Geological Society of America
Special Paper 399
2006

A Late Mississippian back-barrier marsh ecosystem in the Black Warrior and Appalachian Basins

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ABSTRACT

An outcrop of the Mississippian Hartselle Sandstone in north-central Alabama preserves in situ, erect cormose lycopsids, assigned to *Hartsellea dowensis* gen. and sp. nov., in association with a low diversity bivalve assemblage dominated by *Edmondia*. The isoetalean lycopsids are rooted in a silty claystone in which the bivalve assemblage occurs, representing the transition from tidal flat and tidal channel regime into a poorly developed inceptisol. Two paleosols are preserved in the sequence and each is overlain by a fine-grained quartz arenite, responsible for casting aerial stems and cormose bases of the entombed plants. The massive quartz arenites are in sharp contact with interpreted O-horizons of the paleosol, and the lower sandstone displays a lobate geometry. The plant assemblages are interpreted as back-barrier marshes, the first unequivocal marshlands in the stratigraphic record, preserved by overwash processes associated with intense storm surges in a Transgressive Systems Tract. A sample suite curated in the National Museum of Natural History, collected by David White at the turn of the last century in the Greenbrier Limestone of West Virginia, preserves rooting structures, leaves and sporophylls, and sporangia and megaspores of *H. downensis* in a mixed carbonate mud (micrite). The presence of isoetalean lycopsids in both siliciclastic and carbonate peritidal environments within nearshore shelf settings of the Early Carboniferous indicates that adaptation to periodic brackish water, if not tolerance to infrequent fully marine-water inundation during storm surges, had evolved in these marsh plants by the late Paleozoic.

Keywords: Hartselle Sandstone, lycopsid, paleobotany, paleoecology, Alabama.

INTRODUCTION

Marshes are a type of wetland frequently or continuously inundated with water wherein emergent nonwoody plants are adapted to saturated soils generally of an immature nature. There are several different classification schemes for marshlands (Gore, 1983; Keddy, 2000), although a broad dichotomy can be made into non-tidal (freshwater or brackish) or tidally influenced (freshwater, brackish, or fully marine) settings. In coastal environments, the main criterion that separates a marshland from a tidal flat is

Gastaldo, R.A., Gibson, M.A., and Blanton-Hooks, A., 2006, A Late Mississippian back-barrier marsh ecosystem in the Black Warrior and Appalachian Basins, *in* Greb, S.F., and DiMichele, W.A., Wetlands through time: Geological Society of America Special Paper 399, p. 139–154, doi: 10.1130/2006.2399(07). For permission to copy, contact editing@geosociety.org.

the presence of rooted herbaceous plants. Presently, such marshes are restricted primarily to temperate zones because woody mangrove taxa predominate in frost-free latitudes. This probably was not the case prior to the evolution of woody higher plants, with marshes dominating the latitudinal spectrum once plants colonized peritidal environments. Although inference has been made that marshlands are a common component of transitional coastal environments since the evolution of higher plants (e.g., Bateman et al., 1998; Retallack, 1992, 2000; Strother, 2000), few substantive geologic, paleontologic, or taphonomic data exist to support this claim (see Allen and Gastaldo, this volume).

There may be several reasons to account for an absence of autochthonous marsh assemblages in the stratigraphic record. Marshes are restricted geographically along a narrow band of land fringing coastal zones. Sediment accretion in these areas results in better-drained soils and ecosystem replacement by other communities; marsh-to-swamp transitions may be the result of less than a 30 cm change in elevation in modern coastal regimes (Gastaldo et al., 1987). Following sediment compaction, this transition may be recorded in only a few centimeters of stratigraphic section. Sediment accretion is most common in prograding (offlap) sequences that build out onto the shelf, with the last formed marsh at the distal reaches of the wedge. Hence, unless sufficient accommodation during progradation is generated quickly to allow for catastrophic burial (Gastaldo et al., 2004), it is unlikely that recognizable marshlands can be preserved along the way. Coastal-zone transgression (onlap) often results in erosion of coastal plain deposits as the coastline is moved inland by sea-level rise (ravinement; e.g., Liu and Gastaldo, 1992). During ravinement, marsh deposits are reworked and removed from the sediment record. Therefore, it is unusual to encounter equivocal marshes and even rarer to find unequivocal examples of this wetland in the stratigraphic record.

The upper Mississippian (Chesterian [Hombergian]) Hartselle Sandstone crops out in a NW-SE trend along the western margin of the Cumberland Plateau from the Kentucky/Tennessee border south to northeast Alabama, with isolated exposures along the flanks of the Birmingham anticlinorium (Thomas, 1972; Stapor and Cleaves, 1992). It conformably overlies the Pride Mountain Formation, interpreted as part of a lowstand wedge, and represents mainly beach (Stapor et al., 1992), offshore barrier bar and sand-rich shelf deposits (Thomas and Mack, 1982), and tidal facies of an onlap sequence (Stapor and Cleaves, 1992). A small outcrop of the Hartselle Sandstone in Jefferson County, Alabama, exposes in situ erect and rooted cormose lycopsids in an inceptisol that also preserves a macroinvertebrate assemblage indicative of tidal estuarine conditions. A coeval plant assemblage, collected in the early part of the twentieth century by David White in the calcareous Greenbrier Formation, West Virginia, has been identified in the collections of the National Museum of Natural History (USNM), providing for insight into the range of depositional settings for this Late Mississippian plant. Hence, this report provides the first unequivocal evidence for in situ marshlands in the Paleozoic.

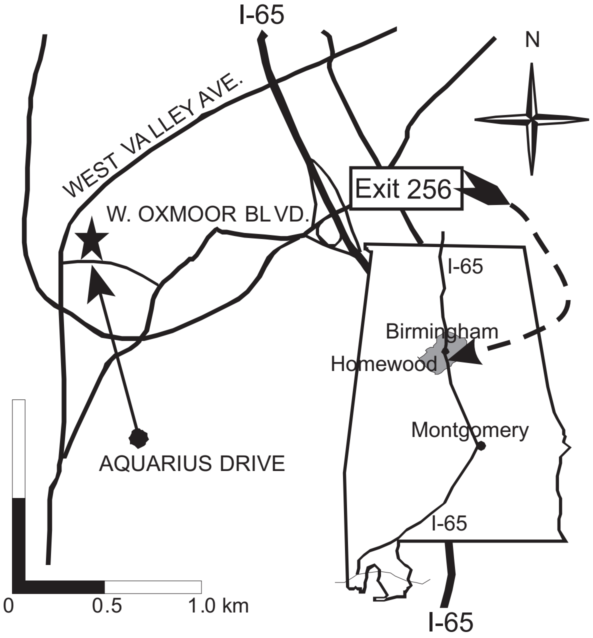

Figure 1. Locality of Hartselle Sandstone outcrop in Homewood, Walker County, Alabama (shaded county within insert map). The collection site is behind a commercial building on Aquarius Drive (NW ¼, NE ¼, Sec. 22, T16S, R3W, Birmingham South 7.5′ Quadrangle, Jefferson County).

STUDY SITE

Collections were made in Homewood, Alabama (NW ¼, NE ¼, Sec. 22, T16S, R3W, Birmingham South 7.5′ Quadrangle, Jefferson County [GPS]), approximately three miles west of I-65 (Homewood-Oxmoor Road exit) behind an industrial building on Aquarius Drive (Fig. 1). Obscured by a stand of pine trees and underbrush, the section crops out in an arcuate trend with a total vertical thickness of 3.5 m. The section consists of two sequences, each beginning with a basal silty claystone overlain by a quartz arenite assignable to the Hartselle Sandstone (Thomas, 1972; Rindsberg, 1994; Fig. 2); a basal quartz arenite underlies the outcrop, which strikes N55E and dips 12° to the southeast.

