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STUDIES ON NORTH AMERICAN PECOPTERIDS. III. PECOPTERIS BUTTSII D. WHITE FROM THE EARLY PENNSYLVANIAN OF ALABAMA

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ABSTRACT—The form genus *Pecopteris* Brongniart is rare in Lower Pennsylvanian strata. Those species originally described from North America need to be reinvestigated to determine their relationship to the more extensively described European forms. The occurrence of early Pennsylvanian pecopterids is significant because they represent the early history of this group, which becomes dominant in the Westphalian D.

Pecopteris buttsii D. White was originally established for a lobate pinnuled pecopterid from the Brookwood coal horizon (New River equivalent, Westphalian A), Warrior coalfield, Alabama. The species was invalidly published and a study of the type specimen was initiated to discern its affinity. Attempts at collecting additional specimens from the type area have failed and the formal description is based upon fragments of seven third or possibly fourth order (?) pinnae. Additional specimens of *P. buttsii* (?) from Tennessee were also examined to discern their relationship with the holotype.

Consideration of parameters necessary to erect form taxa is highly complex and many factors must be assessed prior to establishment of a new form. These parameters include the degree of morphological homology between specimens and their reported temporal isolation or continuation. Frequency of occurrence should not be considered as a delimiting character nor should size or preservational configuration.

Comparison of the holotype of *P. buttsii* with other Westphalian pecopterids reveals that *P. buttsii* is conspecific with *P. volkmannii* Sauveur and that certain forms of *P. vestita* Lesquereux and *P. pseudovestita* D. White may also be synonymous. Based on the continual reported occurrence of *P. volkmannii* throughout the Westphalian and the indistinguishable character of *P. volkmannii* and *P. lamuriana* Heer, *P. lamuriana* is reduced to a synonym of *P. volkmannii*. The Tennessee specimens which may have been classified as *P. buttsii* and curated in the Department of Geology, University of Tennessee, Knoxville, are not conspecific with *P. volkmannii* and are poorly preserved so that clear identification is not possible. These fragmentary specimens are tentatively assigned to *P. unita* Brongniart and the *P. miltonii* Artis complex.

INTRODUCTION

THE PENNSYLVANIAN megaflora of the southern Appalachian region, inclusive of the Warrior, Coosa, Cahaba and Plateau coal fields of Alabama, is poorly documented. Very few coalified compression assemblages have been studied in any detail, and most of the scattered reports concerning fossil plant material either recognize the preservation of a particular form at a particular stratum, or merely note the presence of preserved vegetation. Bunbury (in Lyell, 1846) is the first author to report on the floristic character of the Pennsylvanian System in Alabama after examination of a small suite of specimens provided by Lyell. Sixteen taxa are identified. Lesquereux (1876) published a list of 78 plant species based upon collections of plant fossils provided by Dr. Eugene Smith from various horizons in the Cahaba and Warrior coal fields. Detailed descriptions and illustrations of new species were deferred until the publication of the Coal Flora (Lesquereux, 1879, 1880, 1884).

The first analysis of any specific coalified compression megafloral assemblage from Alabama was published by Lesquereux (1888) when he described and illustrated 26 species from a horizon above a coal mined from Black Creek, northwest of Gadsden. Since the publication of this study only one additional suite of specimens collected from a particular horizon has been documented (Lyons and Meissner, 1982).

The remainder of reports concerning coalified compression plants pertain to specific taxa from particular horizons. McCalley (1896) recognized *Lepidodendron, Calamites* and *Stigmaria* in the lower sandstone units near LaGrange while he noted that "stem and leaf impressions of ferns" are common features within the underclays of coals in the Warrior coal basin (McCalley, 1900). Smith (1903), Prouty (1922, 1923) and Butts (*in*

Adams and others, 1926) reported silicified Lepidostrobus from the Erin Shale, Clay County, which David White had examined and verified to taxonomic status. White (in Adams and others, 1926) also identified, but did not describe, a number of plants characteristic of the Alabama coal fields. D. White (1943) described some forms of *Eremopteris*, Diplothnema, Aneimites and Mariopteris from the southern Appalachians and illustrated new taxa based upon specimens collected in Alabama. Read (in Rothrock, 1949) identified a few specimens from the shales above the Brown coal of the Coosa coal field. In addition, Read (in Metzgar, 1965) documented a small florule, composed of three species, from above the Brookwood coal. Mamay (1955) redescribed three unusual specimens collected near Cordova, Alabama, and assigned them to a new genus, Acrangiophyllum.

One of the few figured specimens collected within Alabama and designated as a new species of Pecopteris, P. buttsii D. White (in Adams and others, 1926), is an interesting form because of its reported occurrence in the Brookwood coal horizon, which has been equated to the early New River by Read (in Metzgar, 1965). Preliminary correlations of lower Pennsylvanian strata with the U.S. Geological Survey stratotype have placed the Brookwood coal horizon at a position equivalent with the uppermost New River or lowermost Kanawha (uppermost Westphalian Alowermost Westphalian B; Barwood, 1981, written communication). In addition, specimens collected in the Kanawha and Allegheny equivalents in the Caryville, Tennessee, area have been assigned to P. buttsii (Barlow, 1969). The occurrence of presumably pteridophyte foliage assignable to Pecopteris in the early Pennsylvanian is rare. Although a few pecopterids have been reported to occur in the lower Westphalian (Wagner, 1960, 1962, 1971), the diversity of form is small. Pecopterids increase in diversity and complexity in the Upper Westphalian and dominate the Stephanian (Upper Pennsylvanian equivalent). This increase in plasticity within the genus accompanies the rise to dominance of ferns in coal swamp environments (Phillips and others, 1974).

Pecopteris buttsii was named as a new tax-

on by D. White and illustrated (*in* Adams and others, 1926, Pl. 70D, figs. 1–2) but never formally diagnosed. The holotype was briefly analyzed in the figure caption, based upon an enlargement of a portion of the specimen. The illustration depicts the lobation of the margins and the coarse, broad veins concealed in a densely villose or rugose lamina. The collection locality is noted to have been the Brookwood coal horizon, Alabama.

