the stratigraphically highest occurrence of any evidence of marine influence found in the Appalachian Basin and may correlate with a global marine transgression and highstand just below the boundary of the Pennsylvanian and Permian (Davydov et al., 2010, 2013).

2.2. Plant fossils in geologic context

Most Dunkard plant fossils have been collected from the coal-bearing portions, frequently from shales immediately above coal beds. Thus, they are composed of typical Pennsylvanian wetland plants. This wetland flora is quite widespread, however, and has been found throughout the outcrop area, including in the redbed facies (Blake and Gillespie, 2011). The flora is diverse and includes many species characteristic of the latest Pennsylvanian (Gzhelian), quantitatively dominated by marattialean tree ferns (Blake et al., 2002; Darrah, 1975; Gillespie et al., 1975; Wagner and Lyons, 1997). There are also some taxa that, in Europe, had been considered characteristic of the Middle Pennsylvanian, specifically the pteridosperms *Neuropteris ovata* and *Macroneuropteris scheuchzeri* (see discussion in Darrah, 1975). Thse forms have been shown to range throughout the Upper Pennsylvanian (Blake et al., 2002) and into the Permian in North America.

Dunkard callipterids do not occur as part of the wetland biofacies, even though some callipterids may have preferred wetter, even swampy substrates in seasonally dry landscapes (Barthel and Rößler, 1996; Kerp and Fichter, 1985). They are well documented first in shales within the Washington Formation, beginning at the approximate horizon of the Washington coal complex, and continuing into the lower half of the Greene Formation. These fossils occur in a variety of lithologies, from dark, micaceous, finely laminated shales, to buff and red mudstones with poor fissility, to limestones. Darrah (1975, in the captions to his Figs. 1 and 3 on page 95) provides the only report of callipterids from below the level of the Washington coal complex. He attributes the collections to James Barlow of the West Virginia Geological Survey, purportedly collected from the lower Washington Formation, between the Waynesburg A and Washington coals, near Williamstown, in Wood County, West Virginia. However, coals are very poorly developed in the Dunkard Group in Wood County, and Darrah neither provides detailed information on the location of the collecting locality nor on the ultimate disposition of the samples; at present, we treat this report with reservation. Callipterids have been described from the immediate roof shales of a coal bed at only one place, the Brown's Bridge locality, by

Fontaine and White (1880), and here they may actually have occurred in a clastic layer at the base of the Lower Washington Limestone (White, 1891).

Other plants typical (but not diagnostic) of Permian-age floras have been reported from the Dunkard and older rocks in the Appalachian Basin including *Taeniopteris*, *Plagiozamites*, and conifers (Blake and Gillespie, 2011), including one collection from near the base of the Upper Pennsylvanian (McComas, 1988; Wagner and Lyons, 1997). These are reported from various horizons, including the Cassville Shale, above the Waynesburg coal, at the base of the Dunkard Group (Darrah, 1975; Fontaine and White, 1880; White, 1904, 1936). These occurrences have led some paleobotanists to conclude that the entire Dunkard Group is of Permian age.

3. Callipterids in Dunkard strata

In this report we illustrate Dunkard callipterids from a number of stratigraphic positions (Fig. 1) and geographic locations (shown regionally in Fig. 2; more specificity is shown in additional maps that follow). We focus here on the following: (1) Collections of callipterids in the National Museum of Natural History, made by David White or T.E. Williard, or acquired from R.D. Lacoe; (2) Collections from the Field Museum of Natural History, made by Aureal Cross; (3) Specimens illustrated or described explicitly in previous publications. Precise identification of the collecting horizons from which these collections were made is often difficult. When the original work was being done, the area had been clear cut and consisted largely of small farms. Infrastructure such as roads and shortline railroads were being actively constructed. Today this area is generally remote and reforested.

3.1. Brown's Bridge, Brown's Mills, Worley

There is some confusion surrounding the site from which Dunkard Group callipterids were originally collected. For this reason, we devote several paragraphs to this matter. The original beds have not been relocated and uncertainty exists about the exact sites and stratigraphic positions at which the original 19th century and subsequent early 20th century collections were made.

Fontaine and White (1880) reported *Callipteris* (*Autunia*) *conferta* and *Sphenopteris coreacea* (*L. oxydata*) from a locality they identified as "near Brown's Bridge, Monongalia Co., W. Va." (p. 42 and p. 54, respectively), specifically noting that they come from the roof shale of the Washington coal. Leo Lesquereux identified a specimen in the R.D. Lacoe collection (USNM specimen 27141) as "*C. conferta*", according to a label affixed to the specimen; a further label identifies it as coming from "Brown's Mills", and gives the stratigraphic horizon only as "Washington coal". On August 12, 1902, D. White collected *A. conferta* and *L. oxydata* from a locality he identified as "Brown's Mills on Dunkard Creek, Monongalia Co., W.Va." (USGS locality 2926); in the USGS locality register, collection 2926 is noted as coming from "just over the limestone above the Washington coal".

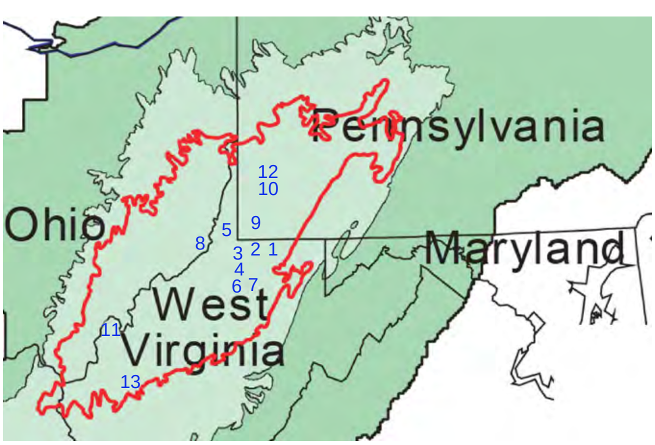

Fig. 2. Dunkard Group outcrop area and location of callipterid collections. Appalachian Basin Province (Dark Green), Appalachian Plateau region (Light Green), Dunkard basin (within red line). 1, Brown's Bridge. 2, Brown's Mills. 3, West of Littleton. 4, Between pumping station west of Littleton and Littleton. 5, East of Bellton Station. 6, Rinehart Tunnel Station. 7, West of Wallace Station. 8, Winkler's Mill. 9, Pleasant Hill Gap. 10, Locations around Waynesburg. 11, Williamstown. 12, Wolfdale. 13, Liberty. Modified from Milici and Swezey (2006, Fig. 3).

From the mid-20th century onward, all of these collections have been treated as having been collected from the same place and stratum. Detailed notes in published papers and official files (field notes and locality registers), however, indicate that Fontaine and I.C. White's "Brown's Bridge" may, in fact, represent a different site from the "Brown's Mills" locality of David White and R.D. Lacoe. In his 1891 report on the bituminous coal fields of Pennsylvania, Ohio and West Virginia, I.C. White (1891, p. 37–38) specifically differentiates "Brown's Mills" from "Brown's Bridge", noting that it is from the second location that callipterids were described in Report PP, Second Geological Survey, Pennsylvania, p. 54 (Fontaine and White, 1880). He goes on further to note that at Brown's Mills the Washington coal (a complex succession of coal, shale and bituminous shale) has a limestone roof, the Lower Washington Limestone, lying immediately above the uppermost bituminous shale. The limestone is noted as containing much iron. He also notes that the Lower Washington Limestone is often interbedded with iron-rich layers that are themselves interstratified with bituminous shales, the latter "covered with fossil plants". I.C. White (1891) specifically writes that it was also on such a layer that callipterids were found at Brown's Bridge.

These observations appear to establish, unequivocally, that (1) the callipterids reported by Fontaine and White (1880) are from a place known then as "Brown's Bridge", (2) that this original site is different from the site described as "Brown's Mills", and (3) that callipterids at both places came from bituminous shale layers, which were variously developed as part of the Lower Washington Limestone.

Also bearing on this matter are the descriptions of the fossiliferous beds in relation to the Washington coal complex. Fontaine and I.C. White reported callipterid specimens at Brown's Bridge from the roof shale of the Washington coal. In contrast, David White reported his specimens as coming from just over the limestone above the Washington coal, thus not from a shale immediately in contact with a coal bed.

The provenance of the USNM Lacoe-collection specimen is equivocal because Lacoe primarily acquired material through purchase, exchange, or by hiring collectors to visit particular sites. It is possible that the specimen was acquired from Fontaine and I.C. White (along with a larger collection of Dunkard specimens now housed in the NMNH, donated by Lacoe). A label affixed to this specimen lists the site of collection as "Brown's Mills". The matrix of the Lacoe specimen, which is heavy, and thus presumably enriched in iron, is similar in color and texture to that of D. White's Brown's Mills specimens. These are the only callipterids in the NMNH collections from dark gray, organic-rich shales, and they are similar enough to infer an origin from the same bed. Lacoe must have acquired this specimen prior to the 1889 death of Leo Lesquereux (who identified it), and turned it over to the Smithsonian as part of the 1895 donation of the bulk of his private collection. David White, who arranged, packed and identified the specimens in the Lacoe bequest, thus would have known of this specimen and the Brown's Mills locality prior to his 1902 field work in the Dunkard.

Finally there are a variety of other, indirect lines of evidence that suggest different sites for Brown's Bridge and Brown's Mills (Fig. 3). According to his 1902, Pennsylvania–Dunkard field notebook (on file at the NMNH), on August 10, 1902 David White collected at Core's Mine on Doll's Run (USGS 2893 — roof of the Washington coal, no callipterids collected), which we presume to have been located near present day Core, West Virginia, south of Dunkard Creek. On August 11, 1902 he

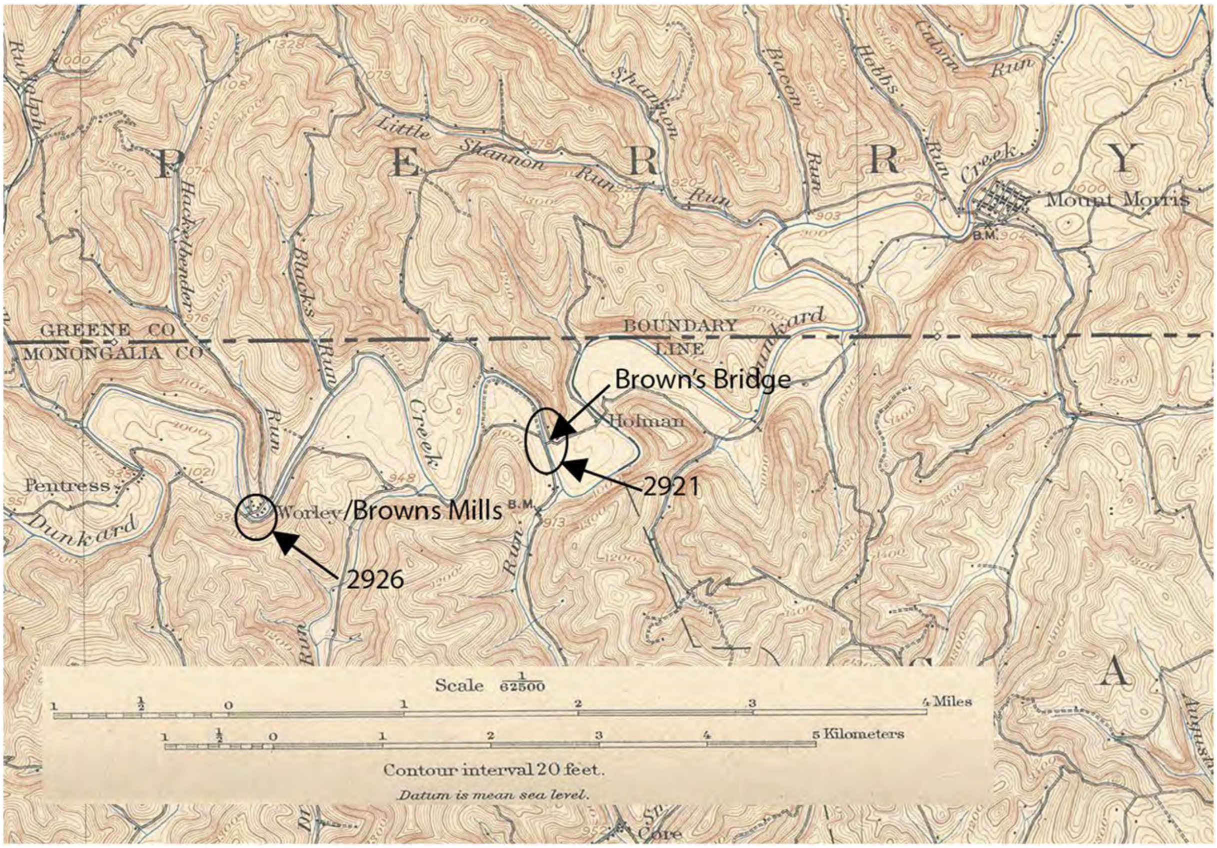

Fig. 3. Blacksville, WV 1904 USGS 15′ topographic map segment showing the locations of the Browns Mills (2926) and Brown's Bridge (2921) sites in West Virginia. Note the spelling of these names. There is ambiguity in field notes, locality registers, the literature and the USGS Geographic Names Information System regarding the spelling of "Brown's" vs "Browns" for both Browns Mills (the official USGS spelling) and Brown's Bridge, as well as Browns Hill, above the Brown's Bridge site. We have split the difference.

collected at a site he designated Brown's Bridge (USGS 2921 — beneath the Washington coal, no callipterids collected), which in his notes is shown to be an unspecified distance north of a bridge over Doll's Run, north of Core. On the 1904 topographic map, a bridge is shown over Doll's Run 1.5 miles (2.4 km) north of Core, and a second bridge is shown over Dunkard Creek, 0.5 miles (0.8 km) north of the Doll's Run bridge. On the 1904 topographic map, this second bridge carries the road that leads to Mt. Morris, Pennsylvania; furthermore, immediately to the north of the bridge, on the Pennsylvania–West Virginia border, is a prominence labeled "Brown's Hill". On August 12, 1902, White collected near Mt. Morris (USGS 2894 — beneath the Waynesburg Sandstone, no callipterids collected) and then at the site he called Brown's Mills (USGS 2926 – just over the limestone above the Washington coal, his callipterid collection, according to the USGS locality register – there are no D. White field notes accompanying this collection). In 1903, T.E. Williard observed that his collection, USGS 3438 (no callipterids), was from the "south side of Dunkard Creek opposite the mill at Worley". The U.S. Geological Survey Names Information System (http://geonames.usgs.gov/pls/gnispublic/f?p=132:3:1293502122222994::NO:3:P3_FID,P3_TITLE:1549998,Worley) shows "Brown's Mills" to be an alternative name for "Worley". The Worley/Brown's Mills site is 1.5 (straight line) to 2 miles (road along Dunkard Creek) (~2.5–3 km) west of the "Brown's Bridge" location, but Worley/Brown's Mills also is on Dunkard Creek and directly opposite a bridge.