The silty claystones are massive and primarily white (10 YR 8/1) with pale red (10R 6/3) and reddish-yellow (7.5YR 7/8) mottling. Mineralogically, the claystone consists of quartz, muscovite, and illite; plant fossils are preserved in both intervals. The basal silty claystone also preserves an erect assemblage, with vertically oriented sandstone casts of cormose bases within the claystone and aerial axes extending more than 35 cm into the lowermost arenite (Figs. 2B, 3). A low-diversity macroinvertebrate assemblage is preserved within the basal rooting interval and a lenticular accumulation lateral to the plant assemblage, as well as the claystone that overlies the lowermost arenite. This upper claystone also preserves a concentrated plant-fossil assemblage consisting of the same systematic diversity found in the lower bed.

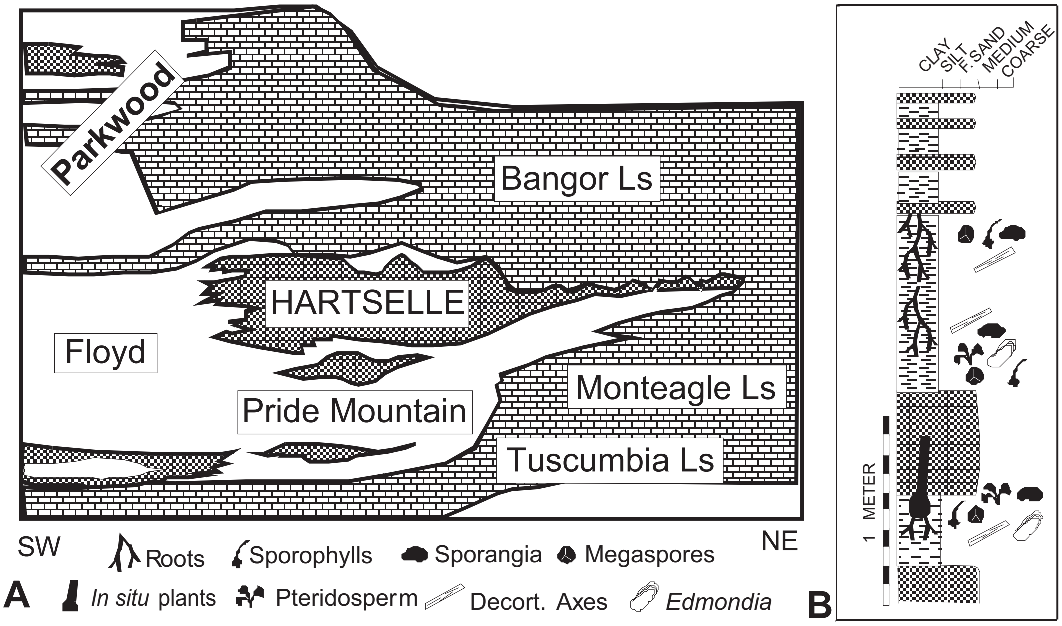

Figure 2. Stratigraphic context of the Hartselle Sandstone and the outcrop from which the present assemblage is described. (A) Southwest-northeast transect of the Mississippian stratigraphy in the Black Warrior Basin showing the intercalated position of the Hartselle Sandstone between the Pride Mountain Formation (lowstand wedge of Stapor and Cleaves, 1992) and Bangor Limestone (highstand deposits) (after Thomas, 1972). The Hartselle is interpreted as offshore beach and barrier deposits in a transgressive systems tract (Stapor and Cleaves, 1992). (B) Stratigraphic column of the Homewood outcrop of the Hartselle Sandstone indicating the position of erect *Hartsellea*, litter horizons of two inceptisols, and macroinvertebrate assemblages. Scale = 1 m.

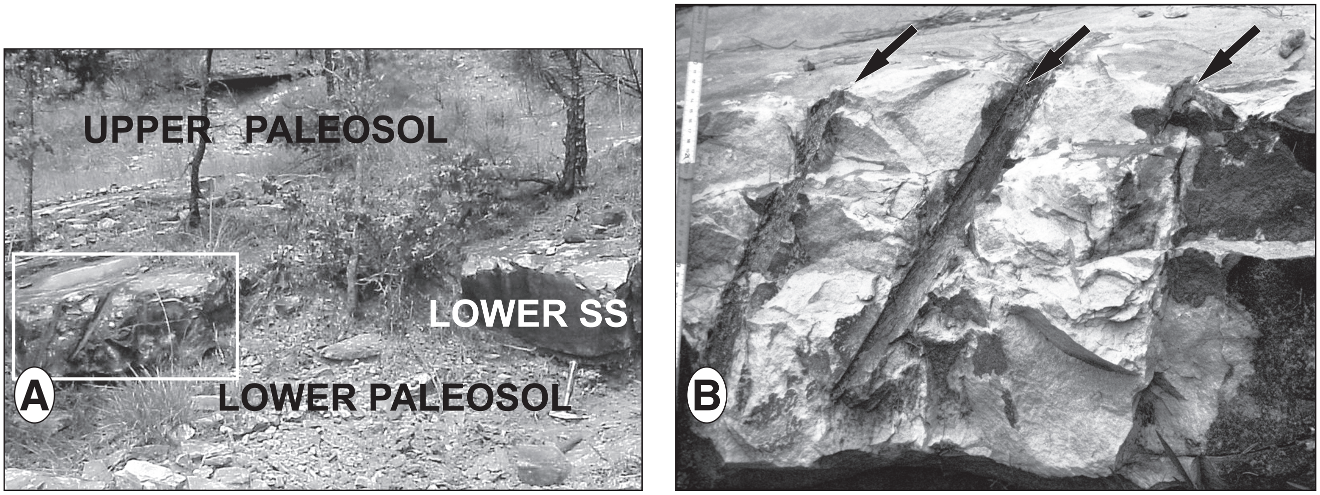

Figure 3. Outcrop photographs of the Homewood locality. (A) The lower paleosol lies above a massive quartz arenite of undetermined thickness, which, in turn, is in sharp contact with the lower sandstone unit in which erect *Hartsellea* are preserved (lower left in box). The lower sandstone is overlain by another interval of rooted silty claystone (inceptisol), which is overlain by thinner beds of resistant quartz arenite (upper center). (B) Enlargement of lower quartz arenite (box in A) in which three erect *Hartsellea* stems were preserved (arrows), indicating the density of the marsh vegetation. Specimens were removed prior to the photograph, with molds of specimens remaining.

Each claystone is overlain by a well-sorted, very fine to fine-grained ($\bar{x} = 3\phi$), white (Gley 1 N8) to light-gray (Gley 1 N7), moderately well sorted quartz arenite. The arenites are massive and in sharp contact with the underlying claystone; tool and sole marks are common at the bed contact. The basalmost arenite is exposed in three dimensions along the outcrop by the weathering and erosion of the overlying silty claystone. That exposure displays a massive sandstone that has a lobate surficial geometry consisting of two lobes, each of which is ~5 m across and a few dm in height. Mineralogically, the arenite consists of monocrystalline, non-undulatory quartz, with minor components including chert, lithics (sedimentary and metamorphic), and mica.

METHODS

Casts of cormose bases were evaluated to identify sites of root initiation, which were mapped to document the range of first-order root diameters and to detect rhizotaxy. Features along aerial stems were analyzed using acetate overlays to determine phyllotaxy. Estimates for growth height were made using the allometric equations of Niklas (1994) based on the six longest stems. Changes in stem diameter were recorded as a function of distance from the stem base. For each specimen, the distances from the stem base were regressed against the stem diameters to determine the allometry of stem taper. Stem diameters taken from levels 5, 10, and 15 cm above each stem base were $\log_{10}$-transformed and inserted into both the "nonwoody and woody" and "nonwoody" species equations (Niklas, 1992) to determine estimated plant height. The choice to use both algorithms was based on previously reported observations by Pigg (1992), Pigg and Rothwell (1983a), and Rothwell and Erwin (1985) on the internal anatomy of isoetalean lycopsids.