According to Articles 32.1 and 38 of the International Code of Botanical Nomenclature (Stafleu and others, 1978), in order for the name of a fossil taxon of specific or lower rank to be validly published on or after 1 January 1912, the name must be accompanied by an illustration or figure showing the essential characters, in addition to a description or diagnosis. Only when publication of the name of a monotypic genus based on a new species prior to 1 January 1908, or the name of a species or of an infraspecific taxon published before 1 January 1908, can an illustration with analysis showing essential characters be considered as validly published. *Pecopteris buttsii* D. White is invalidly published, and therefore, a nomen nudum.

In addition to the taxonomic nomenclatural problems associated with this foliage form, the morphological configuration of the pinnules is unknown in North America at such a low stratigraphic level. The lobed character of the pinnules and venation pattern is suggestive of taxa either recorded from time-equivalent strata in Europe or known only from higher stratigraphic positions in the Euramerican province. In order to validate the taxon, a reinvestigation of the holotype specimens and additional material described as *P. buttsii* (Barlow, 1969) have been studied.

MATERIALS AND METHODS

The holotype of *Pecopteris buttsii* D. White was obtained on loan from the Alabama Geological Survey, Tuscaloosa, in late 1978. After initial examination of the specimen it was deemed necessary to collect additional fossils from the Brookwood coal horizon, Black Warrior coal field, in order to best characterize the morphological plasticity in the taxon. Since Butts reported (*in* Adams and others, 1926) only the coal horizon and not a



FIGURE 1—Outcrop pattern of the Brookwood coal group (McCalley, 1900), depicted by Metzgar (1965) as his stratigraphic interval G. *Pecopteris buttsii* D. White is reported to have been collected from the Brookwood coal horizon.

particular locality, a search of active and abandoned mining operations within Metzgar's (1965) interval G (equivalent to the Brookwood coal group of McCalley, 1900) was conducted (Figure 1). Stratigraphic Interval G consists of those beds between the Johnson coal, at the base, and the top of the Pennsylvanian sequence, or those beds above the Brookwood coal guide seam. These coals crop out in isolated areas in topographically high regions in the southern part of the coal basin and include, in stratigraphically ascending order, the Carter, Milldale, Brookwood and Guide seams. Collections of allochthonous vegetation at a number of different mines and coal horizons have failed to recover additional specimens of P. buttsii.

Darrah (1969, p. 137) noted that *P. buttsii* is one of the polymorphic lobed forms that exhibits pinnae equivalent to *P. miltonii*, *P.* "vestita," *P. pseudovestita* and *P. arborescens* and believed that redescription of this species, based upon "many fine collections will unravel much of the early history of the *P. miltonii* group in America." The collection used as the basis for the aforementioned statement is by Barlow (1969). However, no specimens of *P. buttsii* could be located in Barlow's collection. A duplicate collection from Barlow's research area was sent to Professor W. C. Darrah (J. Barlow, written communication, 1981) and is presently in storage (W. C. Darrah, written and personal communication, 1981). Thus, Barlow's specimens of *P. buttsii* can not be restudied at this time.

DESCRIPTION OF SPECIMENS

P. buttsii D. White.—The seven fragmentary Pecopteris buttsii pinnae (tertiary/quaternary?) with attached pinnules are preserved as coalified compressions and impressions within a light gray to medium gray, horizontally bedded, medium grained siltstone. Scattered within the siltstone matrix are occasional crystals of pyrite. Coalified compressions are preserved throughout the matrix and also include disarticulated pinnae of Neuropteris and unidentifiable axes.

Rachises of the ultimate pinnae are 1.5–2 mm in diameter, striated, and possess small, irregularly scattered projections probably representative of scale or hair bases (Figures 2A, B). The largest rachial fragment measures 12 cm in length (Butts, *in* Adams and others, 1926, Pl. 70D, fig. 1) and the pinnules preserved along this fragment demonstrate only a slight change in length over the entire pinna length. Twenty-eight pinnules are preserved along the dextral side of this fragment; 27 on the sinistral side.

Pinnules are inserted upon the rachis at approximately right angles, although some pinnules are slightly inclined upon the rachis (Figures 2A, B, 3A). Pinnules are inserted alternately upon the rachis, and attachment to the rachis appears to be marginal, although in some, attachment appears to be within the confines of the rachis proper. This latter feature is probably due to diagenetic processes. Dextral insertion of pinnules averages 5 mm between midveins of successive pinnules, whereas distances between dextral and sinistral insertion of midveins upon the rachis average approximately 2.5 mm. The longest preserved pinnule is 18 mm long, 4.5 mm wide and is characterized by a lobed margin and a rounded summit. Most pinnules are poorly preserved and morphological details concerning marginal features are lost. Fusion of the margin lobes occurs for three-fourths the distance from the midvein to the apex of the lobe (Figure 2B). Marginal lobes are 2 mm in breadth, measured from the pinnule





FIGURE 3—Line illustrations of holotype and specimens from Tennessee. A, lobate pinnule of P. buttsii holotype depicting scale/hair bases on rachis, preserved coalified compression and impressional (stippled) features. This pinnule was figured by Butts (*in* Adams and others, 1926) on Pl. 70D, fig. 2. B, specimen BRS 132 (lower Rock Spring coal) illustrating pinnule morphology and lateral venation pattern. C, specimen BPB 103 (Pee Wee coal) figuring pinnule morphology and lateral venation pattern.

midvein, and length of the free lobed portion is 1.5 mm on a pinnule measuring 18 mm long. Eleven to twelve lobes per margin side are present and the first, basal lobe is always larger than subsequently developed lobes. It is difficult to discern the degree of fusion of basal lobes to the pinna rachis, but it appears as if the basal lobes were fused possibly for one-half their breadth.