It appears from this discussion that a site called "Brown's Mills" can be confidently located on the south side of a bend in Dunkard Creek (NW quadrant of the Blacksville 15′ Quadrangle map, and NE quadrant of the Blacksville 7.5′ Quadrangle map), opposite the unincorporated town of Worley, along present-day West Virginia Route 7. We initially believed the Brown's Mills collections to come from close to the grade of a former railroad at that location. However, the contemporary, 1904 USGS topographic map does not show a railroad. If, indeed, the railroad were built after the collections of Lacoe and David White were made, then the original beds may have been buried or significantly altered in outcrop. This may account for the inability of later collectors to relocate any of these early collecting horizons.

3.1.1. Fontaine and I.C. White Collection

The entire original Dunkard collection of Fontaine and White (1880) has been lost. Consequently, their illustrations – all engravings and of variable detail – are all that remain, which has caused significant problems with application of some of the taxonomic names they instituted. In their original publication, they illustrated two callipterid species, only one of which they recognized as a callipterid, *Callipteris* (now *Autunia*) *conferta* (F & W Plate XI, Figs. 1–4, reproduced as Fig. 4a of this paper). The other, which we identify as *L. oxydata* (Goeppert) Kerp and Haubold, 1988, was originally described as *Sphenopteris coreacea* Fontaine and White (F & W Plate 5, Fig. 5, reproduced as Fig. 4b of this paper), which Darrah (1969) identified as *Callipteris lyratifolia*. Fontaine and White (1880, p. 54) describe their plants as coming from a "calcareous iron ore" that occurs in the roof of the Washington coal.

3.1.2. R.D. Lacoe specimen

There is a single specimen of *A. conferta* mentioned above, from the R.D. Lacoe collection, housed at the National Museum of Natural History (USNM specimen 27141 — Fig. 5). The specimen was identified as *C. conferta* by Leo Lesquereux (according to a label affixed to it); it is most likely that this specimen was made available to Lesquereux for identification by Lacoe (see note in Darrah, 1969, p. 153). The specimen is in a heavy, thin bedded, dark gray shale that, from its weight, must indeed contain considerable siderite.

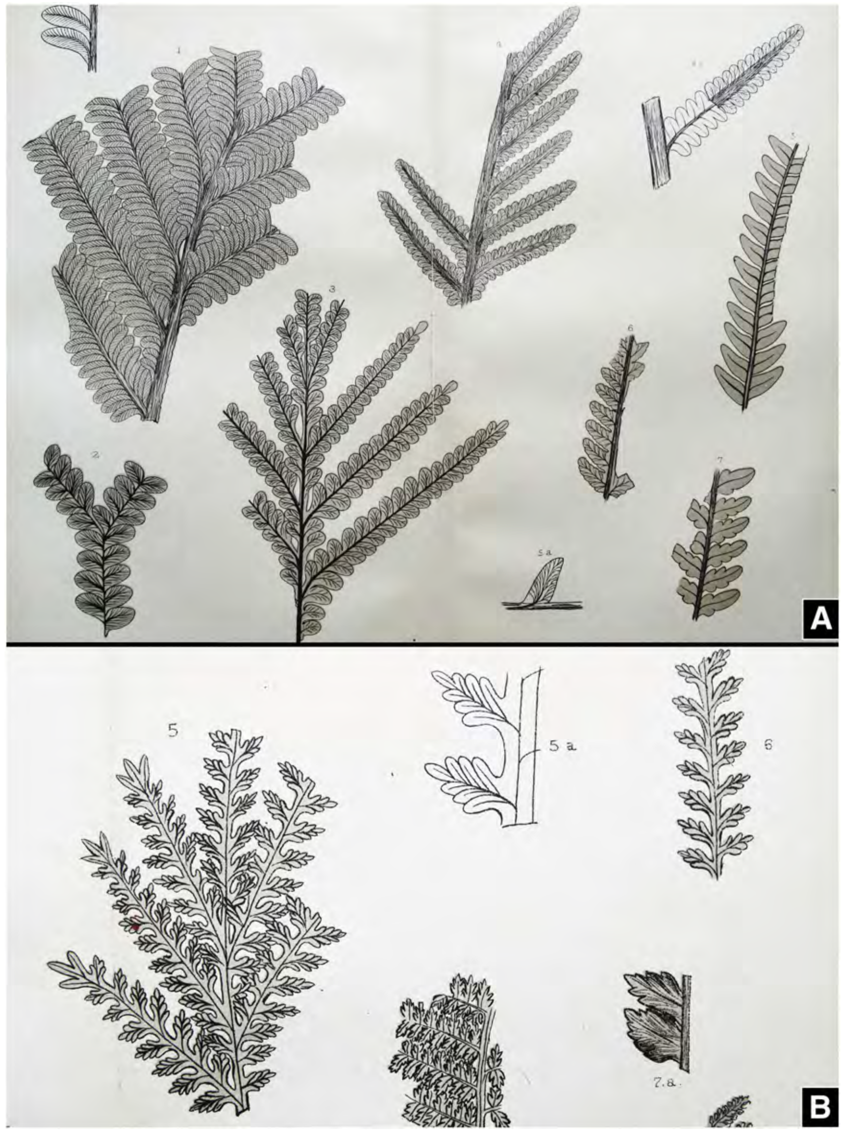

Fig. 4. Original illustrations of callipterids by Fontaine and White (1880), from Brown's Bridge, West Virginia. A. *Autunia* (*Callipteris*) *conferta*. Original Plate XI, Figs. 1–4. B. *Lodevia oxydata* (*Sphenopteris coreacea*). Original Plate V, Fig. 5.

The identification of this specimen as *A. conferta* is supported by the blunt tipped, rectangular pinnule shapes, sunken midveins and associated vaulted pinnule laminae and steep lateral veins. Preservation of the specimen is not good, but this may reflect its age and the fact that it has been coated in the past, probably with a varnish, to preserve what may have been the flaking organic compression.

3.1.3. David White collection

David White's "Brown's Mills" collection (USGS locality 2926) contains both *A. conferta* (Fig. 6) and *L. oxydata* (Fig. 7), the same taxa reported from Brown's Bridge by Fontaine and White (1880). The matrix of the specimens differs slightly from that of the single Smithsonian Lacoe specimen, mainly in being less sideritic and more distinctly laminated, but both are very dark shales with considerable siderite content, so they may represent different parts of or different collecting localities within the same bed. David White's 1902 field notes, frustratingly, do not mention this locality by name. The only record, therefore, is in the US Geological Survey paleobotanical locality register entry, which probably was based on data included with the specimens when shipped from the field. The locality register notes that the collections come from shales above the limestone immediately above the Washington coal.

As previously mentioned, the Brown's Mills geological description is at odds with the Brown's Bridge description of Fontaine and White (1880), who reported their plant bed to be the roof of the Washington coal. Darrah reports that he recollected from the Brown's Mills site in 1932, but does not illustrate it or provide a geological interpretive section; he described the plant bed as a thin, dense, arenaceous shale, which broadly fits the other known collections, but he does not mention the conspicuously dark color.

Environmental interpretation of the callipterid-bearing beds at Brown's Mills is difficult, based on the fragmentary evidence available. Furthermore, the site is presently heavily vegetated and, thus, too poorly exposed to permit location of the original beds. I.C. White (1891), however, described a complex section at the Brown's Mills site and noted that plants occur in layers of bituminous shales within the Lower Washington Limestone. The co-occurrence of large, well preserved fragments of *A. conferta* and *L. oxydata* together on some bedding surfaces, in the same lithology, leaves little question that these species were living together, at least in the organic-shale habitat. These dark-shale, callipterid beds also include a fauna of ostracodes and snails

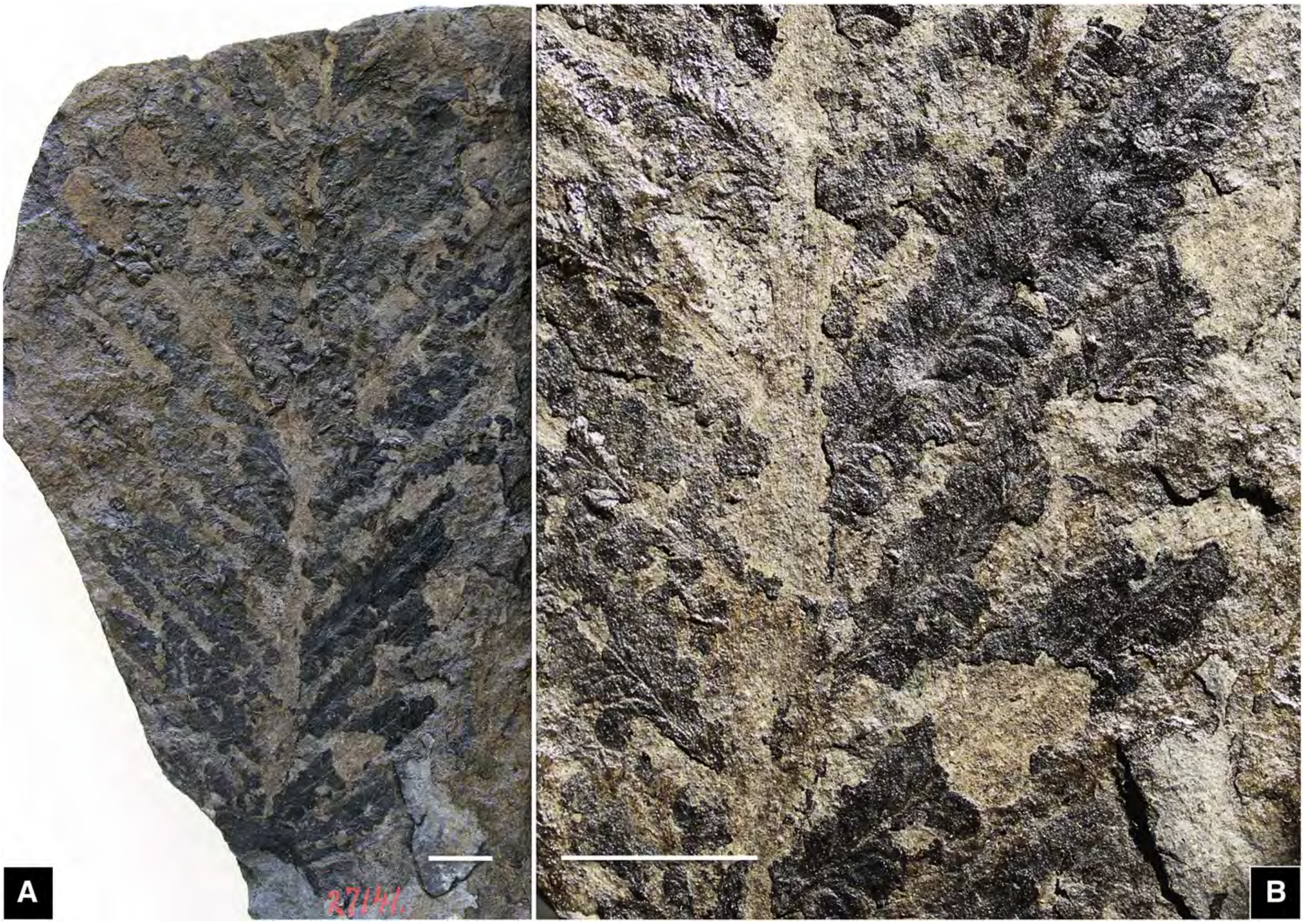

Fig. 5. R.D. Lacoe Collection specimen from Brown's Mills, West Virginia, identified by Leo Lesquereux. *Autunia conferta*. USNM specimen 27141. Specimen has been coated with an unidentified substance. A. Typical small-pinnuled form of *Autunia conferta*. B. Magnification of pinnae from A, illustrating attachment to main rachis and pinnule characteristics, upswept venation. Scale bars = 1 cm.

(Tibert et al., 2011). The snails are heavily calcified and would have required alkaline-rich watersheds, thus they did not likely live in association with the drowning of an acidic, peat-forming swamp. The general inference is that the limestone and the interbedded shales were deposited under a seasonally dry climate (N. Tibert, personal communication, 2013).

We may draw the following conclusions from these observations. (1) The stratigraphic-temporal separation of the callipterid beds from the Washington coal complex indicates that they were not deposited by drowning of the coal swamp. (2) This plant bed contains abundant remains of non-marine ostracodes, snails, fish and serpulid worms (Tibert et al., 2011), suggesting that it may be an interbed facies of the Lower Washington Limestone, which may explain the iron carbonate content of the shales. (3) The position of the plant-bearing shale above, or perhaps even within, a parting of a limestone reflects a shift from a humid climate during coal-swamp development to a sub-humid, seasonally dry climate (terminology of Cecil and Dulong, 2003) during deposition of the non-marine limestone and organic-rich shale interbeds. (4) The density, lack of preferential orientation and excellent preservation of the plant material suggest a parautochthonous to autochthonous environment of accumulation — the foliage was buried where it fell from the parent plant. (5) At the landscape scale, the report of callipterids from sandstones at this site (Gillespie et al., 1975) is ancillary evidence that callipterids were widespread and occurred across the landscape for an extended period, permitting their preservation in a variety of habitats and the lithologies formed therein.