Adpressions and casts of aerial axes, subterranean axes, and megaspores were studied using scanning electron microscopy (SEM) in addition to standard microscopic techniques. SEM resulted in characterization of megaspores and cellular details of roots, but no cellular or stomatal patterns of leaves or sporophylls were preserved. Megaspore measurements were made along the polar and equatorial axes using a digital micrometer to acquire length and width data. Two 5–10 g samples from each silty claystone interval preserving megaspores were macerated to isolate mega- and/or microspores. Preparation techniques followed the standard palynological practices as described by Traverse (1988).

Invertebrate-bearing horizons were mined when encountered during section measuring, rather than in a systematic stratigraphic interval, primarily due to the low numbers of preserved specimens in localized occurrences and their poor preservational state. Friable claystone blocks were broken in the field to expose invertebrates, and additional blocks were returned to the laboratory to systematically split under more controlled conditions. The two quartz arenite beds also were examined for the presence of trace fossils.

TAPHONOMY

Plant Macrofossils

Sandstone- (Fig. 4A–C) and mudstone-cast (Fig. 4D) bulbous plant bases are preserved in the assemblage. Radiating bifurcate rooting structures are found originating from these bases in addition to adpression bifurcating rooting structures in the lower silty claystone. These bifurcate roots occur horizontally and at angles up to 40° penetrating the claystone, with several nodes traceable throughout the fine-grained matrix up to 0.5 m depth (i.e., upper claystone paleosol). Roots are more densely concentrated in the uppermost 15 cm and, although no root sheaths have been recovered because of degradation associated with groundwater leaching, cellular epidermal patterns are preserved. Other rooting structures also occur in the matrix as adpressions, along with aerial plant parts of the herbaceous lycopsids and pteridosperms. Aerial plant parts are a heteromeric assemblage and show no signs of sorting, with parts ranging from centimeter-diameter axes and entire leaves to millimeter-sized megaspores with exine ornamentation. All plant parts are concentrated within the uppermost 20 cm of the bed, with a thin condensed, poorly preserved assemblage directly at the contact with each overlying sandstone. Sporophylls and ?leaves are found typically in isolated zones within 15 cm of the top of the bed, whereas sporangia and megaspores occur throughout the bed.

Erect plants are found originating from within the basal claystone and extend upward into the overlying arenite (Fig. 3). These plants are cast by the same lithology that buried them, but they display no primary structures that can be discerned on the exterior of the sandstone fill. Cast specimens may be oriented either vertically (80°–90°) or in a semi-prostrate position. Aerial axes preserve leaf traces in a helical pattern or as longitudinal striae when axes are decorticated. Often the stele can be observed erect and offset within the cast, and neither leaves nor sporophylls are preserved attached to these stems. Although subterranean corms closely resemble their original shape, aerial axes are elliptical in cross section and somewhat compressed vertically due to compaction and dewatering of the entombing sandstone. Hence, both assemblages at this locality represent autochthonous communities buried in situ by an event that emplaced the overlying, lobate, thick quartz arenite. Hence, the claystone interval in which plant parts are concentrated in the uppermost part of the section is interpreted as an original O-horizon.

Macroinvertebrates

Extensive groundwater leaching has resulted in a poorly preserved macrofauna. Nearly all calcitic shell material is dissolved completely, but some vestiges of highly degraded shell appear to adhere to a few specimens. The invertebrates consists almost entirely of internal, external, and composite claystone molds of bivalve molluscs, with a single partial external mold of a gastropod spire. Compaction has distorted some specimens, producing

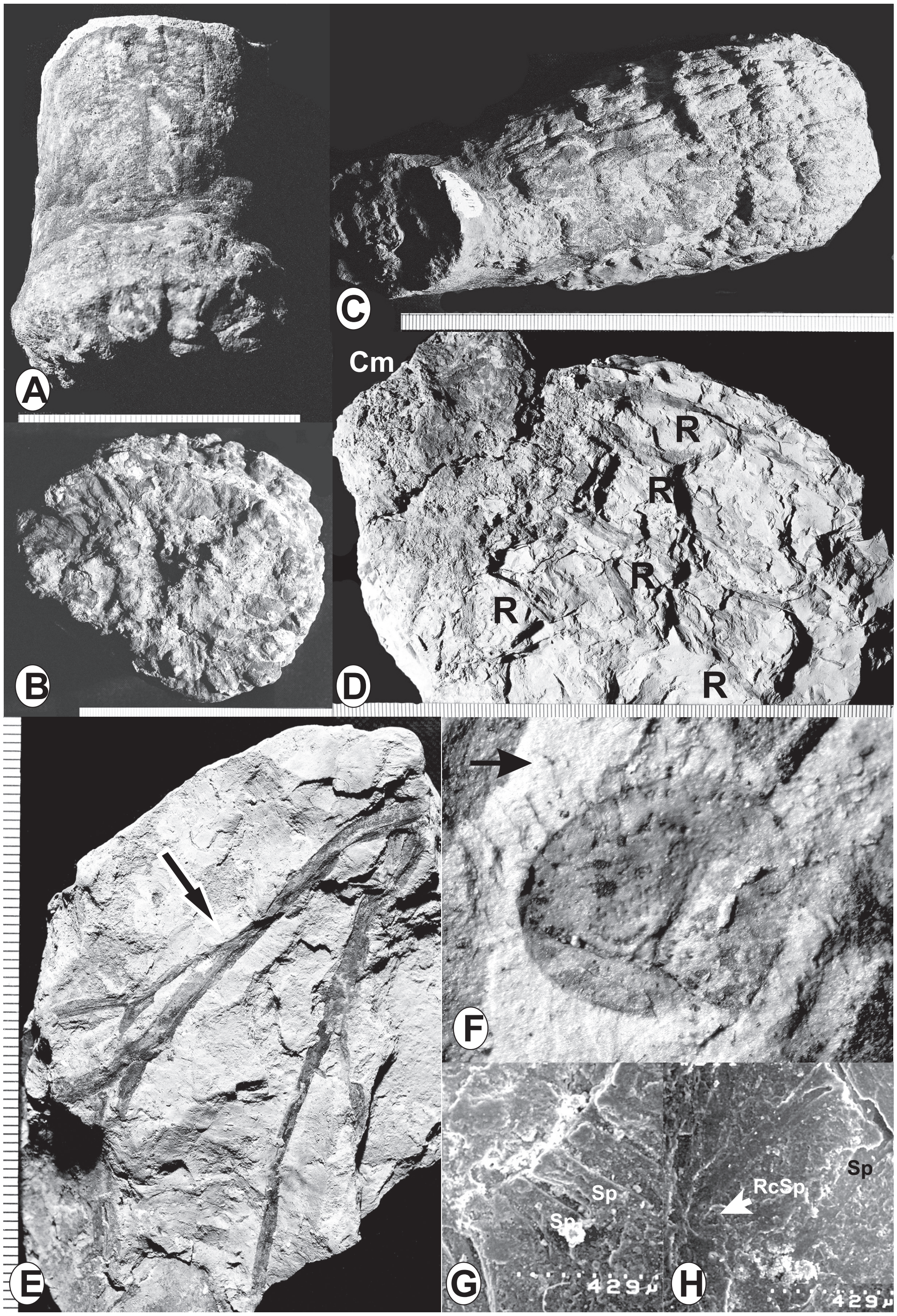

Figure 4. Corms of *Hartsellea dowensis* sp. nov. Scales in A–E in mm. (A) Sandstone-cast basal corm and lower stem transitional area showing the absence of leaf traces. Root bases occur as rounded projections from the bottom of the cast. USNM 527757. (B) Bottom view of specimen shown in A showing root initiation points and central furrow. (C) Top view of a cormose base that was dislodged from vertical during the life of the plant and continued to grow in a subhorizontal orientation. Sandstone-cast roots can be seen to envelope the corm, and the erect stem is shown in cross section at the lower left. Viewed from the side, this specimen is golf-club shaped. USNM 527759. (D) Bottom view of a claystone-cast corm (Cm; upper left) from which bifurcate roots (R) emerge and permeate the inceptisol. USNM 527760. (E) Adpression specimen showing three consecutive bifurcations of the root system. USNM 527761. Arrow points to bifurcation of root. (F) Stereomicrograph of isolated, dispersed megaspore with distorted trilete mark and punctae on the proximal side, as well as radiating apicular and bifurcate (at arrow) spines. USNM 527762. (G) SEM micrograph of proximal megaspore surface showing punctae (Pt) and radiating spines (Sp) along the spore margin. Scale = 429 µm. (H) SEM micrograph showing apicular to retuse (RcSp) nature of megaspore spines (Sp) depending upon the degree of matrix cover. Scale = 429 µm.