The coalified surface of most pinnules either obscures the detail of the venation pattern or

has been subsequently weathered to leave an impression which lacks discernable detail. A few pinnules preserved on the reverse side of the specimen (Butts, *in* Adams and others, 1926, Pl. 70D, fig. 2; Figures 2B, 3A) are well preserved and allow the description of the venation pattern. Lateral veins arise alternately from a stout midvein and each lateral vein bifurcates close to the point of origin. The basalmost lateral vein of the dichotomy ascends in a slight curve to the margin and

[←]

FIGURE 2—Pecopteris buttsii D. White. Scale in mm. A, reverse side of holotype figured by Butts (*in* Adams and others, 1926), a part of which was used to illustrate the lateral venation pattern as figured on Pl. 70D, fig. 2. B, enlargement of pinna to demonstrate hair/scale bases on rachis (at arrows) and to detail the lateral venation pattern and pinnule morphology. Pinnules within rectangular boundary illustrated by Butts (*in* Adams and others, 1926) on Pl. 70D, fig. 2. This figure is not an enlargement of the pinna illustrated on Pl. 70D, fig. 1.

is retained within the lobe. A second dichotomy of the lateral vein occurs immediately after the first dichotomy and the acroscopic vein of this division curves to the margin, again, remaining within the lobe. The residual central vein undergoes an even dichotomy and both veins curve slightly toward the margin and meet the margin edge in an open angle. Gastaldo and Matten (1978) term this fascicular venation pattern complex. The manner in which the midvein terminates at the summit of the pinnule is unknown.

Tennessee specimens.-The lobate pinnuled specimens of Pecopteris curated in paleobotanical collections of the University of Tennessee, Knoxville, also have been examined. Specimens BHA 49, 71 and 72 (High Coal, Cross Mountain) are part and counterparts and are poorly preserved disarticulated fragments of possibly tertiary pinnae (Figure 4A). Most pinnules are highly distorted but some display characteristics which are assessible. Pinnules may attain a length of 15 mm and a width of 4 mm and have lobed margins. A slightly decurrent midvein arises from a nondescript rachis and extends to a rounded(?) pinnule summit. Lateral venation is difficult to discern due to epidermal impressions but a fascicle of veins appears to arise from the midvein and extend to the margin. Each fascicle is contained within a pinnule lobe. It appears that the lateral vein emerges obliquely from the midvein, dichotomizes near the midvein and the basiscopicmost lateral vein continues to the margin. The uppermost vein of the bifurcation dichotomizes again approximately one-third between the midvein and margin and the acroscopic vein of this division curves to the margin. The remaining

vein of the dichotomy dichotomizes approximately halfway between the midvein and the margin and the uppermost resulting vein again dichotomizes three-fourths of the distance between the midvein and margin.

Specimen BRS 132 (Lower Rock Spring Coal, Pine Bald) is also a small, fragmentary pinna but quite well preserved. The specimen (Figure 4B) depicts the acroscopic transition within the pinna of lobate to entire margined pinnules attached to a slightly striated rachis. Lobate pinnules attain a maximum height of 12 mm and a width of 5 mm and a slightly decurrent midvein arises from the rachis and extends to a rounded pinnule summit. Lateral veins emerge obliquely from the midvein and dichotomize producing a fascicle of veins which continues to the margin and is confined within the pinnule lobe. The resultant venation pattern is similar to that previously described for specimens BHA 49, 71, 72 with the exception that the basiscopic pinnule venation pattern is slightly more complex (Figure 3B). The lateral veins emerge and dichotomize near to the point of origin with the resultant lower vein again dichotomizing approximately one-half the distance between the midvein and the margin. The uppermost vein divides at approximately one-third the distance between the midvein and margin and the resultant veins curve towards the margin. The acroscopicmost vein remains simple whereas the basiscopic vein of the dichotomy dichotomizes approximately at the one-half point and the uppermost vein of this dichotomy may, in some cases, dichotomize again near the margin.

Three coalified compression specimens from the Pee Wee and Split Coals (BPB 77,

^{FIGURE 4—Specimens collected by Barlow from New River-Kanawha equivalents in Tennessee and believed to have possibly been identified as P. buttsii. Scale for all figures in mm. A, specimen BHA 49 ultimate pinnae of a pecopterid collected from strata associated with the High coal, Cross Mountain. Probably assignable to P. miltonii complex. B, specimen BRS 132 collected from strata associated with the lower Rock Spring coal, Pine Bald. Ultimate lobate pinnules assigned to P. miltonii. C, specimen BPB 77 (Pee Wee and Split coals north of Clinchmore) showing two ultimate pinnae assigned to the P. miltonii complex. Fragmentary pinnules on the left of the specimen bear resemblance to P. buttsii, but entire pinnules are easily distinguishable. D, specimen BPB 102 assigned to the P. miltonii complex. E, specimen on the left is assignable to P. unita while the specimen on the right is assigned to the P. miltonii complex. F, specimen, BPB 50 showing acroscopic portion of ultimate pinnae assigned to the P. miltonii complex. S, specimen, BPB 50 showing acroscopic portion of ultimate pinnae assigned to the P. miltonii complex. S, specimen, BPB 50 showing acroscopic portion of ultimate pinnae assigned to the P. miltonii complex.}



102, 103; north of Clinchmore) are morphologically similar to P. buttsii, whereas one specimen (BPB 50; Figure 4F) possesses a similar venation pattern but a different pinnule morphology. Specimen BPB 77 is a small fragment of probably a tertiary pinna with attached lobate pinnules (Figure 4C). The pinnules attain a maximum height of 12 mm and a width of 5 mm and are basally fused to the rachis. The rachis is striated but there does not appear to be any evidence of hair/ scale bases. A slightly decurrent midvein arises from the rachis and ascends to a rounded summit. The lateral venation pattern is difficult to discern due to the presence of epidermal features but it appears that lateral veins arise obliquely from the midvein, dichotomize, giving rise to a fascicle of veins that curves towards the margin and is retained within the pinnule lobe (Figure 3C). The resultant fascicle pattern appears homologous to P. buttsii. The same features are preserved on specimens BPB 102 and 103 (Figures 4D, E).

DISCUSSION

Comparison of P. buttsii with lobate pinnuled pecopterids. - Early Pennsylvanian (Westphalian A-B equivalents) pecopterids are quite rare and the diversity of forms encountered is low. Corsin (1951) recorded Pecopteris acuta Brongniart, P. plumosa-dentata Artis Brongniart, P. volkmannii Sauver, P. miltonii (Artis) Brongniart and P. pennaeformis Brongniart from Westphalian B strata in the Sarre and Lorraine. Dalinval (1960) also recognized P. plumosa-dentata, P. pennaeformis, P. volkmannii, and P. miltonii, as well as P. vedrinei Dalinval, P. intermedia Bertrand (MS), P. bourozii Dalinval, P. hirsuta Dalinval, P. dufayi Dalinval, P. lobulata Dalinval, P. avoldensis Stur, and P. simonii Zeiller from Westphalian A-B equivalents in the north of France. Wagner (1959, 1962) recognized Pecopteris plumosadentata (Artis) Brongniart and Pecopteris aspera Brongniart from the Westphalian A-B in northwest Spain. Subsequently, Wagner (1960, 1971) recorded Pecopteris volkmannii, Pecopteris miltonii and Pecopteris pennaeformis from the lower Westphalian.