3.2. West of Littleton

Several plant collections from “West of Littleton”, West Virginia, were made by David White on August 22, 1902. According to White's field notes and a note found with the collections, the site was at the west end of the first railroad cut west of Littleton. The railroad, then the Baltimore and Ohio line, is now gone, but appears on the NE quadrant of the Littleton 15′ USGS quadrangle map from the early 20th century (Fig. 8). T.E. Williard collected from these same exposures in 1903 and noted them as coming from the first railroad cut north of Littleton, just above Fish Creek. Due to the path of the railroad track,, the site is, in fact, north and west of Littleton.

The West/North of Littleton plant collections (USGS Locality Numbers 2909, 2909×, 2911, 3376) consist of several different lithologies. D. White indicates plants at minimally four levels, which may account for his lithologically mixed samples — there are fewer USNM collections than the number of plant-bearing beds indicated in the field notes, indicating mixing of collections made from the various, distinct fossiliferous beds. Similarly, Williard's samples are lithologically heterogeneous, indicating derivation from more than one fossiliferous bed. D. White's notes for this location indicate a relatively large number of limestones in the section, interspersed with red and green shale. The stratigraphic position of these beds appears to be between the Jollytown and Dunkard coals (between which the Tenmile coal occurs, Fig. 1), with some uncertainty. This position would put the collections in the lower Greene Formation, at various distances above the Upper Washington Limestone.

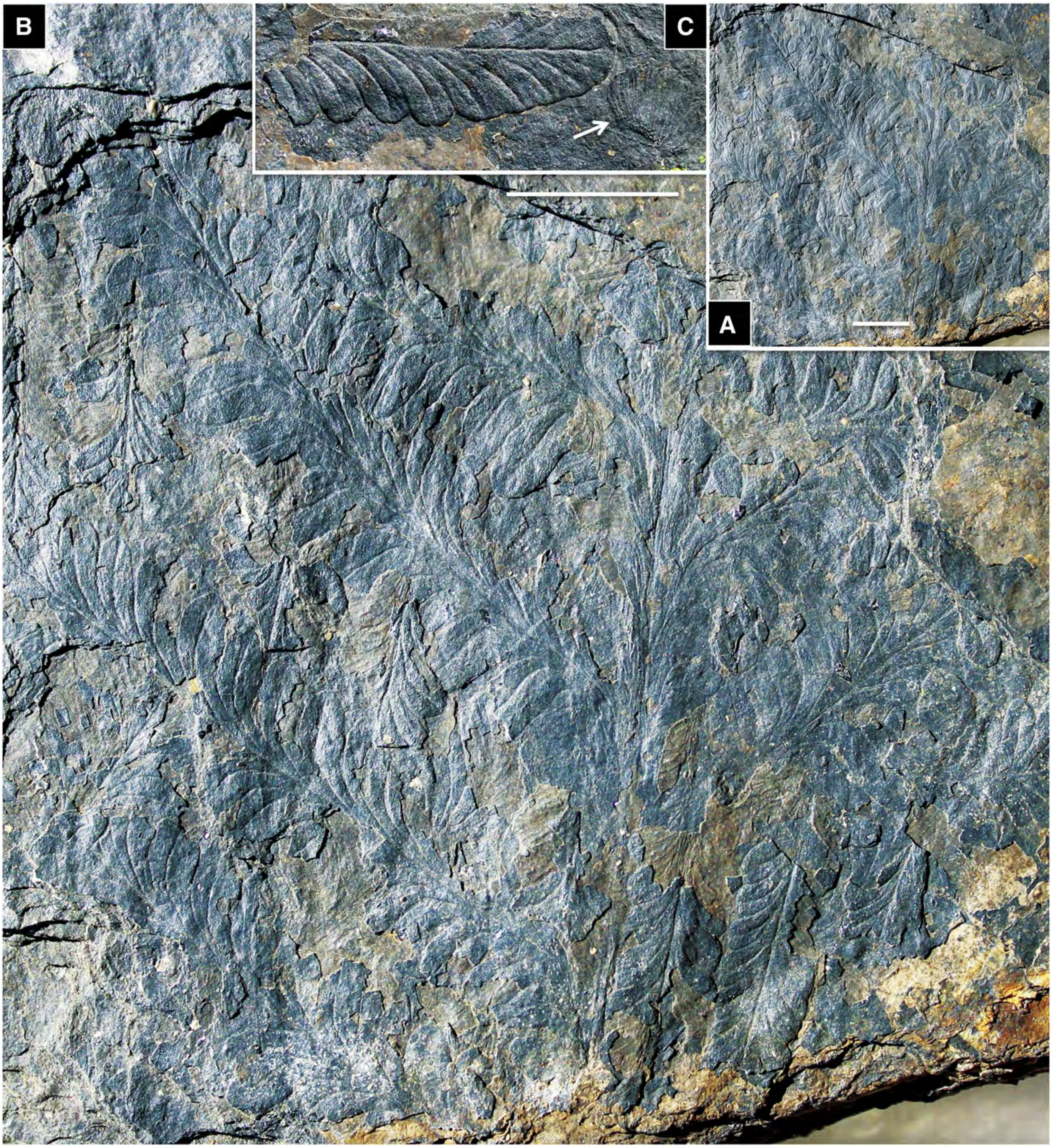

Fig. 6. *Autunia conferta* from Brown's Mills, West Virginia, collected by David White. USGS locality 2926. A. USNM specimen 543957, fragmentary frond with several pinnae. B. 3X enlargement of A, note pinnule shape, which is the same as that of the Lacoe/Lesquereux specimen and those illustrated by Fontaine and White (1880) from Brown's Bridge. Thickness of pinnule laminae obscures steeply ascending lateral veins. C. USNM specimen 543962, pinna tip with acroscopically fused pinnules, steeply ascending lateral veins. B and C at same magnification. Scale bars = 1 cm.

Collections 2909, 2909× and 3376 are mostly hand samples of gray to red clay-rich mudstones with a few buff siltstones. The majority of the assemblage in each collection consists almost entirely of typical Late Pennsylvanian wetland plants, including *Pecopteris* tree-fern foliage, calamitalean remains and possibly *Callipteridium*. There are, however, several specimens of callipterids in these collections, preserved in gray to red mudstones that appear to have been pedogenically overprinted, based on the presence of slickensides, bioturbated texture, and lack of clear bedding. We would characterize all these callipterid specimens as *A. conferta* (Fig. 9A–C), based on the high vaulting of the pinnules, sunken midveins, and dense, steep secondary veins. The D. White and some of the Williard callipterid collections may have come from the same bed, based on the similarity of their respective lithologies. However, the Williard collection includes a specimen in buff siltstone.

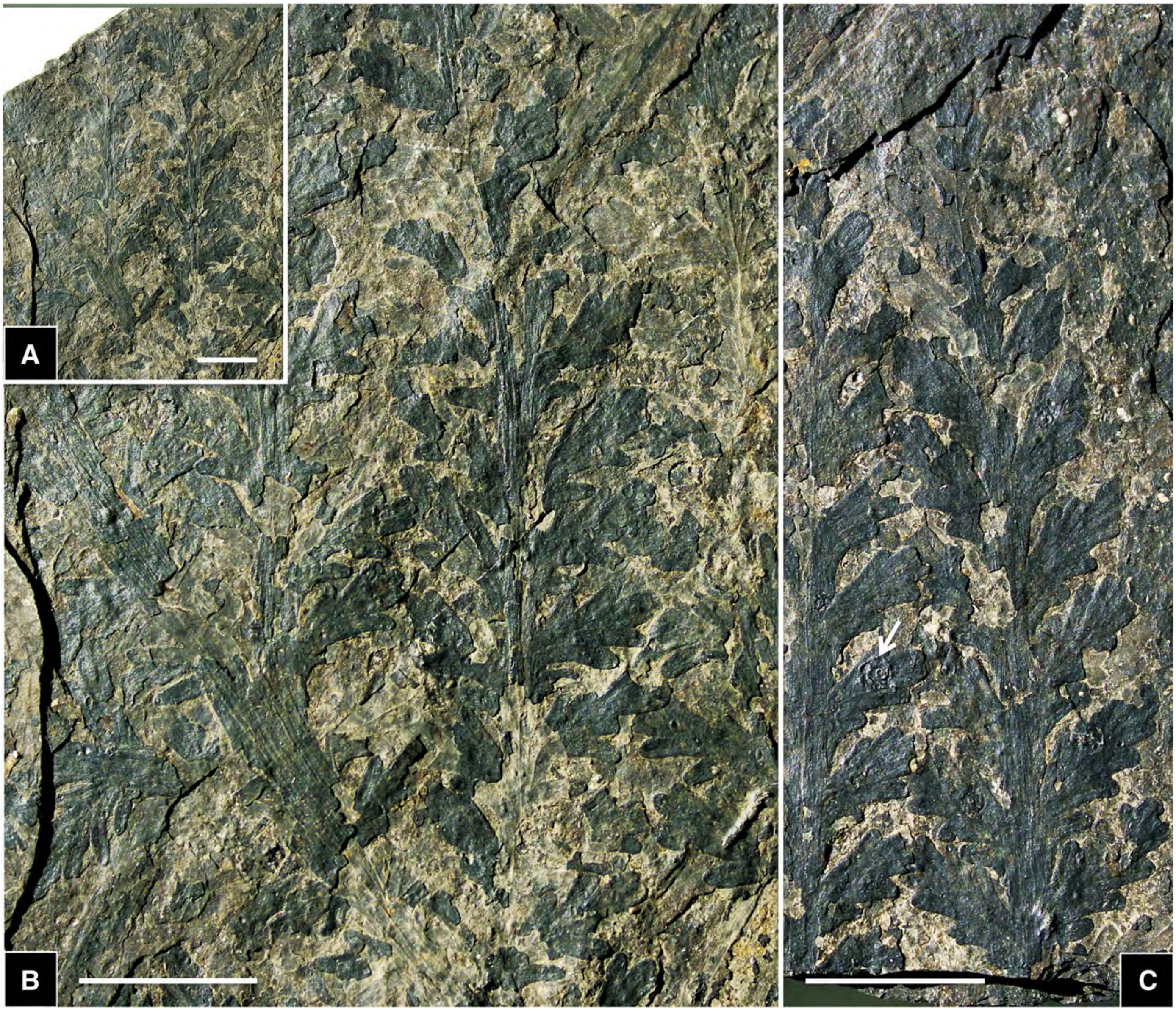

Fig. 7. *Lodevia oxydata* from Brown's Mills, West Virginia, collected by David White. USGS locality 2926; USNM specimen 543958. A. Fragment of frond with attached pinnae. B. 3× enlargement of A, note pinnule shape, steeply ascending lateral venation, and thick pinnule laminae. C. Close up of two pinnae. Note spirorbids attached to the foliage (one at white arrow, others can be seen by scanning the foliage laminae). Scale bars = 1 cm.

Collection 2911 also consists of a mixture of lithologies, including red mudstones and buff, micaceous siltstone. A single possible callipterid is present in this collection in the buff siltstone facies. The specimen most closely resembles *Rhachiphyllum* in the presence of flat pinnule laminae, relatively sparse veins, and a thin, non-sunken pinnule midvein.

Based on the mixed nature of the collections, on the small amount of overlap between the callipterids and wetland species, and on the uncertainty in the field notes that accompany the collections, little can be said about the paleoenvironments occupied by these plants or about the climatic regime under which they lived.

3.3. Between Littleton and the Pumping Station West of Littleton

USGS Locality 2901 is an unspecified distance to the west of the Littleton railroad station (according to D. White's field notes), but perhaps ¼ or less of the distance between Littleton and the Board Tree railroad tunnel along the railroad grade. No pumping station is shown north and west of Littleton on the 1926 USGS 15′ topographic map (Fig. 8).

The specimens from this site are a mixture of lithologies suggesting that they were collected from different beds. Most of the specimens are red mudstone, consisting mainly of wetland taxa such as *Macroneuropteris scheuchzeri*, *Polymorphopteris*, *Pecopteris* and *Sphenophyllum*. However, several pinnae of *A. conferta* occur in a gray, carbonate-rich, fine grained mudstone, on an irregular red-stained surface. The pinnules are vaulted with a sunken midvein and steeply angled lateral veins (Fig. 9D, E).

D. White (field notes) places this collection at the level of a coal horizon between the Jollytown coal and the Dunkard coal (noted as “fide I.C.W.” — presumably referring to I.C. White). If D. White interpreted the section correctly, these collections appear to be from a succession of thin carbonate beds and red shale below a bed of coal and carbonaceous shale, above the Jollytown coal, making the Tenmile coal a candidate.