undulating surfaces on the shell molds, whereas concentric surface ornamentation generally is preserved, if only slightly distorted. Compaction also has produced composite shells in which impressions of bent and folded sporophyll/leaves of *Hartsellea* are impressed into the mold. These sometimes resemble horizontal sinuous shell borings but are distinguished easily by tracing the lamina off of the shell into the adjacent claystone matrix (Fig. 5D). Rooting structures also are found to cross cut the invertebrate-rich horizons, and are in association with disarticulated valves. The highly degraded state of the shells hinders taxonomic identification beyond the level of genus. External ornamentation, where preserved, is usually restricted to small areas and not the entire specimen (Fig. 5C). In spite of the difficulty of species-level identification, the shell outlines and orientations are

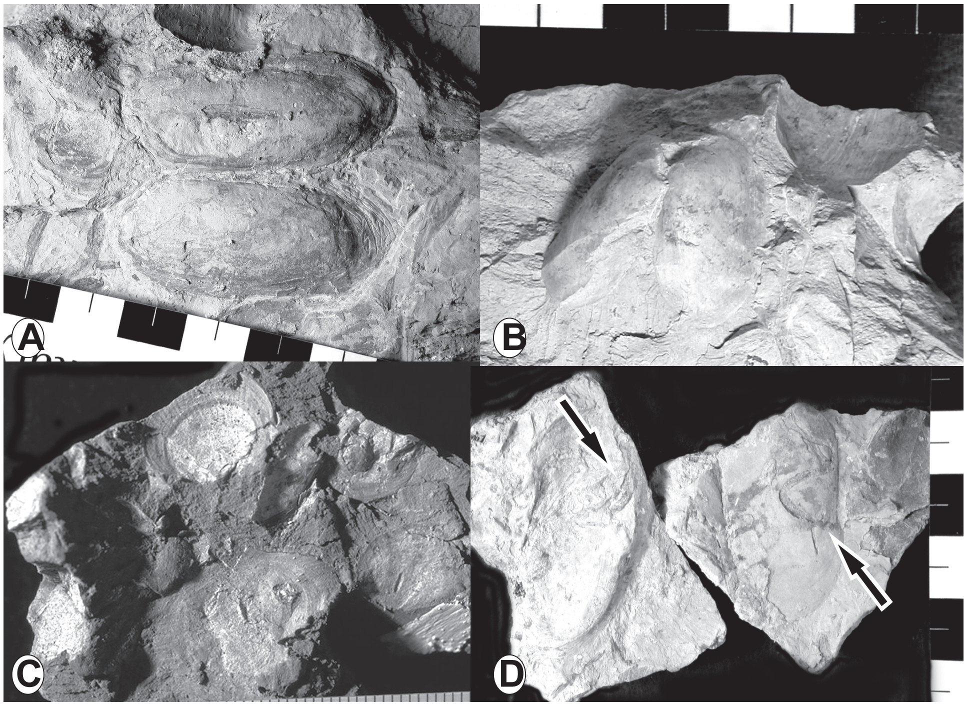

Figure 5. Macroinvertebrates collected from the lower inceptisol and a lenticular assemblage laterally adjacent to the inceptisol. (A) Butterflied *Edmondia*? with portions of other *Edmondia* shells. Note lack of abrasion, breakage, or shell material. Scale in cm. USNM 527753. (B) Butterflied *Edmondia* cutting across claystone laminae. Scale in mm. USNM 527754. (C) Claystone block with several partial *Streblochondria* clustered together. Scale in mm. USNM 527755. (D) Two claystone blocks showing *Hartsellea* gen. nov. roots (arrows) adpressed onto *Edmondia* shells, resembling burrowing structures. Scale in cm. USNM 527756.

preserved sufficiently well to allow for taphonomic observations concerning the assemblage.

Bivalve shells consist of disarticulated or butterflied valves oriented horizontal to bedding (Fig. 5A, 5B). Occasionally valves are found inclined across claystone laminae (Fig. 5B); however, these appear to be slightly agape, butterflied, or isolated valves indicating that specimens are not in life position. There is no difference between the claystone infilling the concave surfaces and that of the exterior convex interior surfaces of the valves. The bivalve shells are not broken, nor do they show obvious signs of abrasion, although the latter would be difficult to demonstrate conclusively considering the lack of preserved shell material. Size range of the bivalves, as measured by variation in maximum length within taxa, indicates some degree of probable sorting; no very small or juvenile shells were encountered. But, there is no evidence for size sorting or preferred orientation of valves on bedding surfaces. Taken together, these characteristics suggest that the invertebrates represent localized sparse shell accumulations preserved within their habitat rather than in situ assemblages.

HARTSELLE SANDSTONE ASSEMBLAGE

Cormose Lycopsid Base

The vertically oriented bases (rhizomorphs) are roughly club-shaped with an upright, unbranched, cylindrical aerial stem

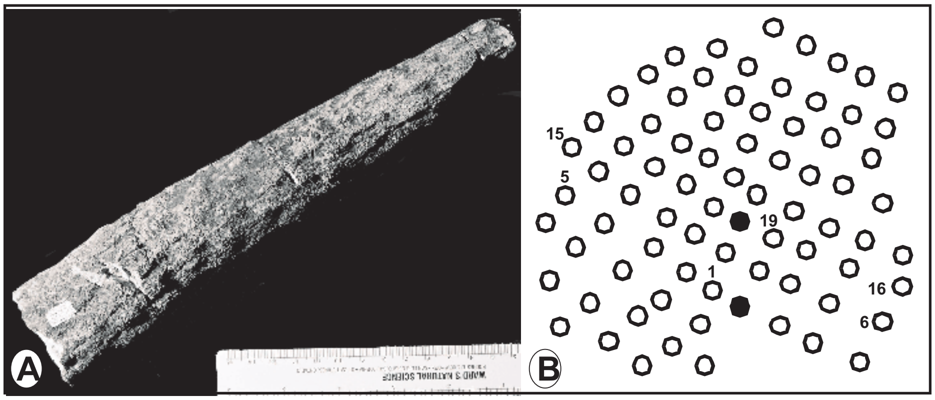

Figure 6. *Hartsellea* stem characters. (A) Erect, sandstone-cast, partially decorticated stem on which leaf traces can be identified as approximately equidimensional ellipsoid or rounded scars arranged in a helical pattern. Scale in cm. USNM 527763. (B) Leaf-trace pattern traced onto a cellulose-acetate overlay from which a 2/19 phyllotaxis can be seen. The base of the axis shows some distortion by compression, as is evident from the displacement of the leaf scars.

(Fig. 4); semi-prostrate bases resemble a golf club covered in roots (Fig. 4C). Basal diameters range from 4.1 to 10.5 cm ($\bar{x}$ = 6.64 cm), and numerous, spirally arranged roots appear to diverge from a centrally located circular furrow (Fig. 4B). There is no evidence that the bases are quadripartite or quadrilobate (K. Pigg, 2004, personal commun.). Rootlet initiation points on casts are preserved as elongate bulges, whereas the first-order roots are cylindrical, imparting an overall irregular surface to the rhizomorph. The number and diameter of roots originating from the furrow are related to the diameter of the corm. First-order roots range from 2.5 to 7.8 mm in diameter ($\bar{x}$ = 5.0 mm ± 1.2 mm; $n = 90$), and smaller rhizomorphs produce smaller first-order rootlets. Although cast specimens preserve root initiation points and primary roots, it has not been possible to determine the rhizotaxy. Above the basal corm is a transitional zone where neither leaf nor root traces are preserved (Fig. 4A).