In North America, Bell (1944) reported *Pe-copteris plumosa* var. *crenata* and *P. pilosa* Bell from Westphalian B equivalents in east-

ern Canada. Darrah (1969) recognized P. cf. aspera in Westphalian A equivalents and P. abbreviata Brongniart (=P. miltonii), P. miltonii, and P. dentata in Westphalian C equivalents as characteristic species. Gillespie and Pfefferkorn (1979) utilized P. miltonii as a biostratigraphic marker for Kanawha (Westphalian B/C equivalents) and younger strata in the U.S. Geological Survey Stratotype in West Virginia. Since the establishment of Pecopteris, over 290 species have been recognized (Boureau and Doubinger, 1975) and the few species recorded from the Early Westphalian compose less than 5% of all established forms.

In order to delimit the affinity of *P. buttsii*, a survey of all early Pennsylvanian lobate pinnuled pecopterids was conducted. Distinguishing taxonomic characteristics similar to those described for *P. buttsii* were found to exist in nine early Pennsylvanian forms (*P. miltonii*, *P. vedrinei*, *P. intermedia*, *P. dufayi*, *P. lobulata*, *P. avoldensis*, *P. simonii*, *P. pennaeformis* and *P. volkmannii*) and three Middle to Late Pennsylvanian forms (*P. lamuriana*, *P. vestita*, and *P. pseudovestita*).

Pecopteris miltonii (Artis) Brongniart is a species in which the frond is very variable in pinnule morphology. Although the holotype is no longer available for examination, and the illustrations by Artis (1838) depict only a fertile portion of a frond where the pinnules appear lobed, well documented specimens have provided a basis for comparison (Kidston, 1924; Corsin, 1951; Dalinval, 1960). Specimens assignable to *P. miltonii* may have pinnules that are small and entire margined or elongated and have a lobed margin, depending upon the position of the pinnule within the frond. On upper tertiary pinnae, pinnules are lobate and the upper surface is covered by small, fine, appressed hairs. The pinnules are adherent to the base and are obliquely inserted upon a striated rachis. The pinnule is usually enlarged at the base and the inferior (basiscopic) border is decurrent. The median vein extends to near the summit and divides; lateral veins are inclined and divide either in a pattern of unequal dichotomous, twice equal dichotomous or complex. Each lateral vein bundle ends within the pinnule lobe. The venation pattern of P. buttsii is complex and fascicular morphology is similar to that of P. miltonii. The degree of pinnule lobation, the regularity of lateral venation pattern and the punctate character of the rachis, though, do not allow their synonymy.

Pecopteris buttsii can neither be synonymized with P. vedrinei, P. intermedia, P. dufayi, P. lobulata, P. avoldensis, P. simonii nor P. pennaeformis. Pinnules characteristic of P. vedrinei are not as lobed as those in P. buttsii and venation patterns differ drastically. Lateral veins in *P. vedrinei* arise obliquely from the midvein and dichotomize only once near their point of origin. The resultant venation is not restricted to the interior of the pinnule lobe but venation is equally spaced along the pinnule margin. The terminus of the dichotomized vein may end either within a pinnule lobe or between two pinnule lobes. In addition, the pinnules are smaller in stature and the ultimate rachis is striated.

Pecopteris intermedia is distinguished by possessing large pinnules (up to 10 mm long and 3 mm wide) that have slightly undulating margins. The smaller acroscopic pinnules are entire margined. Lateral venation arises from the slightly decurrent midvein and undergoes twice equal dichotomization. Rarely is the lateral vein fascicle unequal dichotomous. The median vein extends to a pointed apex where the ultimate lateral veins given off are undivided. Each lateral fascicle of veins is contained within a pinnule lobe. The rachises are pubescent.

Pecopteris dufayi possesses rachises which are spinose and striated, upon which are preserved elongated pinnules that are lobate or smaller contiguous pinnules with entire borders. Lobate pinnules attain a length of 15 mm and a maximum width of 3 mm. The inferior (basiscopic) pinnule base is enlarged and decurrent, and a median vein extends to near the apex of the pinnule. Although the venation pattern is diagnosed as being masked due to the pubescent character of the pinnules (Dalinval, 1960), the venation is described as being obliquely inserted and either once equal dichotomous or twice equal (?)/unequal (?) dichotomous. Rarely does a second bifurcation occur midway between the midvein and the border. Dalinval (1960) does not document whether both resultant lateral veins dichotomize or if only one vein dichotomizes. The lateral vein bundle arrives at the border and apparently is restricted to within the pinnule lobe. The specimens are fructified and are assigned to *Asterotheca*. Due to the ambiguity concerning pinnule venation pattern, *P. buttsii* is not assigned to this species.

Pecopteris lobulata was established for weakly lobate pinnuled pecopterids with quaternary rachises finely striated. The elongated pinnules, measuring 8-9 mm long and 2.5-3 mm wide, have rounded summits and are inclined upon the rachis. A strong midvein continues to the apex of the pinnule and secondary veins are obliquely inserted, dividing near the point of origin and again approximately halfway between the midvein and border. The resultant lateral venation pattern per fascicle is either unequal dichotomous or twice equal dichotomous. Each fascicle is contained within a pinnule lobe. The differences in degree of pinnule lobation, fascicle venation pattern and rachial features separates these two taxa. The same character differences allow the separation of P. buttsii from P. avoldensis. Rachises of P. avoldensis preserve striations representing 'fibers' and possess slightly lobed, obliquely inserted pinnules measuring 7-8 mm long and 2-3 mm wide. The median vein extends to a rounded to pointed apex and lateral veins divide such that the resulting bundle meets the border of the pinnule within a pinnule lobe. The lateral venation pattern is variable and can be either twice dichotomous, unequal dichotomous or complex.