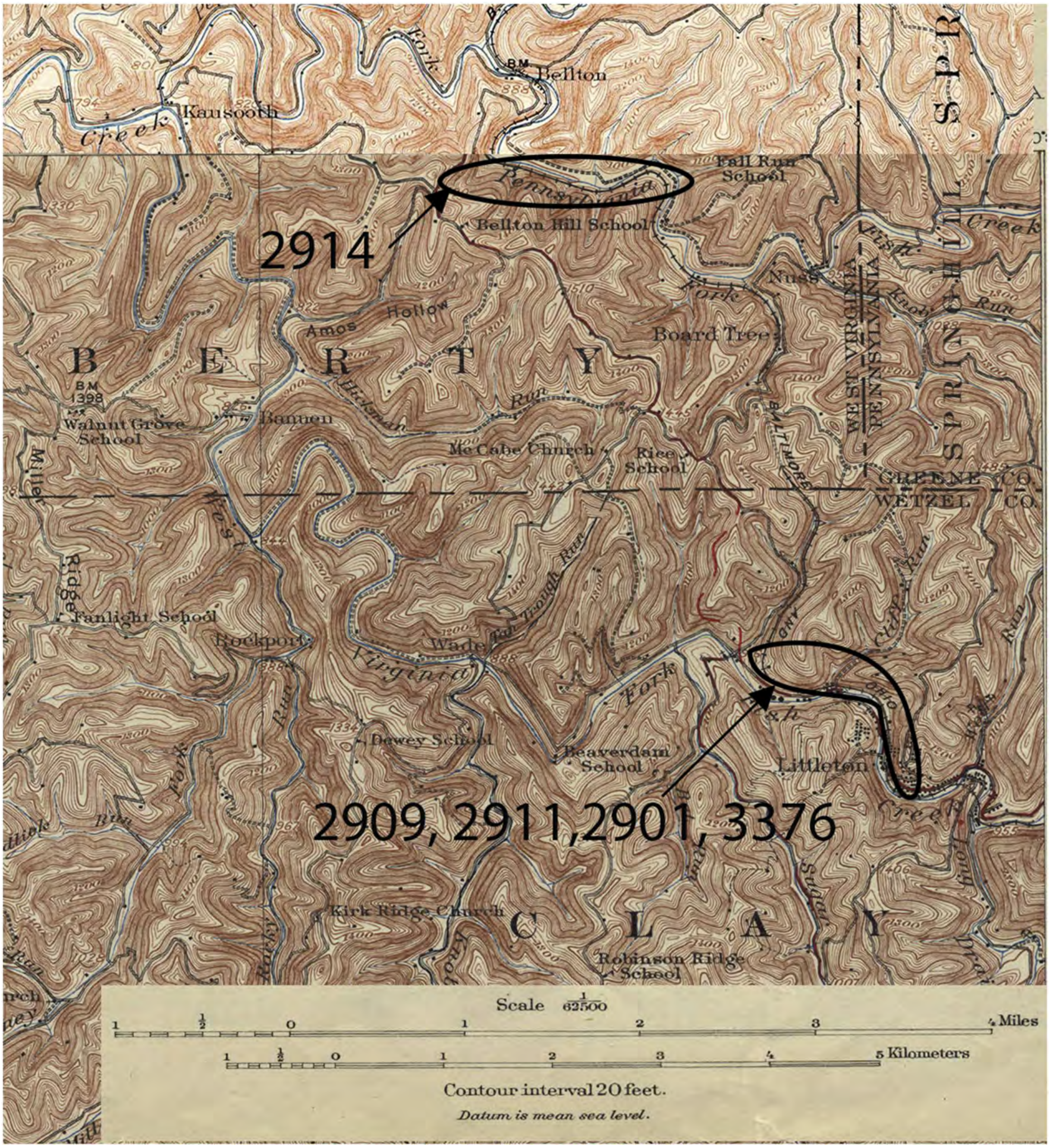

Fig. 8. Cameron, WV 1904 and Littleton, WV 1926 USGS 15′ topographic map segments showing fossil plant localities from West of Littleton (2909 and 2911), North of Littleton (3376) and Between Littleton and the Pumping Station West of Littleton (2901). Fossil plant locality 2 miles east of Bellton (2914). All in West Virginia.

3.4. Two Miles East of Bellton Station

Along the former Baltimore and Ohio Railroad, two miles east of Bellton, West Virginia (Fig. 8), D. White collected specimens from red and gray shales, an unspecified distance above what he identified as the "Dunkard (or perhaps the Jollytown) coal" (field notes), which would place this collection (USGS Locality number 2914) in the lower portion of the Greene Formation. The coal is noted as 6 in. (15 cm) thick. Red beds lie above the Dunkard coal (Fig. 1), separated from it by gray shales and sandstone, which is broadly in conformance with D. White's field sketch, perhaps explaining his identification of the coal bed. From White's notes, it appears that the plant-bearing beds are separated from the coal by more than a meter but less than 10 m.

Consisting, again, of mixed lithologies and a mixed flora, D. White's field notes record "*Callipteris reginum* [*Callipteris conferta*]". We found a single specimen with callipterid impressions in this collection; it contains parts of two pinnae, preserved in a hard, buff, siltstone. They are referable to *A. conferta* based on pinnule shape, sunken midveins, steep lateral veins and vaulted pinnule surfaces (Fig. 10).

3.5. Rinehart Tunnel Station

On August 23, 1902, the final day of his summer field season, D. White stopped near a newly excavated railroad tunnel on the West Virginia Shortline Railroad (field notes page 34), a site he referred to as "Tunnel Sta." (?Tunnel Station). A possibly later addition to the notebook by D. White or an unknown person locates this site "…in SE corner of Wetzel County in Centerpoint 15′ quad and Folsom 7 1/2′ quad. It is between Rinehart and Folsom" (Fig. 11). White notes "*Callipteris* in plenty at the tunnel in the [illegible] dump and in dump at the w. end

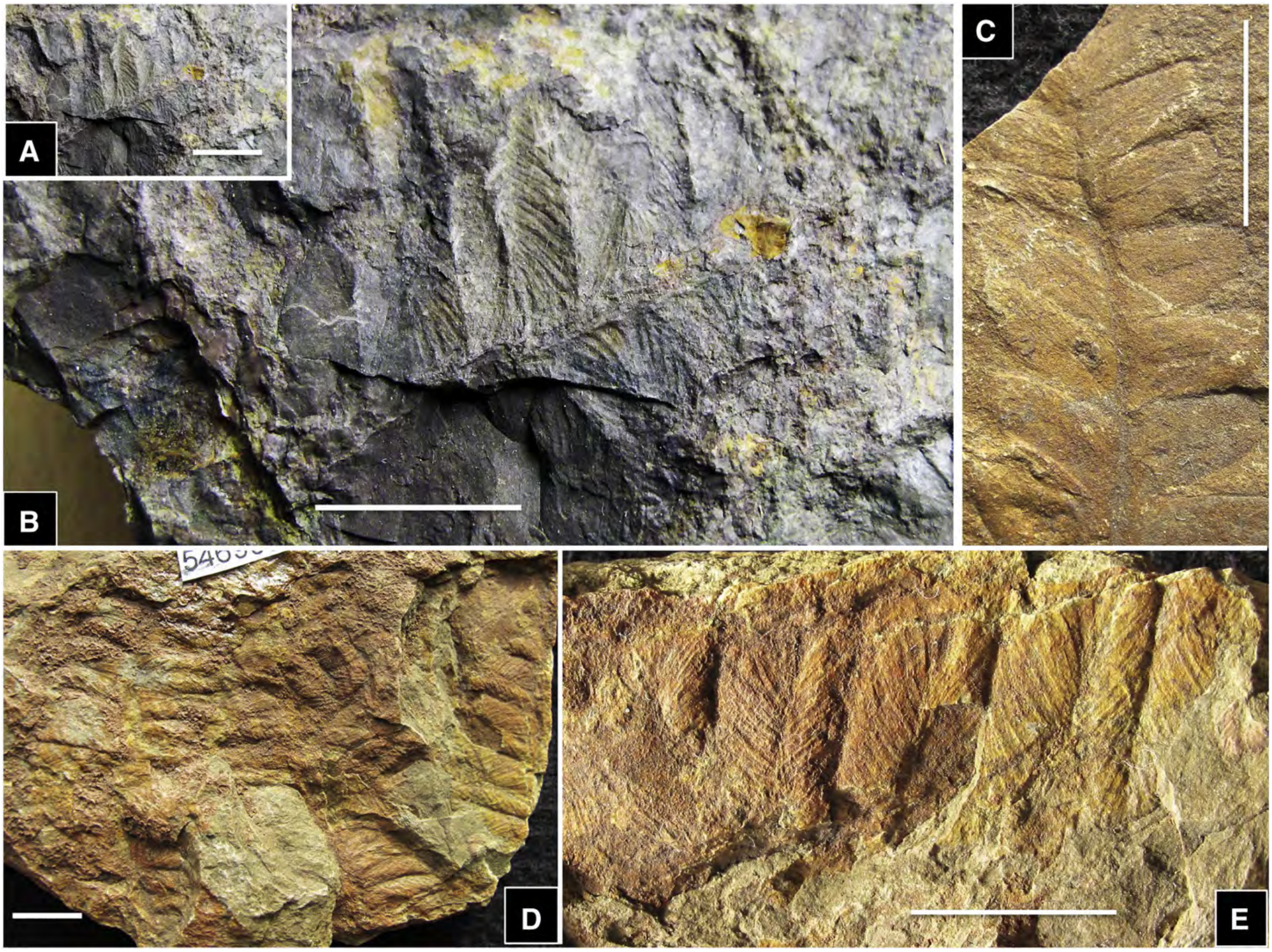

Fig. 9. *Autunia conferta* from sites northwest of Littleton, West Virginia. A. West of Littleton, USGS locality 2909, USNM specimen 543959. Red and gray mottled mudstone. B. 3X enlargement of specimen illustrated in A1, showing the bluntly acute pinnule apices, nearly centrally located pinnule midvein, and steeply ascending but convexly arched lateral veins. C. North of Littleton, USGS locality 3376, USNM specimen 546905p. Preserved in buff siltstone. D. Between Littleton and pumping station east of Littleton, USGS locality 2901, USNM specimen 546909. Red-stained, gray, calcareous mudstone. E. 3× enlargement of USNM specimen 546909. Scale bars = 1 cm.

of switch below tunnel sta." Although we were able to relocate and reach the eastern portal of the tunnel, we could not find evidence of waste rock dumps from tunnel excavation, the presumed source of the callipterid fossils. Because of the profile of the hill and location of the tunnel mouth, excavated rock probably needed to be hauled away from the site and may have been used as fill in the construction of the railroad bed through the uneven terrain.

Although there is no indication of any collections made from this site in D. White's field notes, an NMNH collection (USGS Locality number 2930) is identified as "Tunnel Station". The callipterids in these collections are molds of *A. conferta* of characteristic form, with strong, sunken midveins, steeply ascending lateral veins, vaulted pinnule laminae and blunt pinnule apices (Fig. 12A, B).

The callipterids are preserved in a poorly bedded, coarse grained, gray limestone. The Tunnel Station collection also contains red shales, but no callipterids were identified from this matrix.

These fossils appear to have come from the Greene Formation. The beds through which the tunnel was excavated lie approximiately 375 m (1225 ft) above the Pittsburgh coal bed.

The presence of fossils in a limestone bed places these plants presumably at a time in depositional history when limestone beds were forming as the lateral equivalents of calcareous paleosols (Fedorko and Skema, 2013), thus on seasonally dry landscapes with significant periods during which evapotranspiration exceeded precipitation.

3.6. West of Wallace Station

Williard, found plant fossils in limestone at the first railroad cut west of Wallace Station, West Virginia (USGS Locality number 3427), which is approximately 3.2 km (2 miles) southeast of the east end of the, then, West Virginia Shortline tunnel at Rinehart (Fig. 11). Based on an early 1900s photograph of Wallace (showing oil derricks within the town, and a mostly treeless landscape) and on a contemporary topographic map, there were rock exposures quite close to Wallace, probably within walking distance of the station to the west of where the railroad crosses present-day West Virginia Route 20.

As at Rinehart, the fossils are molds of *A. conferta*. The pinnule shape is somewhat more round than found in typical *A. conferta* and the venation is not as steep as usually seen (Fig. 12C, D). However, larger specimens have intercalary pinnules, consistent with a callipterid affinity, and of the relatively small size (Fig. 13, at arrows), consistent with those known from *A. conferta*. Kerp (1988) reported great variability

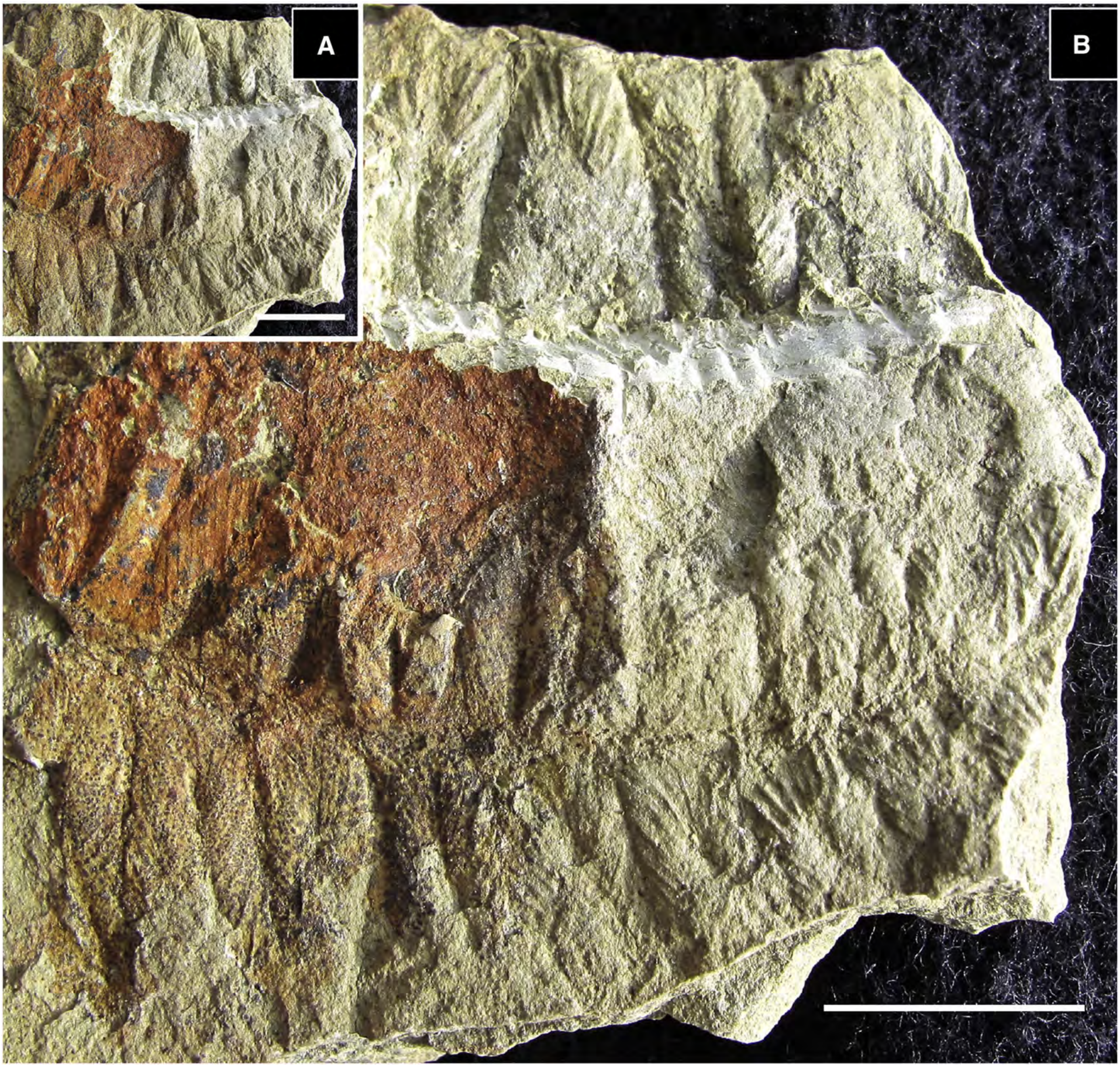

Fig. 10. *Autunia conferta* from 2 miles east of Bellton, West Virginia, USGS locality 2914, USNM specimen 539443. Specimen is preserved in hard, gray to buff siltstone. Scale bars = 1 cm.

in *A. conferta* morphology; the present specimens are within the known range of that variability.