Roots

Preserved roots are geopedally oriented, bifurcate, and crosscut the silty claystone at low to moderate angles, with complete rooting systems generally occupying several bedding planes (Fig. 4D). The depth of preserved root penetration is between 5 and 7 cm, based upon measurements from the more densely rooted horizons (decompaction of the claystone at 15:1 would result in original root penetration of at least a half meter). The longest root segment collected is 4.8 cm, with an average root segment being less than 2 cm. A centrally located vascular trace, identified as a darkened carbonaceous line, runs the length of the roots. All roots bifurcate, and there are at least five orders of axes in the rooting zone with specimens typically displaying three orders of branching (Fig. 4E). Roots bifurcate at angles ranging from 32° to 52° ($\bar{x}$ = 43°; $n = 50$). Diameters of second- and higher-order roots range from 3.8 to 0.6 mm with an average length between each successive bifurcation of 5.75 mm. Root lengths between successive bifurcations are variable and range from 0.30 to 20.85 mm. Root epidermis is composed of rectangular epidermal cells that average 76 × 43 µm ($n = 30$).

Stems

Aerial, decorticated axes are preserved primarily as in situ erect sandstone casts, although vestiges of decayed axes occur prostrate in the assemblages as adpressions and claystone-infilled stems. Erect axes range in height from 13.0 to 43.0 cm with basal axial diameters equal to that of each plant's transitional zone (Fig. 6). Aerial axes taper upward, show no signs of branching, and exhibit helically arranged ellipsoid or rounded leaf scars that are approximately equi-dimensional (6.2 × 5.6 mm; $n = 20$). Decortication of most axes prevented estimation of phyllotaxy; however, one specimen preserved faint but definite scars from which a 2/19 phyllotaxis was determined (Fig. 6B). Owing to the nature of the casting lithology, none of the leaf scars provide evidence of a vascular trace or parichnos tissue, and no leaves have been found attached to any stem axis. Remnants of a central stele are preserved in several cast specimens, and the "star-shaped" configuration is suggestive of exarch maturation. Using the allometric equations developed by Niklas (1994), predicted growth heights are estimated to be 3.35 m ("nonwoody" species equation) and 3.22 m ("woody and nonwoody" species equation).

Leaves (Sporophylls) and Sporangia

Leaves and/or sporophylls are preserved isolated and mostly incomplete because of fracturing across bedding; complete specimens are observed rarely (Fig. 7). The best, most

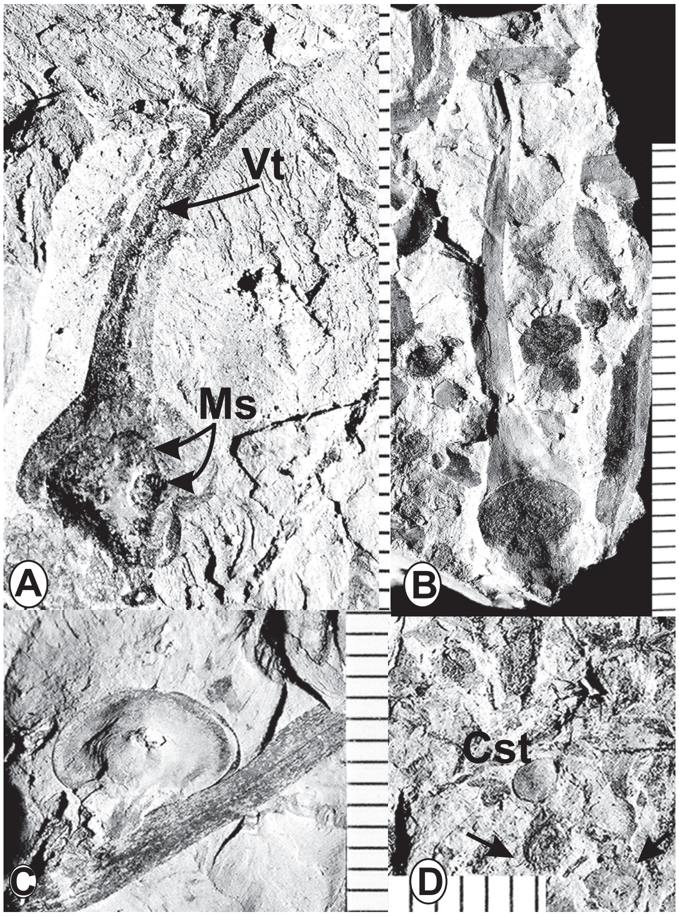

Figure 7. *Hartsellea* sporophylls and leaves. (A) Adaxial side of megasporophyll on which 5 megaspores (Ms) can be seen. Sporophyll pedicels are more inflated than those of vegetative leaves, providing surface area for the development of the sporangium. A linear-lanceolate lamina with central vascular trace (Vt) developed distal to the pedicel. UNSM 527764. (B) ?Abaxial side of a leaf showing non-inflated pedicel congruent with the linear-lanceolate lamina with central vascular trace. Note compressed megaspores in the matrix. USNM 527765. (C) Isolated, reniform sporangium. USNM 627766. (D) Dispersed, isolated megaspores assigned to *Triletes* preserved as impressions with apicular ornamentation (arrows) and claystone casts (Cst) on which no ornamentation can be seen. Scales in mm. USNM 627767.

complete leaves/sporophylls are lanceolate and taper logarithmically in an apical direction. A central vascular strand constitutes approximately one-fifth of the leaf width. Overall, leaves range between 1.3 and 4.1 cm in length (× = 22 mm; *n* = 11) and possess an inflated, diamond-shaped base that is typically 1.7–5.5 mm high and 3.1–12.2 mm wide (Fig. 7B). The lanceolate lamina expands where it is contiguous with the inflated base. Because of specimen orientation within the matrix and the presence often of only the distal lanceolate lamina, it is not possible to distinguish between vegetative leaves and sporophylls in many instances. Sporophylls in the Hartselle suite can be distinguished from vegetative leaves only when the adaxial surface of the diamond-shaped base is visible and a sporangium is present (compare Fig. 7A and 7B). No evidence of strobilar organization has been found.

Compressed, isolated sporangia and sporangia attached to sporophylls are kidney shaped (reniform), averaging 7.5 mm high and 8.3 mm long (Fig. 7A, 7C). The surfaces of sporangia are smooth. No microsporangia have been identified; however, several of the sporangia preserve densely packed megaspores (Fig. 7D). The maximum number of megaspores per megasporangium is unknown, but sporangia containing four and eight megaspores have been observed (Fig. 7A).

Palynomorphs

Isolated trilete megaspores are found in abundant numbers throughout the rooted interval. These may be preserved as either compressions or claystone casts retaining three-dimensional features; both preservational modes exhibit ornamentation originating from the outer wall and extending into the matrix (Figs. 4F, 7D). The megaspores are circular to triangular in outline with a mean diameter of 1.9 mm (standard deviation = 0.3 mm; *n* = 200). The distal side of each is covered with punctae, small bumps, or both, whereas the proximal side is relatively smooth, with a trilete mark that extends nearly to the margin of the megaspore. Punctae are moderately dense, averaging 57 per 0.5 mm^2. There is no pronounced cingulum. Most megaspores in the matrix exhibit long spines that protrude from the margins. The most complete spines exhibit a taper and appear apicular. In rare instances a bifurcation, or "hook," can be seen terminating the spine (Fig. 4H). Spines are up to 600 µm in length, and under high magnification it is possible to see a linear thickening within the spine axis, with ridges running parallel to the middle of the spine. Spine density based on three well-preserved specimens is 15 spines per mm^2. Evidence of spore-wall structure also is visible, but megaspore ultrastructure is unknown. No microspores have been recovered from processed claystone samples.