Zeiller (1888) established P. simonii for lobate pinnuled forms that possess a tapered and somewhat obtusely pointed apex. The relatively large pinnules (5-10 mm long; 3-4 mm wide) are attached to a punctate third order rachis and are characterized by 5-11 lobes per pinnule side. The base of the pinnule is slightly enlarged and the decurrent midvein extends to the summit. The lateral venation arises obliquely from the midvein and divides by a dichotomy. Dalinval (1960) depicted specimens referable to P. simonii as small, entire bordered pinnules with variable lateral venation. Lateral veins can primarily be either twice equal dichotomous, unequal dichotomous or complex. The lobate pinnules differ from P. buttsii in pinnule apical shape and lateral venation pattern.

Pecopteris pennaeformis possesses lobate and entire margined pinnules. Ultimate rachises of *P. pennaeformis* possess scale/hair bases and lobed pinnules that are generally confined to the basal portion of the frond. The lobate pinnules differ from P. buttsii pinnules by being smaller, up to 6 mm long as opposed to a maximum of 18 mm, and having lateral vein bundles that can be characterized as being twice equal and unequal dichotomous. The lateral venation pattern in P. buttsii can be termed complex and there is no documentable variability in fascicle configuration within the pinnule.

Of all early Pennsylvanian (Westphalian A/B) pecopterids recognized, Pecopteris volkmannii is the only form with which P. buttsii should be synonymized. The ultimate rachises (third order) are pubescent or preserve hair/ scale bases, and pinnules of the lower region of the frond (basiscopic) are lobed. The summit of the pinnule is rounded as in P. buttsii and the pinnules are attached to the rachis by contracted acroscopic and basiscopic lobes. Both basiscopic pinnule lobes are slightly enlarged and a strong midvein extends towards the summit of the pinnule. Pinnules attain a length of 13 mm and a width of 3 mm, with a length: width ratio between 1:3 and 1:4 (Corsin, 1951). The lateral venation fascicle pattern has been depicted as unequal and complex (Zeiller, 1888; Kidston, 1924; Corsin, 1951; Dalinval, 1960), as is the configuration in P. buttsii. The pinnule morphology and accompanying venation pattern are variable with respect to the position of the specimen within the frond. P. buttsii is represented by fragments of a large frond and, therefore, cannot depict the plasticity of the complete parental organ. The pinnule and rachial morphology is homologous to those specimens figured by Zeiller (1888) and conforms to some specimens illustrated by Corsin (1951) and Dalinval (1960). In all reported collections, *Pecopteris volkmannii* is a rarely encountered form.

The synonymy of *P. buttsii* with *P. volk-mannii* would be considerably easier if *Pecopteris* was not a form genus. As this taxonomic status implies, a form genus is established to encompass any morphological configuration which possesses specific characteristics, and those species established within a form genus are variants of the generic parameters. In addition to this typological concept used for erection of new taxa, the element of time has also been considered a factor in establishing species. Although two

populations of specimens may be almost identical in morphological characters, a difference in stratigraphic position may be sufficient enough to separate the specimens as two distinct species. Due to this inherent complexity, three additional species of *Pecopteris* characteristic of Upper Middle and Upper Pennsylvanian (Westphalian D/Cantabrian/Stephanian equivalents) strata must be discussed in order to assess best the affinity of *P. buttsii*. The status of two of these species, *P. vestita* and *P. pseudovestita*, is controversial, but no attempt will be made in this present study to unravel the chaos.

Pecopteris vestita was erected by Lesquereux (1879, 1880), based upon a variety of specimens some of which possess pubescent rachises and pinnules, others which have rachises and pinnules that are smooth. In addition, the pinnule morphology is either that of elongated lobate pinnules or smaller, entire bordered pinnules, depending upon the position of the pinnule in the frond. The lateral venation pattern of a fascicle within a lobed pinnule has a variety of complex configurations. The lateral vein emerges from the midvein and divides up to 5 times on the way to the border. In effect, the venation configuration can be interpreted as a lateral vein emerging from the midvein and each time the vein dichotomizes, the newly created outside vein continues to the pinnule margin. The initial lateral vein, therefore, simulates a median vein within the pinnule lobe from which simple veins arise. Due to the multifaceted character of the specimens included within P. vestita by Lesquereux, D. White (1899) separated two distinctive species from the P. vestita complex: P. vestita and P. pseudovestita. Pecopteris vestita is restricted to those specimens which possess punctate rachises, with a sulcus on the ventral surface. upon which are borne pubescent pinnules that may be either lobate or entire margined depending upon their position in the frond. The nervation is composed of a slightly decurrent midvein, which extends to near the apex, with lateral veins in the larger pinnules dichotomizing near the base and the upper fork of the dichotomy forking again. White (1899, Pl. 26, fig. 1; Pl. 33, figs. 1–6) illustrated both the lobed pinnule and entire margined forms and two specimens appear to be morphologically similar to P. buttsii, with the exception that both specimens (USNM 5808, Pl. 26, fig. 1; USNM 5647, Pl. 33, fig. 3) possess an additional bifurcation of the interior vein within the fascicle near the border. It is difficult to discern if there is an additional forking of the lateral bundle in this position within *P. buttsii* because apices of the pinnule lobes are poorly preserved. A preliminary reexamination of White's specimens has shown that the venation pattern depicted by White (1899) is accurate and characteristic of some pinnules found upon the pinnae. A detailed study of the specimens is necessary to determine the degree of variability in this taxon.

Kidston (1924) equated all illustrations of P. vestita published by D. White (1899, Pl. 26, fig. 1, Pl. 33, figs. 1-5, cf. 6, 7) with P. *miltonii* although the type material was not examined. There appears to be some confusion on the part of Kidston (1924, p. 502) concerning the taxonomy of P. vestita because in the synonymy he questioned the affinity of White's material with that of Lesquereux's. Corsin (1951), on the other hand, separated lobate forms of P. vestita (White, 1899, Pl. 26, fig. 1 and Pl. 33, figs. 2-4) from the entire margined forms and placed them within a newly erected species, P. pilosa Corsin. Unfortunately, P. pilosa Corsin is an invalid species because Bell (1944) transferred specimens described by Dawson (1868) as Sphenopteris pilosa to Pecopteris erecting a new combination, P. pilosa (Dawson) Bell. According to the International Code of Botanical Nomenclature (Stafleu and others, 1978, Art. 55, 64 and 72) P. pilosa Corsin is a nomonym of P. pilosa (Dawson) Bell and must be rejected. This taxon will not be renamed in this present study and this problem will only be taken into consideration after a reinvestigation of the *P. vestita* complex.