The Wallace Station specimens are preserved in gray micritic limestone, and thus different from the matrix of the specimens from D. White's nearby Tunnel Station collection. The information provided by Williard for inclusion in the USGS locality registers does not provide any stratigraphic interpretations or make any note of the horizon from which the plant fossils came, or, in fact, whether they were collected from float or in-place. Given the geographic location, however, these specimens are probably from the lower part of the Greene Formation.

Like the Tunnel Station collection, the presence of plants in a limestone is a significant environmental indicator, even in the absence of larger context. It suggests plant growth, accompanied by deposition of plant remains, during the drier portions of climate cycles. The callipterids in these deposits are probably indicators of seasonally dry habitats, conducive to the formation of limestone, and possibly laterally equivalent to calcic, vertic paleosols.

3.7. Winkler's Mill

"Winkler's Mill" is a location from which plant fossils were collected by Aureal Cross on August 27, 1948. The site is in the NW quarter of the New Martinsville 15′ Quadrangle, approximately due west of New Martinsville, WV (Fig. 14).

Among the plant fossils from this site are several specimens of *A. conferta*. These specimens are intermediate in form between those from Wallace Station, with rounded pinnules and relatively lax, widely spaced venation, and those of many other localities with rectangular, blunt-tipped pinnules with steep lateral venation. The Winkler's Mill specimens are relatively rounded and with bluntly acute apices. In addition, the lateral veins, while not extremely steep, do show a

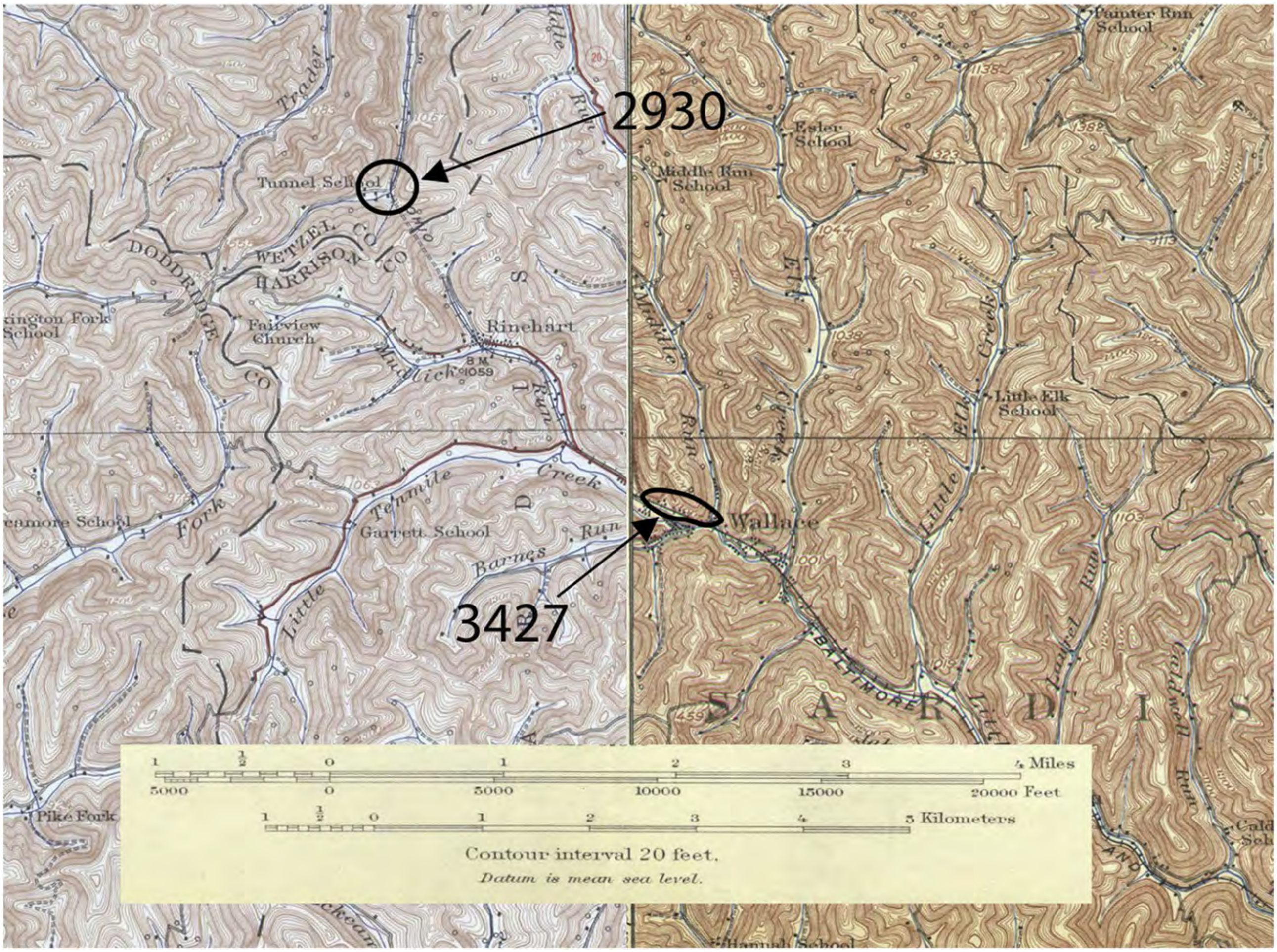

Fig. 11. Clarksburg, WV 1925 and Centerpoint, WV 1924 USGS 15′ topographic map segments showing fossil plant locations Rinehart Tunnel Station (2930) and West of Wallace Station (3427), West Virginia.

characteristic S-shape, with an upward inflection prior to meeting the pinnule margin (Fig. 15).

The geology of the general area is described in Cross et al. (1950), in a field-trip road log, specifically Day 1, Stop 12, Geological Sections 8C, 8D, and 8E on Bares Run, on the drainage to the immediate east of Winkler's Mill. This area exposes the youngest Greene Formation rocks in Ohio. The specific callipterid collecting location does not appear to be discussed, and fossil beds containing callipterids, which would be a noteworthy observation, are not mentioned in the field guide. Plants are noted in several locations among these geological sections, but only in Geological Section 8E are the plants *not* associated with the immediate roof shales of coaly layers, making these the most likely beds from which this collection might have been obtained. These particular rocks are described as gray-green to purple in color; purple, however, is often used to describe rocks with hematitic inclusions or red staining, so red coloration is not ruled out by this description.

The Winkler's Mill collection presently resides at the Field Museum of Natural History, Chicago, A.T. Cross locality the numbers C-339(2) and B-3667.

A. conferta specimens in this collection are intimately associated with other taxa, from the same rock matrix, including *Alethopteris* cf. *zeilleri* and *Annularia carinata*. That the plant fossils are not associated with a coal bed or organic-rich horizon leaves open the possibility that they were deposited under conditions of seasonality, less favorable to organic accumulation. However, there are many collections from the Dunkard that are dominated by wetland plants that similarly are found in sedimentary settings not associated with coals. *A. zeilleri* and *A. carinata* are sufficiently widespread that attribution of these species to wetlands alone cannot be assumed, prima facie.

3.8. Pleasant Hill Gap

The youngest callipterids known from the Dunkard Group, well up into the Greene Formation, were collected near Pleasant Hill Gap in southwestern Pennsylvania, a landscape feature located between New Freeport and Jollytown. It can be found in the southeast corner of the New Freeport 7.5′ Quadrangle map. David White (field notes) placed the site on the west side of the gap, 1½ mile (2.4 km) east of New Freeport. The 1904 road configuration (refer to the Rogersville 15′ Quadrangle map, southwest quadrant, Fig. 16) appears to be only slightly different from today, and a church is located at the gap as today. The old road is still visible, along which highly weathered, overgrown outcrops remain (photo in DiMichele et al., 2011).

The "Pleasant Hill Gap" (also known as "Rice's Gap" or "Rice's Church") plant collections constitute USGS Locality numbers 2915 and 3411. The fossils occur in a brown siltstone with poor fissility, not a claystone as indicated by Darrah (1969), who reports collecting at this site after discussions with David White. In addition, Darrah's identification of the coal horizon was given with reservation due to his inability to identify any limestones in the section. However, White did note limestone at more than one level in the local outcrop, and the identification of thin limestone by Skema and Harper in 2011, in a position consistent with its identification as the Nineveh limestone, mitigates this concern.

The callipterids from this site are *A. naumannii* (Fig. 17). All specimens are relatively small, but preservation is good and, despite the

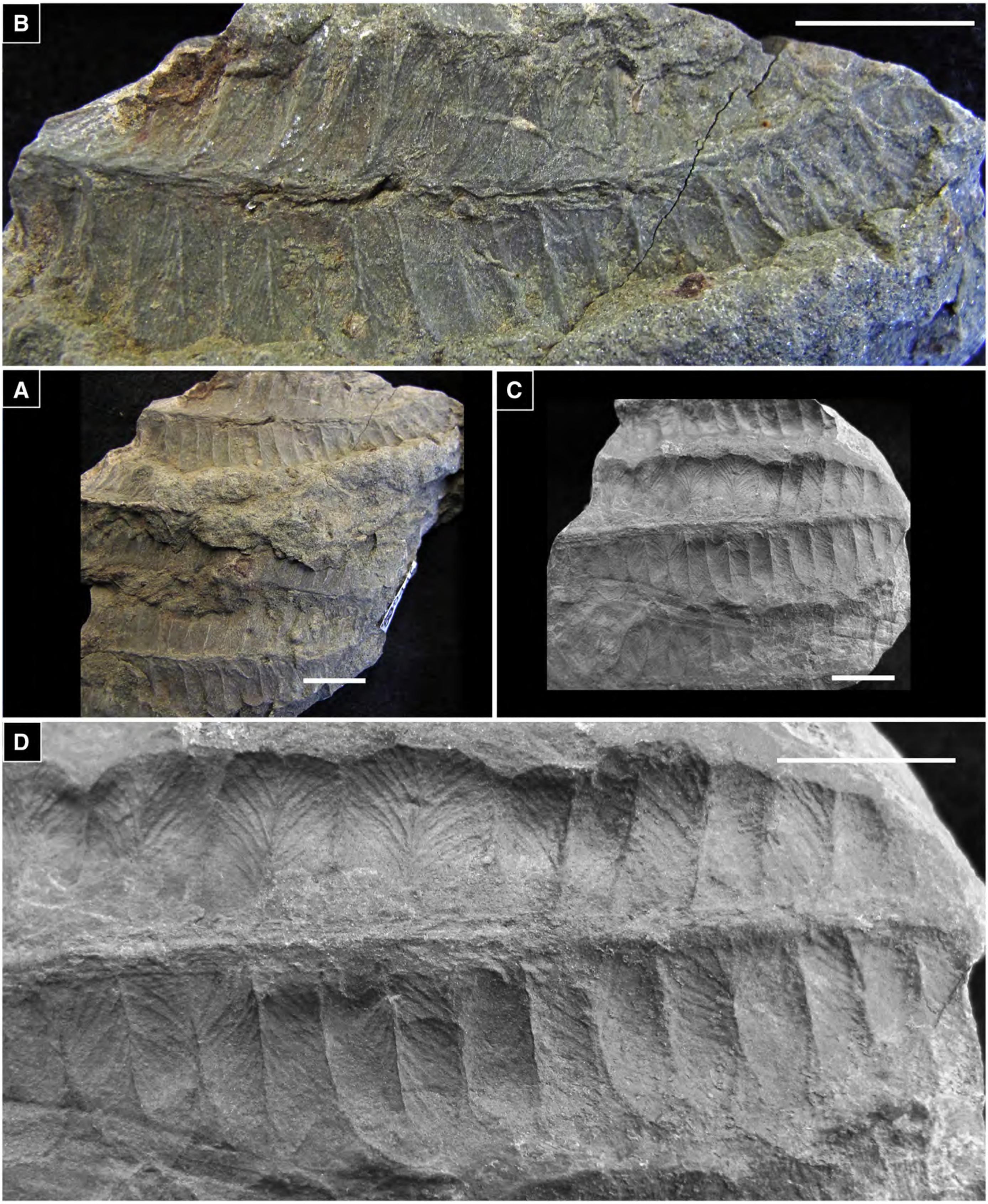

Fig. 12. *Autunia conferta*. A. Rinehart Tunnel Station, West Virginia, USGS locality 2930, USNM specimen 539445, preserved in coarse grained limestone. B. Enlargement of A, one pinna with rectangular pinnules, strong midvein, steeply upswept lateral veins. C. West of Wallace Station, West Virginia, USGS locality 3427, USNM specimen 46908, preserved in micritic limestone. D. Enlargement of C, ovoid pinnules with strong midvein and ascending s-shaped lateral venation. Scale bars = 1 cm.