ASSOCIATED HARTSELLE MEGAFLORA

Preserved in association with the cormose lycopsid, within both rooted intervals and at the contact with the overlying quartz arenite, are a variety of rooting, axial, vegetative leaf, and reproductive structures (Fig. 8). Non-bifurcate rooting structures include elongate and contorted axes (due to compression) that are less than 5 mm in width and several centimeters in preserved length. Small, millimeter-diameter, lateral roots emerge at enlarged nodal areas and penetrate the matrix (Fig. 8A). Aerial axial fragments often are decorticated and occur in two morphologies: bifurcate axes reminiscent of pteridosperm rachides (Fig. 8B, 8C) and linear axes of a smooth and striated nature. Axes bearing helically arranged scars also are encountered. Bifurcate axes may be up to 0.75 m in length and 7.24 cm in width, with most axes on the order of a centimeter in width. Pinnatifid leaves, which probably are of pteridosperm affinity, are found isolated from any axial fragment. They possess a petiole and central axis from which sessile, broad, rhombic and trilobed pinnules occur (Fig. 8D), and conform to *Genselia* (R. Ianuzzi, 2004, personal commun.). Fertile structures conforming to the pteridosperm reproductive structure *Telangiopsis* consist of free sporangia, fused at the base into a synangial organ, that are borne in clusters terminally on branching axes that lack foliar units (Fig. 8F). Rare, isolated seedlike structures also are preserved (Fig. 8E).

GREENBRIER FOSSILS

The small specimen suite curated in the paleobotany collections of the USNM (SM7727) is from the Greenbrier Limestone, of middle Chesterian (Hombergian) age (Yeilding, 1984). The exact collection site is not recorded in the museum's records. The fossil assemblage consists only of plant material—roots, leaves and sporophylls, sporangia, and megaspores—preserved in a light-gray (5Y 7/1) mixed carbonate-siliciclastic lithology (Fig. 9). The rock is predominantly micrite with scattered polycrystalline, medium-sand grains within this matrix.

Greenbrier roots are bifurcate with diameters ranging between 3.2 and 0.7 mm, and angles of bifurcation averaging 42°. Only three orders of bifurcation are displayed in the sample suite, representing distal parts of the root system (Fig. 9B). A single, medial vascular strand runs the length of each root and divides within the axial bifurcation.

The Greenbrier suite appears to preserve both vegetative leaves and sporophylls. Vegetative leaves are distinguished by a greater overall laminar length and less well developed inflated base (Fig. 9A). These are linear-lanceolate in shape and up to 7 cm in length. Although expanded, the leaf base is less inflated and presents a more gentle spindle-shaped taper. Sporophyll morphology is similar to that of the Hartselle material, with leaf bases characterized by flared, diamond-shaped inflations above which short, linear-lanceolate laminae extend for a maximum of 3 cm (Fig. 9D). Sporophyll bases appear more bulbous, not broad and flattened as in the Hartselle specimens, and this may be a taphonomic bias because the latter have been compressed significantly.

Sporangia are isolated and reniform, measuring 4.9 mm in height and 6.8 mm length (Fig. 9D). The surfaces of sporangia

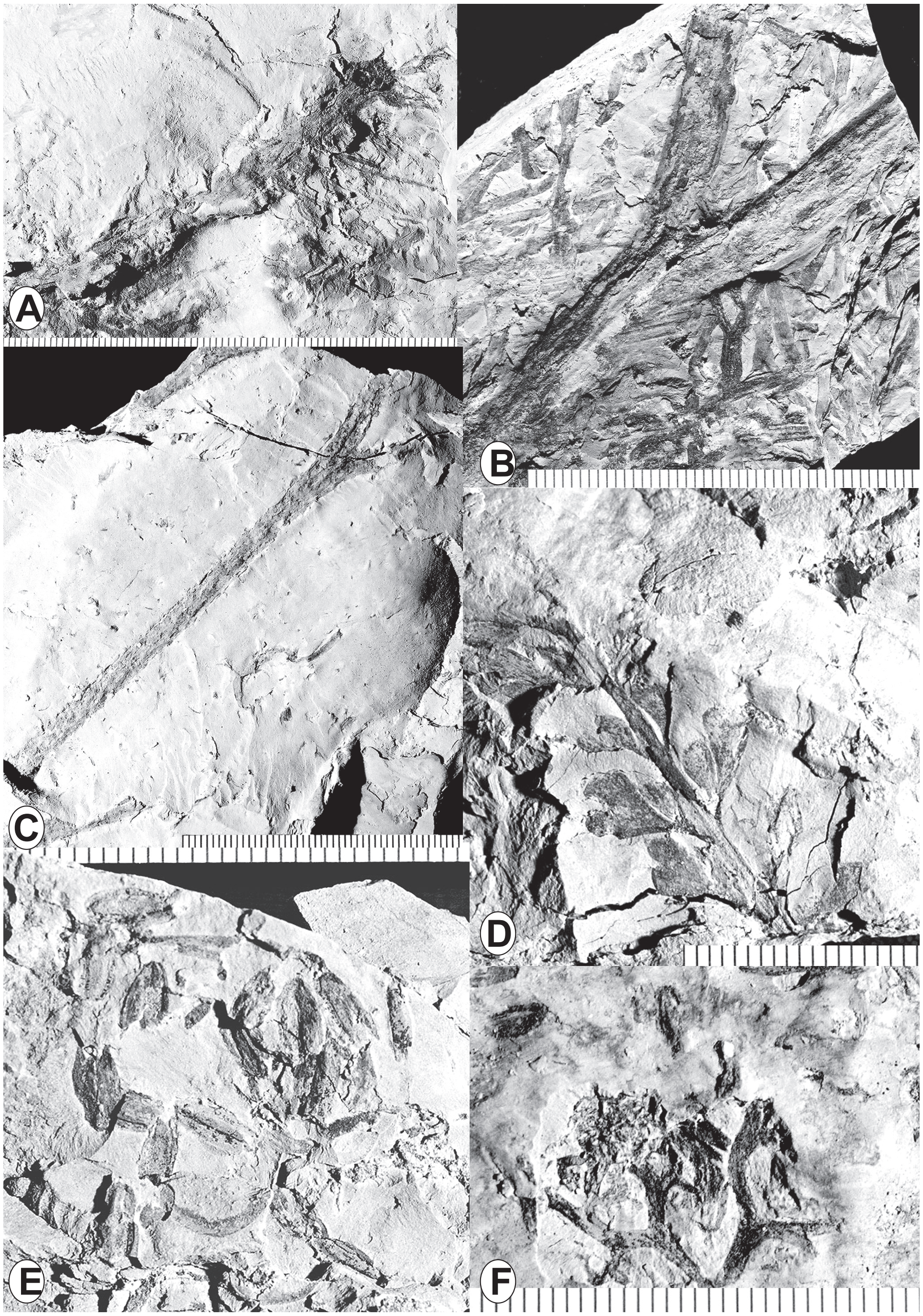

Figure 8. Non-lycopsid macrofloral elements preserved within Hartselle inceptisols. (A) Non-bifurcate roots that are elongate and contorted from compression with small, mm-diameter, lateral roots emergent at enlarged nodal areas. USNM 527768. (B) Large, bifurcate, decorticated axis of undetermined systematic affinity. USNM 527769. (C) Small axis reminiscent of a pteridosperm rachis consisting of elongate petiole and basal leaf bifurcation. The surface of the axis is covered with small punctae. USNM 527770. (D) Isolated pinnatifid leaves of an unidentified pteridosperm. USNM 527771. (E) Isolated small seedlike structures found in association with pinnatifid leaves and *Telangiopsis*. USNM 527772. (F) Elongate sporangia developed from the apices of bifurcate branching system assigned to *Telangiopsis*. All scales in mm. USNM 527773.

are smooth, although carbonaceous residue imparts a punctate appearance. Isolated megaspores average 2 mm in diameter, are circular to triangular, and exhibit the same surficial distribution of long, apicular spines along the megaspore (Fig. 9C, 9D). The number of megaspores per sporangium could not be determined from the available specimens, and no microspores have been recovered from the macerations.