Pecopteris pseudovestita was erected by White (1899), based upon those specimens described and illustrated by Lesquereux (1880, p. 252 pars, Pl. 43, figs. 5, 5a) as entire pinnuled, non-villose forms with some acroscopic lobate pinnules that are attached to a smooth rachis. In addition to considering the specimens of Lesquereux (1880), D. White (1899, Pl. 30, fig. 1; Pl. 31, fig. 2; Pl. 32, fig. 1) illustrated specimens which possess lobate pinnules with a highly variable venation pattern dependent upon the position of the pinnules within the frond. The lobed pinnules in the acroscopic portion of the pinna (Pl. 30, fig. 1a) possess lateral fascicles of veins that are of a complex pattern homologous to the lateral venation of *P. buttsii*. The number of dichotomies in the lateral fascicle increase as the pinnules are positioned in a more basiscopic portion of the pinna.

Since the specimens of P. buttsii are disarticulated, at least, tertiary pinna, they could be representative of the most acroscopic pinnae of *P*: *pseudovestita*, as illustrated by White (1899). In turn, then, the morphology of these acroscopic pinnules is equivalent to P. volkmannii. White (1899) assigned the sporangial masses of *P. pseudovestita* to *Asterotheca* and, although Corsin (1951) placed P. volkmannii in Group P. pennaeformis (Senftenbergia-type sporangia), the true fertile state of P. volkmannii is unknown (Kidston, 1924; Corsin, 1951). Therefore, it may be possible that P. buttsii, P. volkmannii and portions of P. pseudovestita may be considered homologous. Corsin (1951), though, believed that lobate forms of *P. pseudovestita* (White, 1899, Pl. 30; Pl. 31, fig. 2; Pl. 32) are homologous with P. miltonii and synonymized these specimens. The concept of P. pseudovestita, according to Corsin, therefore, is reduced to entire margined forms which were initially identified by Lesquereux (1879, 1880) as Alethopteris ambigua.

The last species which is very similar morphologically to P. buttsii is P. lamuriana. Pinnules of P. lamuriana have lobate margins, are attached by their entire base with the acroscopic border slightly contracted and the basiscopic border decurrent, and are inclined upon a rachis that is spinose. The median nerve is slightly decurrent on the rachis and extends to a rounded summit. Lateral veins arise obliquely and are disposed in bundles with one fascicle per lobe. The venation pattern of the fascicle is variable and the lateral vein may divide at least 3 times giving rise to a complex venation pattern which, in some specimens, is indistinguishable from that of P. volkmannii. Corsin (1951, p. 310) stated that P. lamuriana can be often confused with some forms of P. volkmannii. Corsin (1951) believed the difficulty in discerning these two taxa is relieved due to two parameters: abundance and stratigraphic position. Pecopteris volkmannii is restricted to Westphalian A strata and is rare, whereas *P. la-muriana* is found abundantly in Westphalian D and younger strata (Corsin, 1951).

Taxonomic considerations. - If some forms of *P. lamuriana* are indistinguishable from P. volkmannii (Corsin, 1951), and the acroscopic position of some pinnae of P. pseudovestita are homologous with P. volkmannii, then specimens of P. buttsii are indistinguishable from some forms of all the aforementioned species. To which taxon should these specimens be assigned? The reported fertile material of these taxa does not help in delimiting species because P. buttsii and P. volkmannii are only known from sterile material, whereas P. pseudovestita and P. lamuriana possess Asterotheca. The question is, then, whether seemingly identical fragmentary forms should remain as separate taxa based upon their frequency of occurrence and stratigraphic position.

The frequency of occurrence of a particular form should not be a parameter used to determine taxonomic affinity. It has been demonstrated (Phillips and others, 1974; Di-Michele and Phillips, 1981) that during the Westphalian the climate generally became drier. The development of extensive peataccumulating swamps decreased, with a documented shift in coal swamp vegetation from hydrophytic lycopods to a more mesophytic pteridophyte dominated forest. If the lower Westphalian was indeed wetter, fewer mesophytic forms would have existed close to the depositional environments. In fact, if the extensive lowland system was primarily marsh conditions, the frequency of extrabasinal forms, those adapted to a drier habitat, would be expected to be low. In addition, if coalified compression taphocenoses are generated by storm activity (Scheihing, 1980), those arborescent forms not abundantly represented in the immediate erosional environment should not be abundantly represented in the depositional environment. If the forms were not arborescent, the probability of their preservation would be further reduced. Therefore, one would expect to find few representatives of those plants considered to be adapted to a much drier habitat. Of course it must be assumed that the physiological conditions for growth of these pteridophytes had not changed during the Westphalian.

Should the stratigraphic position of a par-

ticular homologue be the criterion for taxonomic separation? This is a difficult question to answer and the answer is based upon individual philosophy. Since Pecopteris is a form genus created for convenience, an artificial taxon based upon specific morphological criteria, two philosophies may be valid. When a particular morphology is documentable, that is, if it occurs throughout a particular stratigraphic interval, then all specimens conforming to the specific diagnosis should be assigned to that taxon. Fragments of disarticulated plants found within the stratigraphic interval that demonstrate those characters used to delimit that taxon should be assigned to the established form.

New taxa should not be created when the delimiting parameter may have been a function of available nutrients (i.e., size), nor should new taxa be created to accommodate slight variance in some of the defining characters. For example, if one pinnule of a pinnae does not conform to a specific diagnosis, but all other preserved pinnules can be accommodated, this factor alone is not worthy of consideration as a delimiting feature of a new species. Morphological variability within portions of pecopterid fronds is extensive and can be drastic within a short distance (Gastaldo, in press). In addition, population variability is probably as extensive as individual variability, if not more so. Rather than pigeon-holing discrete isolated variants, attempts at discerning population variations are needed to determine a more realistic diversity factor. All available data should be assessed and utilized in the assignment of a specimen to a form genus or species.