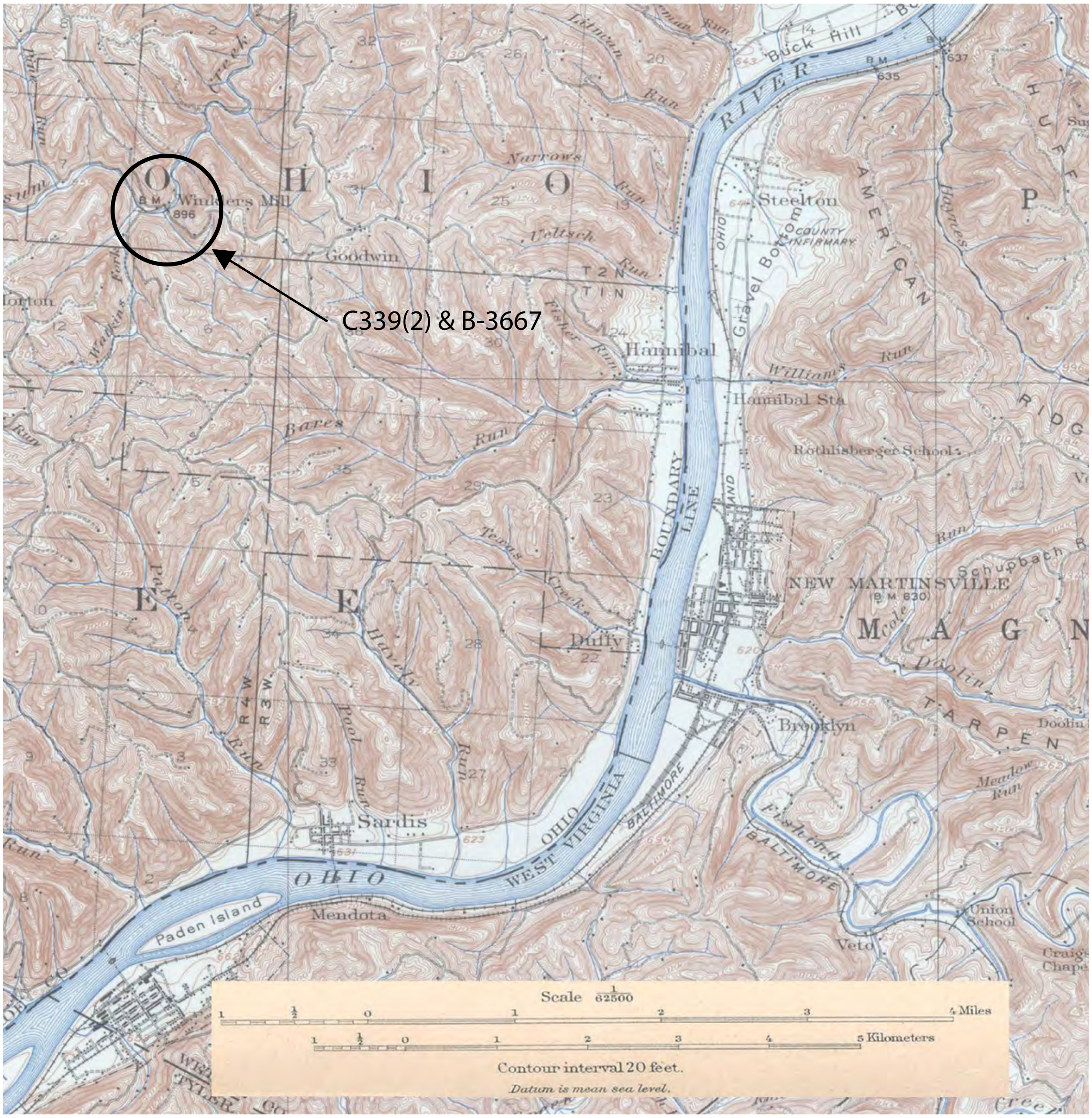

Fig. 14. New Martinsville, OH 1924 USGS 15′ topographic map segment showing the location of fossil plant locality Winkler's Mill (C339(2) and B-3667), Ohio.

delicacy of the architecture of the leaves, the pieces preserved are in good condition. Darrah (1969, p. 17) also reported, but did not illustrate, *A. conferta* and two small conifer specimens (attributed to *Lebachia*) from this locality.

The exact stratigraphic position of the collections of White, in 1902, and Willard, in 1903, are problematic, and there is considerable ambiguity among the sources of information, not the least of which is White's field notebook itself. In his notes, the exact position of the plant bearing bed is ambiguous, and appears more likely to be below a coal bed (labeled "Nineveh coal" in the notes) than above. Furthermore, both the name of the coal and the plant identification appear to have been entered into the field notebook later. A line runs from the word "Plants" to a sketch of the outcrop, along side of which is penciled "drk sh"; the callipterids are from a gray-to-buff colored shale however, not a dark shale. Consequently, despite the notations, it cannot be said for certain, on the basis of White's notes, exactly where he collected in relation to any of these beds.

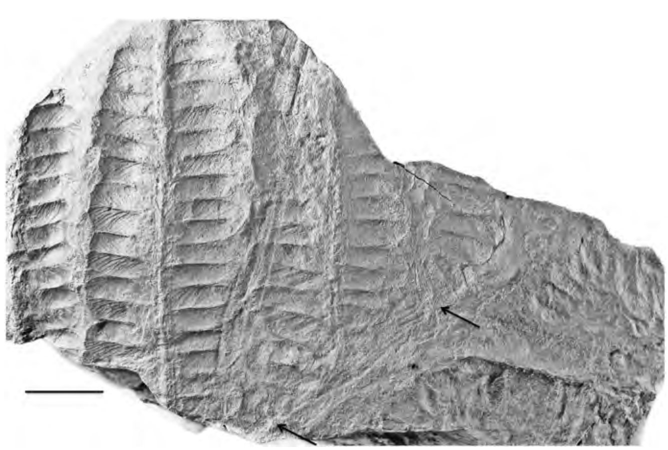

Fig. 13. *Autunia conferta*. West of Wallace Station, West Virginia, USGS locality 3427, USNM specimen 546908. Leaf fragment with several pinnae. Arrows indicate positions of small intercalary pinnules. Specimen preserved in micritic limestone. Scale bar = 1 cm.

Later fieldwork also has some bearing on this matter. Willard collected additional specimens; his collections, although poorly documented (due to the absence of field notebooks — only the USGS locality register entries remain), are from the same lithology and consist of the same flora as D. White's, and are presumably from the same horizon. A better exposure of this same portion of the stratigraphic

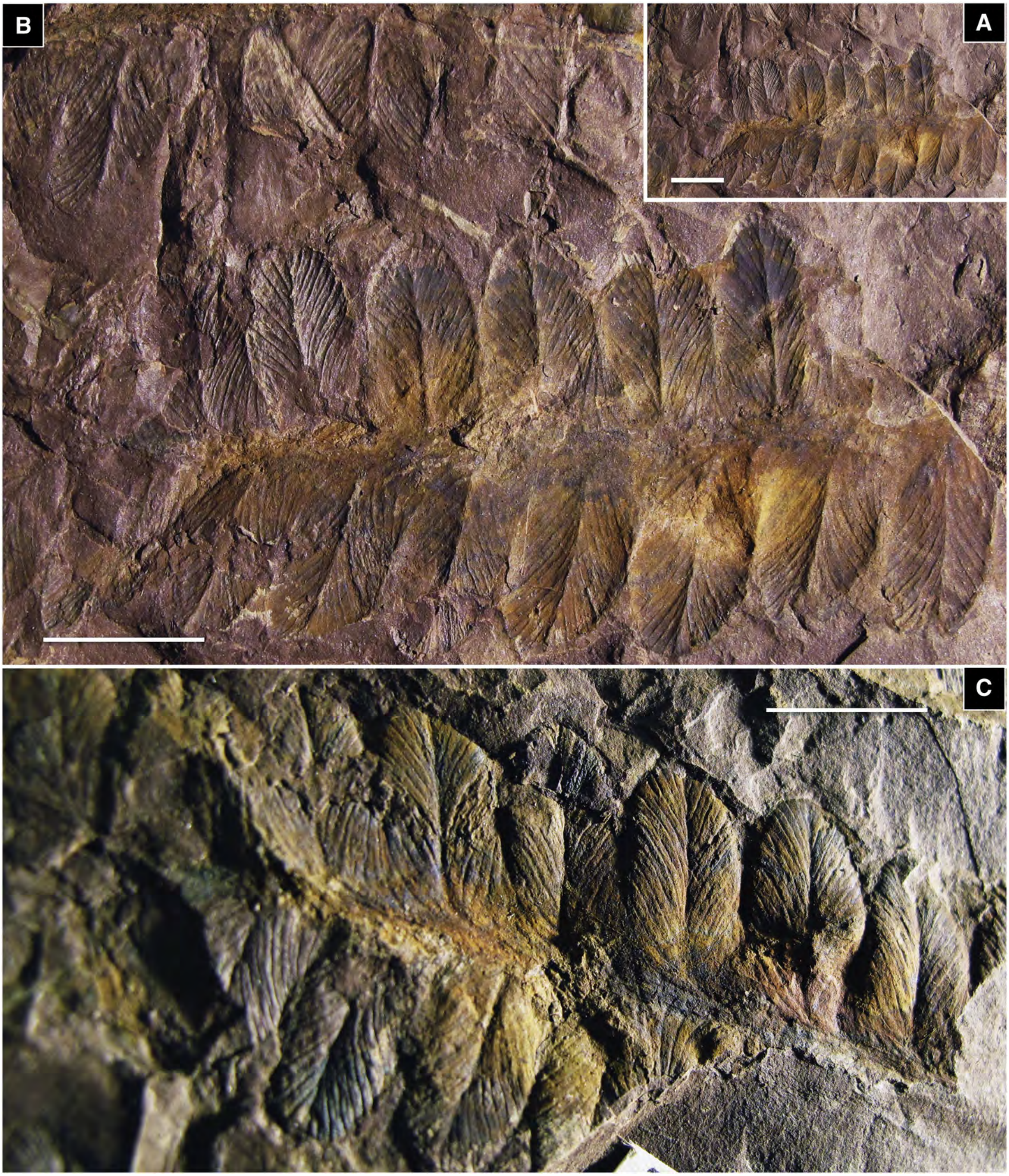

Fig. 15. *Autunia conferta* from Winkler's Mill, Ohio, collected by Aureal Cross. A.T. Cross locality numbers C-339(2) and B-3667. A. Field Museum of Natural History specimen PP55102-B. Single pinna preserved red and gray mottled siltstone. B. 3× enlargement of specimen illustrated in A; note bluntly acute pinnule apices, strong centrally located midvein, and steeply ascending convex to s-shaped lateral veins. C. FMNH PP55102-A, positive counterpart of specimen in A; note sunken decurrent midvein, vaulted pinnule lamine and showing the pinnule shape and venation. As a "positive", this specimen is an impression of the underside of the leaf. Scale bars = 1 cm.

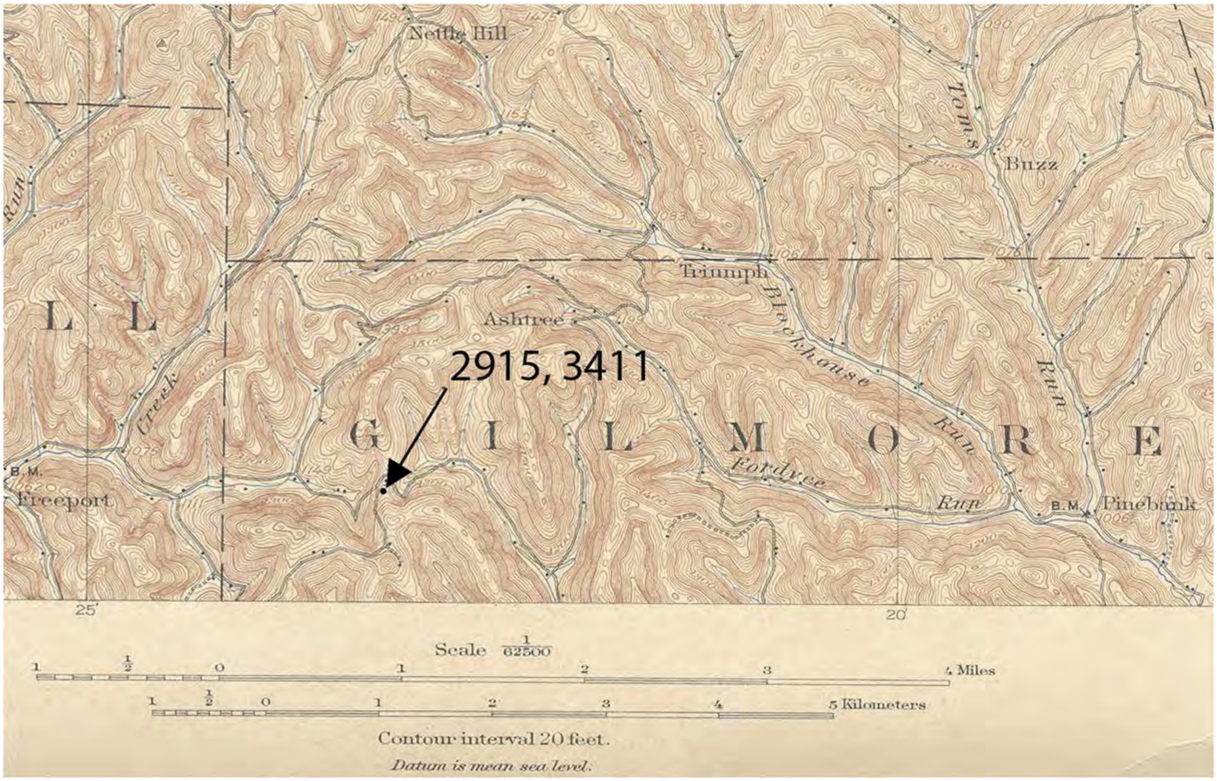

Fig. 16. Rogersville, PA 1905 USGS 15′ topographic map segment showing location of fossil plant locality Pleasant Hill Gap (2915 and 3411), Pennsylvania.

interval was located (V. Skema and J. Harper, personal observation, 2011) about 1.6 km southwest of White's original collecting site. There, an organic clayshale occurred at the horizon of the Nineveh coal, immediately above a limestone, probably the Nineveh limestone (Fig. 1). The limestone is at approximately the same elevation as the limestone and dark shale indicated in White's notebook drawing.