SYSTEMATIC PALEONTOLOGY

The combined Hartselle/Greenbrier specimen suite consists of material that, in part, conforms with *Cormophyton mazonensis* (Pigg and Taylor, 1985), an authigenically preserved cormose lycopsid base discovered in nodules of the Francis Creek Shale, Carbondale Formation, Middle Pennsylvanian of Illinois

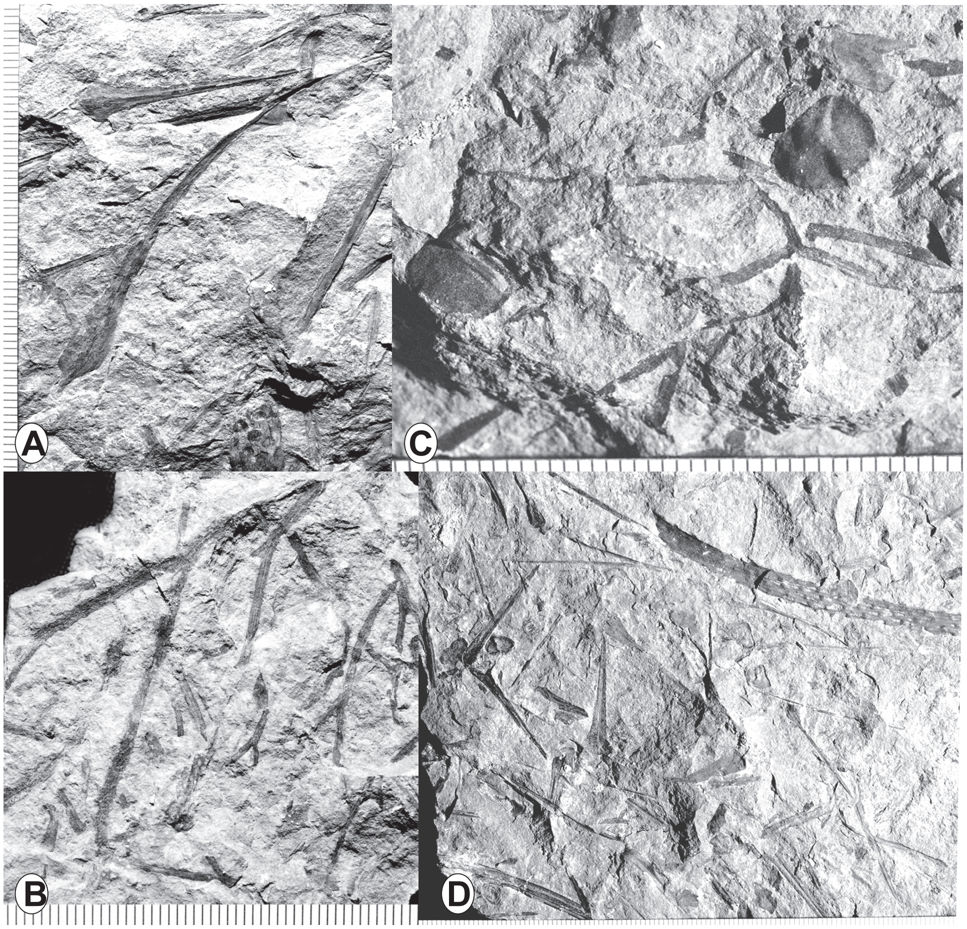

Figure 9. Representative specimens of *H. dowensis* from the Greenbrier Limestone, West Virginia (USNM SM7727) . (A) Isolated, vegetative leaves preserved within a micrite inceptisol. (B) Inceptisol roots showing successive bifurcations and spinose megaspore (lower center). (C) *Triletes* micrite-cast megaspores with proximal surface exposed within rooted micritic limestone. (D) Dispersed megasporophylls, sporangia, and punctate axis (?pteridosperm rachis).

(Westphalian D). *Hartsellea* is interpreted as a plant similar to *Chaloneria cormosa*; however, preservational criteria and the absence of anatomical detail preclude its incorporation into this latter genus. Bases from Mazon Creek and those organs described herein provide a wealth of information concerning external features of *Chaloneria*-type plants.

Class **Lycopsida**

Order **Isoetales**

Family **Chaloneriaceae** Pigg and Rothwell, 1983a

Genus ***Hartsellea*** gen. nov. Gastaldo, Gibson, and Blanton-Hooks

Diagnosis. Herbaceous plant with rounded, club-shaped base and conical, unbranched stem; circular root scars arranged helically; bifurcate roots; leaves and sporophylls arranged helically; rounded leaf scars, wider than high. *Triletes*-type dispersed megaspores.

Hartsellea dowensis **sp. nov.** Gastaldo, Gibson, and Blanton-Hooks

Type species. *Hartsellea dowensis*

Diagnosis. Cormose base; bifurcate roots from central basal furrow, up to 5× bifurcate; lanceolate, elongate leaf lamina with single, central vascular strand and dilated base; megasporophyll pedicels diamond-shaped and inflated with short, lanceolate lamina; adaxial reniform sporangium; trilete megaspores, four to eight per megasporangium, rounded to triangular, spines on distal surface appear apicular, hooked, or bifurcate.

Type locality. Jefferson County, Alabama (NW ¼, NE ¼, Sec. 22, T16S, R3W, Birmingham South USGS 7.5′ Quadrangle, Jefferson County, Alabama [33° 27.675’ N, 86° 50.340’ W])

Stratigraphic Position. Upper Mississippian Hartselle Sandstone

Age. Late Mississippian, Chesterian

Etymology. The generic designation *Hartsellea* refers to the Mississippian Formation in which the plant is preserved. The specific epithet is named after Doug Owens who discovered the fossil assemblage and collected the erect plants for the present study.

Type specimen. Holotype—USNM 527757: Figure 4A. Paratypes—USNM 527759: Figure 4C; USNM 527760: Figure 4D; USNM 5277561: Figure 4E; USNM 5277562: Figure 4F; USNM 527763: Figure 6; USNM 527764: Figure 7A; USNM 5277645: Figure 7B; USNM 527766: Figure 7C; USNM 527767: Figure 7D.

Repository. National Museum of Natural History, Department of Paleobiology, USNM Loc. 42130.

Description

Late Mississippian *Hartsellea* attained a calculated height of ~3.5 m and consisted of an unbranched, monopodial aerial stem that developed from a cormose root base. Aerial axes attained basal diameters of at least 10 cm, with subterranean corms expanded beneath the stem-corm transition. A small, central "star-shaped" stele encountered in several specimens is used to infer that these plants were nonwoody. Aerial stems tapered apically, but the apical terminus is unknown. It is also unknown whether the plant underwent a determinate or indeterminate growth strategy.

Aerial axes were enveloped with helically arranged vegetative leaves up to 7 cm in length and smaller sporophylls, both of which typically produced near-equidimensional leaf scars when the axis was decorticated. Linear lanceolate leaves consist of a distal lamina and a distinct pedicel or keel. Leaf bases are flared, or diamond shaped, with vegetative leaf bases less expanded than those of sporophylls. Leaves narrow distally from the widest portion of the leaf base and sporophylls taper logarithmically. Reniform sporangia occur on the adaxial surface of sporophylls, but it is not known if the plant produced fertile regions interspersed with vegetative zones (as in *Chaloneria*; Pigg and Rothwell, 1983a) or terminated in a strobilar structure (as in *Clevelandodendron*; Chitaley and Pigg, 1996). Only megasporangia have been identified, each of which contains four to eight megaspores. Trilete megaspores, assignable to the dispersed taxon *Triletes* (Bennie and Kidston) ex Zerndt 1930, average 2 mm in diameter and possess numerous, bifurcate spines that may be up to 600 µm long. Because retuse or bifurcate spines (depending upon preservational state) are not always evident owing to sediment cover, megaspores appear apiculate. In the dispersed condition, this ornamentation would have been lost during sample preparation. An unsuccessful search was made for reported dispersed Mississippian megaspores with these morphological features, although those of *Bothrodendrostrobus–Setosisporites* are similar (Stubblefield and Rothwell, 1981). Microspores are unknown.