On the other hand, when discrete populations of homologous morphological entities exist in different intervals of time without a documented bridge between these intervals, it may be convenient to retain these two entities as discrete taxa. The occurrence of particular morphological forms in association with other taxa may be useful in biostratigraphy. A form taxon represents a particular association of characters that are genetically controlled. In the case of *Pecopteris*, the most dependable character has been deemed the venation pattern (Darrah, 1969), but venation pattern must be related to a number of other factors including laminar dimensions and physiology. It is, therefore, possible to

have portions of plants which appear the same, particularly those pecopterid pinnules and pinnae in the most acroscopic portions of the frond, that may not be related biological forms. And if these forms occur discretely in time, then the disjunction in time may be a valid criterion for separation. Because this particular form may exist in the time between the documentable populations, stratigraphic evidence is needed to support the synonymy of populations in order to combine the forms into a single taxon. Until specimens are discovered which allow the synonymy of stratigraphically discrete forms, the negative evidence may be utilized.

Based upon the morphological suite of characters available for study, Pecopteris buttsii is considered conspecific with the concept of P. volkmannii as defined, discussed and partially illustrated by Corsin (1951). As previously documented, P. volkmannii is stratigraphically restricted to the Westphalian A (Corsin, 1951), although Kidston (1924) recorded this species from higher strata. Corsin (1951) utilized Kidston's (1924) synonymy as a basis for the species concept. Therefore, if P. volkmannii is reported from throughout the Westphalian and it is indistinguishable from P. lamuriana (Corsin, 1951), then these taxa should also be synonymized and the reported variability be considered a feature of a population of specimens. In both taxa the rachises possess either small hairs or spines (or remnant bases) upon which are borne lobate pinnules in some portion of the frond. These pinnules are characterized by a well marked medial vein that is slightly decurrent upon the rachis and that extends to near the pinnule apex. Lateral veins arise obliquely and divide into a fascicle which meets the border at a variable angle (oblique to almost perpendicular) and is contained within a pinnule lobe. The fascicle is composed of the lateral vein, which initially divides near the point of origin with the lowermost vein normally continuing to the margin. The uppermost fork divides at approximately one-fourth of the distance to the margin and the basalmost vein of this dichotomy forks again at approximately onehalf of the distance to the margin. The uppermost vein may either remain simple (as in P. lamuriana, Corsin, 1951; Kidston, 1924; and P. volkmannii, Zeiller, 1888; Jongmans

and Gothan, 1915) or may dichotomize once approximately one-third to one-half the distance to the margin (as in P. volkmannii, Corsin, 1951). The acroscopicmost lateral veins within the pinnules are not as dichotomized as those basiscopic veins. The only apparent morphological difference used by biostratigraphers is the size difference in pinnae of ultimate order, but most often the pinnae of P. lamuriana are figured as fragmentary extreme acroscopic portions of fronds. This may account for the difference in size that has been traditionally used for separation. Pecopteris volkmannii Sauveur (1848) has priority over *P. lamuriana* Heer (1872) and, therefore, *P.* lamuriana is herein synonymized with P. volkmannii. The reported and illustrated specimens of P. volkmannii (Zeiller, 1888; Gothan, 1913; Jongmans and Gothan, 1915; Kidston, 1924; Corsin, 1951) conform (in part) to the concept proposed by Sauveur (1848).

Tennessee specimens.-Specimens from shales associated with the High coal, lower Rock Spring coal, Pee Wee and Split coals are considered not to be homologous with P. buttsii (= P. volkmannii). Although the pinnules are lobate and possess lateral venation of a complex character within each lobe, the absence of a pubescent rachis, the more squat character of the pinnule and the venation diversity does not allow their synonymy. Some small fragments may appear similar to P. buttsii (BPB 77, 103; Figures 2C, E) but there are notable differences. Those portions which appear nearly identical are incomplete pinnules, which do not preserve the entire acroscopic part of the pinnule. This may give the impression that the pinnules are longer than in actuality, but comparison with complete pinnules preserved upon the same rock and other specimens in the collection allow the separation. The lateral venation that originates from the midvein in these specimens arises at a more acute angle and dichotomization results in a pattern reminiscent of P. pseudovestita and P. vestita, and some forms are probably acroscopic pinnules of *P. unita*. At the present, the suite of specimens curated at the University of Tennessee, Knoxville, and examined in this study is considered not to be *P. buttsii*, but rather taxa including *P*. unita (BPB 103 pars) and the P. miltonii complex (BPB 77, 102, 103 pars, 50; BHA 49,

71, 72; BRS 132). Recollection of the localities and the acquisition of larger fragments, though, are needed to confirm these taxonomic assignments.

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REFERENCES

- ADAMS, G. I., C. BUTTS, L. W. STEPHENSON and C. W. COOKE. 1926. Geology of Alabama. Alabama Geological Survey Special Report 14: 208–230.
- ARTIS, E. T. 1838. Antediluvian Phytology. London, 24 p.
- BARLOW, J. A. 1969. Stratigraphy and paleontology of the youngest Pennsylvanian strata in the Caryville, Tennessee, area. Unpubl. Ph.D. dissert., University of Tennessee, Knoxville, 393 p.
- BELL, W. A. 1944. Carboniferous rocks and fossil floras of northern Nova Scotia. Geological Survey of Canada Memoir 238:1–276.
- BOUREAU, D. and J. DOUBINGER. 1975. Traité de Paléobotanique. IV(2):1–178, Paris.
- CORSIN, P. 1951. Flore fossile bassin houiller de la Sarre et de la Lorraine. Fasc. 4e. Pécoptéridees. Études des Gites Mineraux de la France, p. 177–370.
- DARRAH, W. C. 1969. A critical review of the Upper Pennsylvanian floras of eastern United States with notes on the Mazon Creek Flora of Illinois. Privately published, Gettysburg, Pa., 220 p.
- DALINVAL, A. 1960. Contribution a l'étude des Pécoptéridées. I. Flore Fossile, 3 Fasc. Les *Pecopteris* du bassin houiller du Nord de la France. Études Geologie pour l'atlas de Souterraine Geologique Serice des H.B.N.P.C. Lille, 222 p.