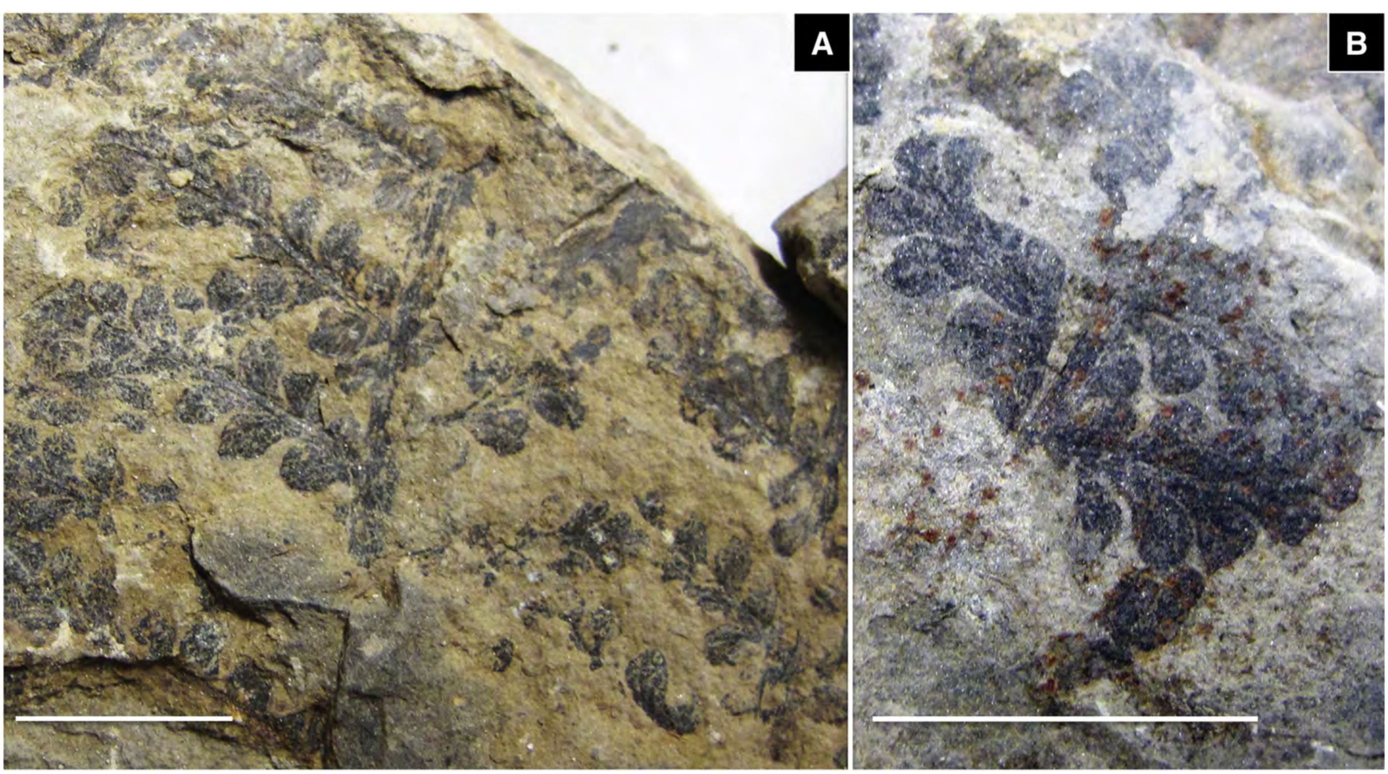

Fig. 17. *Autunia naumannii* from Pleasant Hill Gap, Pennsylvania. USGS locality 2915. A. General aspect showing weakly lobed nature of the pinnule margins and steeply ascending venation. USNM 543960. B. Rounded to weakly lobed pinnule shape and steeply ascending venation. USNM 543961. Both specimens magnified to larger than natural due to very small size of the pinnules. Scale bars = 1 cm.

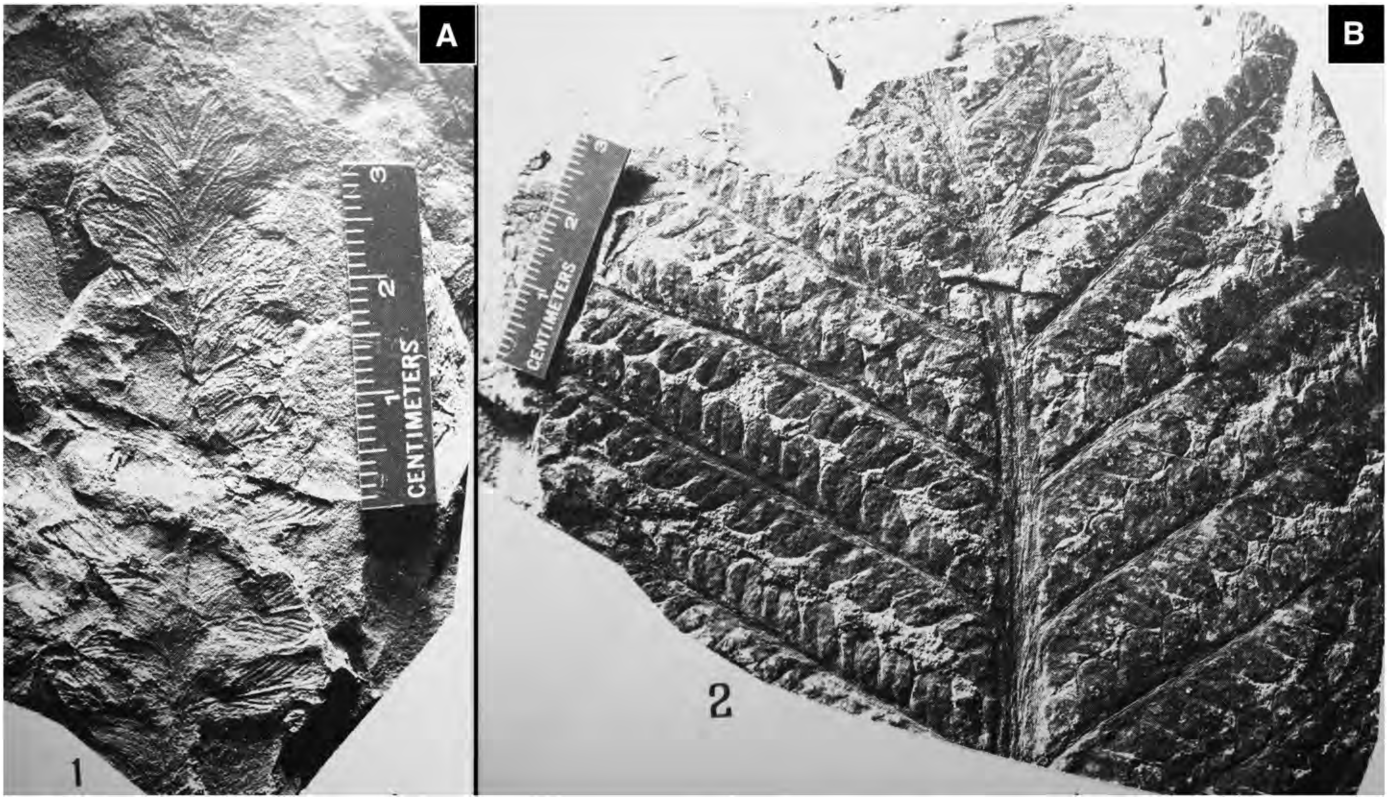

Fig. 18. Callipterid specimens originally illustrated by Darrah (1975). A. *Autunia conferta*. Reproduced from Darrah's original Fig. 1. Note pinnule apices bluntly acuminate, midvein strong and decurrent, lateral veins steeply ascending, pinnules partially fused near apex. B. *Autunia conferta.* Reproduced from Darrah's original Fig. 2. Multi-pinna frond segment with small rachial pinnules.

Plant material, though no callipterids, were found in beds of several different lithologies above the limestone.

Based on the limited present evidence, only cautious environmental interpretation of this deposit is possible. An association of two callipterid species and a conifer is consistent with a subhumid climatic setting, based on their occurrences elsewhere in equatorial Pangea. In the upper parts of the Greene Formation, compared to the Washington and lower Greene formations, coals are thinner and less numerous, indicators of climatic seasonality are stronger (Cecil et al., 2011; Eble et al., 2013), and red beds become predominant. Such indicators are broadly consistent with the presence, at some times during glacial–interglacial cycles, of plants more tolerant of seasonal drought.

3.9. Other callipterid occurrences illustrated or described in the literature

Darrah (1975) illustrated three callipterid specimens, assigning all to *C.* (*A.*) *conferta*. This identification appears to be correct for the specimens illustrated in his Figs. 1 and 2 (Fig. 18). Darrah's Fig. 3 shows a small, fragmentary specimen with lobed pinnae that make an assignment to *A. conferta* questionable.

The specimens illustrated in Darrah's Fig. 1 (Fig. 18A) and Fig. 3 were collected by J.A. Barlow on Williams Run near Williamstown, West Virginia (Fig. 19). The specimen illustrated in Darrah's Fig. 2 (Fig. 18B) is reported to come from a ravine north of Wolfdale in Canton Township, northwest of Washington, Pennsylvania. These specimens would represent the oldest known callipterids in the Dunkard Group, from below the Washington coal zone. Unfortunately, they are not well documented, so their stratigraphic position remains uncertain.

Darrah (1969, p. 17) made note of, but did not illustrate, *Callipteris* (*A.*) *conferta* at eight or more sites in Pennsylvania and West Virginia, in addition to the Brown's Mills and Pleasant Hill Gap localities of David White, described above. Most of the sites are north and northwest of Waynesburg, Pennsylvania, in red shales and dark gray sandstones, primarily above the Lower Washington Limestone.

Gillespie et al. (1975) illustrated two callipterid specimens (Fig. 20A, B) collected four feet (1.2 m) above the Lower Washington Limestone, approximately one mile (1.6 km) east of Waynesburg, Pennsylvania. Identified as "possibly *C. conferta*" (Gillespie et al., 1975), both specimens are most likely *Rhachiphyllum schenkii*. (Heyer) Kerp, a form originally described by Heyer (1884) that has long been confused with *A. conferta*; because Heyer's publication remained largely unnoticed, it can be assumed that it was unknown to these authors. We base our determination on the long, slender shape of the pinnules, the flat laminae (lack of pinnule vaulting, as seen in *A. conferta*, and with veins apparently superficial, not sunken in the lamina), more or less pointed pinnule apices, strongly decurrent pinnule attachment to the rachises, distinct lobes on decurrent portions of the basiscopic margins near the point where the lamina contacts the pinna rachis and large intercalary pinnules. The specimen illustrated in Fig. 20A appears to be an apical portion of a frond.

At the other end of the Dunkard outcrop belt from all the collections discussed above, Gillespie and Pfefferkorn (1979) reported and illustrated several specimens attributable to *A.* (*C.*) *conferta* (Fig. 20C). The specimens were found in red shales exposed near Liberty, Kanawha County, West Virginia. This locality occurs in a basin-margin setting, over 160 km south of the main coal- and limestone-bearing portion of the Dunkard Group. The rocks are likely lateral equivalents of the Washington coal interval at the base of the Washington Formation. These specimens are of special significance, demonstrating the occurrence of callipterids in presumably better drained areas where soil moisture was likely seasonal in distribution.

4. Discussion

A diversity of callipterid peltasperms has been identified in the Dunkard Group. Based on what we have observed personally in

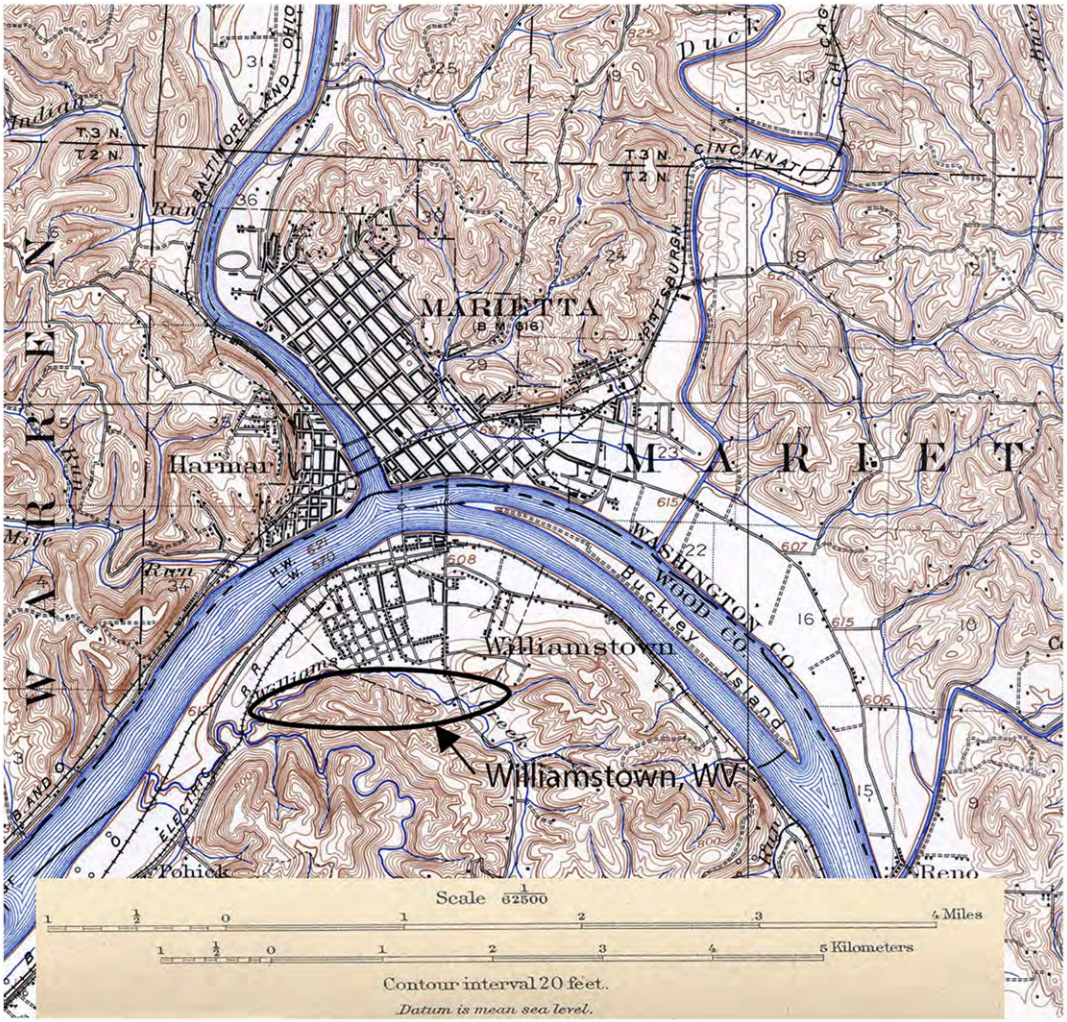

Fig. 19. Marietta, OH 1924 USGS 7.5′ topographic map segment showing location of South of Williamstown, West Virginia.

collections or from published images, this group includes *A. conferta*, *A. naumannii*, *L. oxydata*, and *Rhachiphyllum schenkii*. The most widespread of these is *A. conferta*.

The mostly widely known of the Dunkard callipterids are those from the original Brown's Bridge locality of Fontaine and I.C. White, which appear to be the same as those from the nearby Brown's Mills locality. The identity of these fossils has not been universally agreed upon. Gillespie et al. (1975, p. 229) note that David White described the Brown's Mills fossils he collected by a number of names (*C. lyratifolia*, *Callipteris diabolica*, and *Callipteris currettiensis*) but not as *C. conferta*. Gillespie et al. also note that Bode (1958) reported examining the D. White specimens first hand in 1956, while the collection was on loan to Aureal Cross at West Virginia University. Bode doubted *C. conferta* affinities and attributed all the specimens to *C. lyratifolia*, suggesting that they were rather poorly preserved (an opinion with which we respectfully disagree).

Kerp (1988) demonstrated that *A. conferta*, as currently understood, shows a considerable morphological variability in European deposits, a pattern seen also in collections from the Dunkard Group. The West of Littleton, Pumping Station, Bellton, Tunnel Station, Wallace Station and Winkler's Mill localities have yielded specimens with medium-sized to large, bluntly pointed or rounded pinnules that are overall similar to some *Autunia* specimens from Asselian to Kungurian red beds of North-Central Texas (Chaney and DiMichele, 2007). *Autunia conferta* with smaller pinnules occurs commonly in the Asselian-Artinskian Abo Formation red beds of central New Mexico (DiMichele et al., 2013) and from the Rotliegends of Europe (Kerp, 1988). There also is considerable variation in the apparent lamina thickness among the various *A. conferta* specimens found in Dunkard strata; those from Brown's Mills, which are preserved as organic compressions, are thick enough to obscure many details of lateral venation. In contrast, many of the impressions in limestone and mudstone from other locations appear to be considerably thinner limbed. Venation also varies widely among these *A. conferta* specimens. All have strong, sunken midveins that, where visible, are decurrent. Lateral veins, in contrast, vary from strongly ascending (as in Fig. 12B) to rather lax (Fig. 12D), with many forms between these extremes, repeatedly showing an s-shape typical of lateral venation in many peltasperms.

There is general agreement that the earliest stratigraphic occurrence of callipterids in Dunkard rocks is near the middle of the Washington Formation (in the two-formation scheme). Callipterids continue to occur, sporadically, far into the Greene Formation. Darrah (1969) reports more callipterid occurrence data than anyone else, though it is primarily anecdotal — surviving correspondence indicates that he planned a comprehensive paper on the Dunkard flora, which he did not complete prior to his death. He noted (Darrah, 1969, p. 47) that *C.* (*A.*) *conferta*, *C. lyratifolia* (*L. oxydata*) and *C.* (*A.*) *naumanni* occur at several horizons and usually are abundant where found. However, the number of localities at which these species have been found are few and scattered when compared to the known occurrences of the typical wetland flora. Darrah (1969, p. 154) states: "The occurrence of *Callipteris* is much more sporadic than I had long ago assumed. … When *Callipteris* does occur, however, it is abundant almost to the exclusion of other forms, at many localities." This is a particular kind of rarity, few known occurrences but abundant where occurring.

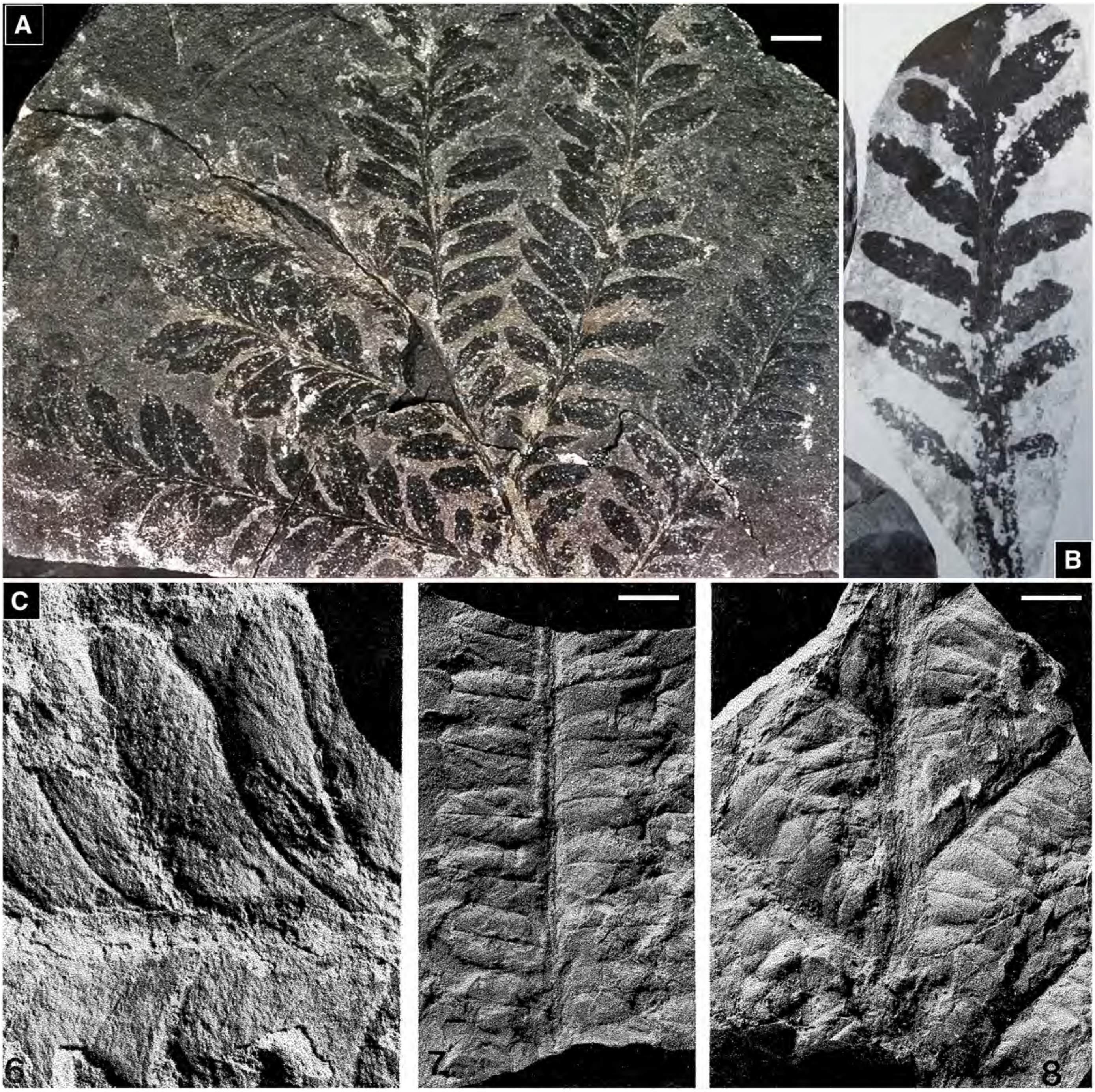

Fig. 20. Callipterid specimens originally illustrated by Gillespie et al. (1975) from east of Waynesburg, Pennsylvania, and by Gillespie and Pfefferkorn (1979) from Liberty, West Virginia. A. *Rhachiphyllum schenkii*. Specimen originally illustrated as Gillespie et al. Plate IA. Partial frond segment showing fusiform pinnule shape, flat pinnule laminae, large intercallary pinnules. B. *Rhachiphyllum schenkii*. Reproduced from Gillespie et al.'s original Plate VIIIA, which was identified as "Possible *Callipteris conferta*". Note flat aspect to the pinnules, midvein not sunken, pinnule margins are wavy, pinnules lobed at base, terminal pinnule free. No scale in original illustration. C. *Autunia conferta* reproduced from Gillespie and Pfefferkorn (1979) original Plate 3, Figs. 6–8. Scale bars = 1 cm.

Despite their sporadic occurrence, what can be said with some certainty is that Dunkard callipterid-bearing beds are not closely associated with coaly or organic-rich facies, instead occurring mainly in various kinds of shales and limestones. Thus, in the Greene Formation in particular, a focus on collecting plant macrofossils and palynological samples from the organic-rich coaly layers will certainly tend to produce wetland plants of a type generally considered to be a "Pennsylvanian" flora.

Ecologically controlled biofacies considerations are a potentially significant confounding matter when using terrestrial plants for biostratigraphic purposes. Plant distribution, both of individual species and of species pools, strongly reflects the interplay of climatic and local habitat conditions (e.g., see many references to this in DiMichele et al., 2008; Roscher and Schneider, 2006). As a consequence, it is essential that biostratigraphic schemes be established on the basis of species pools with ecological and evolutionary continuity in space and time, the plants living under similar climatic and environmental conditions. Only at the extremes of their environmental tolerances might plant species be expected to reflect primary effects of such factors as elevation or latitude — ample evidence from the study of warm-climate floras in Earth history, or of the recent Pleistocene ice ages and the modern day, indicate that it is climatic conditions plants respond to, not elevation or latitude per se.

To bring this back to the matter of callipterids in Dunkard stratigraphy, whatever callipterids may signify about the age of the Dunkard, they most certainly indicate periods of seasonally dry, subhumid paleoclimates. Physical evidence strongly points in this direction, such as the association of these plants with sequences dominated by Calcisols and Vertisols, both in the Washington and Greene formations, and the steep decline in coal bed frequency and thickness coinciding with the appearance of callipterids (Eble et al., 2013). As Darrah (1969, p. 68) noted, significantly, "…the *Callipteris* Permian flora…appears to be indicative of physiologically xerophytic conditions. It is a biofacies usually associated with a peculiar lithofacies." Darrah (1969), for example, interpreted the coriaceous leaves of the Dunkard callipterids to indicate "a facies flora of drier environments." He noted that he "never found *Callipteris* in fine grained gray or black shales. … but in the upper Dunkard section it always occurs in coarse micaceous sandstone of yellow brown to chocolate brown color." He also noted finding conifers (which he identified as *Lebachia*, but did not illustrate) in association with callipterids (*A. naumannii*) near the level of the Nineveh coal (at the Pleasant Hill Gap locality), which is in keeping with an overall interpretation of these plants as indicative of seasonally dry conditions. A similar pattern has been noted in Europe. However, Kerp and Fichter (1985) and Barthel and Rößler (1996), both demonstrated environmental segregation among the callipterids themselves. In particular, *A. conferta* appears to have preferred or been tolerant of environments with significant soil moisture deficits, whereas *Rhachiphyllum schenckii* preferred habitats with high levels of soil moisture, where it may have been a ruderal. These patterns of segregation are found in Dunkard Group strata in which the co-occurrence of callipterid species is documented only at Brown's Bridge and Brown's Mills.

The larger scale pattern of punctuated intercalations of callipterid-dominated floras into a succession of more typical Pennsylvanian wetland plants indicates oscillations of climatic conditions, although the temporal framework of these oscillations cannot be resolved on the basis of Dunkard exposures. These oscillations are, however, superimposed on a shift to "drier" conditions in equatorial Pangea during later Pennsylvanian time (Roscher and Schneider, 2006; Tabor and Poulsen, 2008), when the Monongahela Formation and lower Dunkard were deposited. A consequence of this longer-term shift is that in continental basins of the US and Europe the Pennsylvanian–Permian boundary, no matter how it is defined (paleontologically or by absolute age dates), is lithologically gradational, to the point of being described as "indistinct".

Perhaps the most telling occurrences are those from non-marine limestones or shaley partings of limestones, such as the Brown's Mills, Tunnel Station, and Wallace Station collections. In these instances the callipterids occur in close association with non-marine invertebrates (non-marine ostracodes and gastropods of the Brown's Mills shales), or in the limestone matrix itself (Tunnel Station and Wallace Station collections). Such occurrences suggest environments of high evapotranspiration, resulting in at least seasonally increased concentrations of dissolved solids in lacustrine environments. It is noteworthy that biofacies and lithofacies similar to those of the Dunkard occur in the Appalachian section in the older Missourian (Kasimovian) Conemaugh Formation and, to a lesser extent, in the Virgilian (Gzhelian) Monongahela Formation. In those rocks, callipterids seem to be absent, although conifers have been found (Blake et al., 2002; Darrah, 1969; Martino and Blake, 2001). Missourian (Kasimovian) age callipterids have been reported, however, in intra-coal deposits in the U.S. Midcontinent (Cridland and Morris, 1963) and in association with sabkha facies from New Mexico (Falcon-Lang et al., 2011a). An even older occurrence (attributed to *Rhachiphyllum*) has been documented from deltaic mudstones of Desmoinesian-age (Moscovian) in the Illinois Basin (Pšenička et al., 2011). So, we must assume that these plants were "out there" someplace on the Pennsylvanian equatorial landscape, beyond the favored times and places for preservation, much earlier than they appear in the Dunkard Group. The entirety of these temporal, spatial and environmental occurrences, as commented on by many other authors, suggests that callipterids indeed had strong ties to climates and environments with seasonal moisture deficits, calling for caution when making biostratigraphic determinations in those stratigraphic sections where both wetland and seasonally dry floras occur.

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