- Dawson, J. W. 1868. Acadian Geology, 2nd ed., London, 694 + 102 p.
- DIMICHELE, W. A. and T. L. PHILLIPS. 1981. Stratigraphic-geographic patterns of change in Pennsylvanian coal-swamp vegetation. Botanical Society of America Miscellaneous Series Publication 160:44.
- GASTALDO, R. A. In press. Studies on North American pecopterids. II. Morphological plasticity in a heteromorphic organ from the Middle Pennsylvanian of southern Illinois. 9th International Congress Carboniferous Stratigraphy and Geology, Compte Rendu.
- GASTALDO, R. A. and L. C. MATTEN. 1978. Studies on North American pecopterids. I. *Pecopteris vera* n. sp. from the Middle Pennsylvanian of southern Illinois. Palaeontographica Abteilung B, 165:43–52.
- GILLESPIE, W. H. and H. W. PFEFFERKORN. 1979.
 Distribution of commonly occurring plant megafossils in the proposed Pennsylvanian System stratotype, p. 87–96. *In*, K. J. Englund, H. H. Arndt and T. W. Henry (eds.), Proposed Pennsylvanian stratotype Virginia and West Virginia. American Geological Institute Selected Guidebook Series No. 1.
- GOTHAN, W. 1913. Die oberschlesische Steinkohlenflora. Königlich Preussischen Geologische Landesanstalt, p. 278.
- HEER, O. 1872. Monde Primitif de la Suisse, p. 182.
- JONGMANS, W. J. and W. GOTHAN. 1915. Paläobotanisch-Stratigraphische studien im Niederlandischen Carbon nebst vergleichen mit umliegended Gebielen. Herausgegeben von der Königlich Preussischen Geologische Landesanstalt. 18:186.
- KIDSTON, R. 1923–1925. Fossil plants of the Carboniferous rocks of Great Britain. Geological Survey Great Britain Memoir Paleontology 2, Parts 1–6:522.
- LESQUEREUX, L. 1876. Partial list of coal plants from the Alabama fields and discussion of the geological position of several coal seams. Geological Survey of Alabama, Report of Progress, 1875:75-82.
- —. 1879–1884. Description of the coal flora of the Carboniferous formation in Pennsylvania and throughout the United States. Second Pennsylvania Geological Survey P, 3 vols. (1879, Atlas; 1880, Vol. 1–2; 1884, Vol. 3), p. 977.
- —. 1888. List of fossil plants collected by Mr. I. C. Russell, at Black Creek, near Gadsden, Alabama, with descriptions of several new species. Proceedings United States National Museum, 11:83–87.
- LYELL, C. 1846. Observations on the fossil plants of the coal field of Tuscaloosa, Alabama with a description of some species by C. J. F. Bunbury. American Journal of Science, 2nd series, 2:228– 233.
- LYONS, P. C. and C. R. MEISSNER. 1982. Age of

the Black Creek and Jefferson coal beds, Warrior coal field, Alabama. Geological Society of America Abstracts with Programs, 14:36.

- MAMAY, S. H. 1955. *Acrangiophyllum*, a new genus of Pennsylvanian pteropsida based on fertile foliage. American Journal of Botany, 42: 177–183.
- MCCALLEY, H. 1896. Report on the Valley regions of Alabama (Paleozoic strata) Pt. 2. Alabama Geological Survey Special Report 8:1–436.
- —. 1900. Report on the Warrior coal basin. Geological Survey of Alabama Special Report 10, 327 p.
- METZGAR, W. J. 1965. Pennsylvanian stratigraphy of the Warrior Basin, Alabama. Alabama Geological Survey Circular 30:1–80.
- PHILLIPS, T. L., R. A. PEPPERS, M. J. AVCIN and P. F. LAUGHNAN. 1974. Fossil plants and coal: Patterns of change in Pennsylvanian coal swamps of the Illinois basin. Science, 184(4144):1367– 1369.
- PROUTY, W. E. 1922. Age of Talladega slates of Alabama. Pan American Geologist, 37:363–366.
- — 1923. Geology and mineral resources of Clay County. Alabama Geological Survey County Report 1:1–190.
- ROTHROCK, H. E. 1949. Geology and coal resources of the northeastern part of the Coosa coalfield, St. Clair County, Alabama. Alabama Geological Survey Bulletin 61(1,2):1–163.
- SAUVEUR, M. 1848. Végetaux fossiles des terraine houillers de la Belgique. Academie Royal des Sciences, des lettres et des Béaux Arts de Belgique, 69 p.
- SCHEIHING, M. H. 1980. Reduction of wind velocity by the forest canopy and the rarity of nonarborescent plants in the Upper Carboniferous fossil record. Argumenta Palaeobotanica, 6:133– 138.
- SMITH, E. A. 1903. Carboniferous fossils in Ocoee slates in Alabama. Science, 18:244–246.

- STAFLEU, F. A., V. DEMOULIN, W. GREUTER, D. HEIPKO, I. A. LINCZEVSKI, R. MCVAUGH, R. D. MEIKLE, R. C. ROLLINS, R. ROSS and J. M. SCHOPF. 1978. International code of Botanical Nomenclature. Bohn, Scheltema and Holkema, Utrecht, 457 p.
- WAGNER, R. H. 1959. Flora fossil y estratigrafia del Carbonifero de Espana NW. y Portugal N. Estudios Geologicos, 15:393-420.
- —. 1960. Middle Westphalian floras from northern Palencia (Spain) in relation with the Curvacas phase of folding. Estudios Geologicos, 16:55–92.
- ----. 1962. A brief review of the stratigraphy and floral succession of the Carboniferous of NW Spain. 4th Congres pour l'avancement des Études de Stratigraphique et de Géologie du Carbonifére. III:753-762.
- 1971. The Westphalian D floras of the Olloniego and Esperanza formations in the central Asturian coal field. Trabajos de Geologia, 4:641– 505.
- WHITE, D. 1899. Fossil flora of the lower coal measures of Missouri. United States Geological Survey Monograph 37, 307 p.
- —. 1943. Lower Pennsylvanian species of *Mariopteris, Eremopteris, Diplothmena* and *Aneimites* from the Appalachian Region. United States Geological Survey Professional Paper 197-C:85-103.
- ZEILLER, R. 1888. Flore fossil bassin houillere de Valenciennes. Études Gîtes Mineraux France, Paris, 731 p.

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