Cormose bases grew up to 10.5 cm or more in diameter, and bore numerous root-initiation points that average 5 mm in diameter on the largest specimens. Roots originate from a central basal furrow on the corm, and it is not possible to determine whether the corm is more than bilobed. Primary roots can be preserved as elongate cylinders or bulges that give the base an overall irregular appearance. In compressions, these can be seen as departing from the base and then bifurcating within 5 cm. Five orders of roots bifurcate at angles of ~42° and are characterized by a single, central vascular strand. Roots penetrate a weakly developed soil (inceptisol) and extend geopedally for up to 15 cm in compacted sediment. The total length of the rooting system may have been up to 0.5 m. Evidence indicates that once a plant was displaced from a vertical position, growth continued with elongation of the cormose base in a prostrate orientation (Fig. 4C).

COMPARISON WITH OTHER CORMOSE LYCOPSIDS

Cormose lycopsids are assigned to the Isoetales, an extant clade whose origin was thought to be somewhere between the Late Devonian and Early Mississippian (Pigg, 1992; Retallack, 1997), but now is known since the Late Devonian (Cressler and Pfefferkorn, 2005). The primary character distinguishing this clade is an unusual rhizomorph generally described as a swollen, nonbranching, or lobed base, although Chitaley and Pigg (1996) used a monopodial growth habit and a terminal bisporangiate strobilus as criteria for systematic assignment of a Late Devonian lycopsid to the order. Debate continues as to the phylogenetic origin of the cormose structure and derived lineages (Jennings, 1975; Jennings et al., 1983; Rothwell and Erwin, 1985; Pigg, 1992; Bateman et al., 1992; Bateman, 1992). Some authors favor the evolution of *Stigmaria*-type rooting, found in the Lepidodendrales, as an evolutionary derivation from a cormose base (Bateman et al., 1992), while earlier workers proposed that cormose bases are the result of reductionism (e.g., Mägdefrau, 1956) or that structures in lepidodendraleans and isoetaleans had separate origins (Jennings, 1975; Stubblefield and Rothwell, 1981). There is general agreement that rhizomorphic lycopsids belong to one monophyletic "plexus" (Pigg, 1992; DiMichele and Bateman, 1996). Regardless, early representatives of the clade were identified solely on the basis of aerial (Chitaley and Pigg, 1996) or subterranean parts (Cressler and Pfefferkorn, 2005; Bateman, 1992).

Of all the non-arborescent taxa described from the Late Devonian, Mississippian, or Pennsylvanian, morphological features of the present material conform most closely with younger described isoetaleans. Two Late Devonian forms—*Cyclostigma* (Chaloner, 1984) and *Otzinachsonia* (Cressler and Pfefferkorn, 2005)—have similar basal configurations, but Pigg (1992) considered the bilobed nature of *Cyclostigma* to be ambiguous. And, although *Otzinachsonia* possesses a lobe-and-furrow architecture, the cormose base is definitely four-lobed. The compact anchoring structures in the Early Mississippian form, *Oxroadia* (Bateman and Rothwell, 1990; Bateman, 1992) are unlike those in *Hartsellea dowensis*.

Two taxa of the Pennsylvanian-aged Chaloneriaceae—*C. periodica* and *C. cormosa*—are most similar architecturally to the plant described herein. The ligulate taxon *Chaloneria periodica* is known from permineralized peat of the Middle Pennsylvanian, and is characterized by an aerial axis that possessed alternating vegetative and fertile zones (DiMichele et al., 1979; Pigg and Rothwell, 1983a, 1873b, 1985; Pigg, 1992). Neither vegetative leaves nor sporophylls show evidence of dehiscence, and these structures differ considerably in size. Sporophylls are smaller and thinner than the vegetative leaves, with adaxial sporangia preserved in the axils of some sporophylls (DiMichele et al., 1979). No basal organs are known for this plant. *Chaloneria cormosa*, a permineralized Pennsylvanian form, is an unbranched, upright plant with a cormose base (Pigg and Rothwell, 1979; 1983a, 1983b; Pigg, 1992). The plant is estimated to have been ~2 m in height, with a maximum stem diameter of ~10 cm.

Helically arranged leaves were dehiscent and produced irregular axial leaf scars on the axis. The plant was heterosporous with fertile regions located toward the stem apex (Pigg and Rothwell, 1983a; Pigg, 1992). Dispersed megaspores and microspores are assigned to *Valvisisporites auritus* and *Endosporites globosus*, respectively (Gastaldo, 1981; Pigg and Rothwell, 1983a; Pigg, 1992). Hence, although the morphological features and overall bauplan of *Hartsellea downesis* are comparable to *Chaloneria*, the megaspores of these plants are very different.

Megaspores are more similar to those in *Bothrodendrostrobus* (Stubblefield and Rothwell, 1981). *Setosisporites praetextus* is similar in overall shape, possessing a robust trilete mark. The spore is smaller in maximum dimension (1.5 mm) with a smooth proximal surface adjacent to the trilete mark, whereas the distal surface is covered with branched, elongate spines. Spines may be up to 250 µm (reportedly broken at the spine tips) and when completely broken off leave small, rounded punctae on the distal surface. Stubblefield and Rothwell (1981) documented the embryogenesis of this plant and compared it with that of extant Isoetales. They concluded that *Bothrodendrostrobus* was probably a small plant with a cormose rooting system and, hence, similar in bauplan to *Hartsellea*.

HARTSELLE INVERTEBRATES

The invertebrate assemblage is restricted to discrete horizons within the claystones. These are not laterally continuous; rather, they occur in lenticular pockets where the claystone thickens above thinner parts of the quartz arenites. The macrofauna is nearly a monospecific accumulation of bivalves, with only three tentatively identified taxa ($n = 34$ total specimens from two excavated pockets). *Edmondia* (Fig. 5A, 5B; $n = 29$) is found primarily as disarticulated valves occurring on 29 claystone blocks, and three specimens articulated and butterflied open. *Streblopteria* ($n = 2$) is uncommon and encountered as disarticulated valves, whereas *Streblochondria* ($n = 3$) is found only as disarticulated valves, although two valves may belong to the same individual. *Edmondia* shows the greatest size range, with length ranging from 1 to 4.5 cm; unfortunately other taxonomic features, such as hingeline characteristics and musculature, are not preserved. Poorly preserved *Streblopteria* and *Streblochondria* specimens all occur closely clustered on two claystone blocks (Fig. 5C).

Some very small cf. *Lockeia* (Rindsberg, 1994) traces were encountered on the surface of quartz arenite blocks, but their morphology varied enough to preclude positive identification. No shelly fauna corresponding to the size of the potential *Lockeia* were found. A few sinuous structures resembling horizontal traces, similar to *Planolites*, were found to be distinct enough to differentiate them from tool marks.

DISCUSSION

The Chesterian Series in the Black Warrior (BWB) and Appalachian Basins consists of mixed carbonate-siliciclastic deposits that reflect major changes in the tectonic and paleogeographic setting of the region. Most of the Mississippian in the BWB is characterized by limestones that accumulated within a variety of carbonate-ramp environments (Pashin and Gastaldo, in press) including shoals and tidal flats. Subsequently, the area was influenced by siliciclastic input from the developing Alleghenian orogenic province to the east-southeast (Mack et al., 1983). Carbonates accumulated when the area was under highstand conditions followed by cyclically interbedded shale, sandstone, and limestone of the Pride Mountain Formation (BWB), interpreted as a lowstand wedge within a lowstand systems tract (Stapor et al., 1992). During sea-level rise, the Hartselle Sandstone, consisting of beach, barrier island, and tidal facies (Thomas, 1982; Smith, 1983), was deposited within a nearshore regime of the overlying Transgressive Systems Tract. Hartselle sandstones are barrier strandplains, each of which was deposited during a stillstand, with barriers and back-barrier lagoonal and tidal-flat facies sequentially stacked in the sequence (J. Pashin, 2004, personal commun.). Hence, nearshore subaqueous and subaerial, tidally influenced environments were available for colonization by plants capable of inhabiting poorly developed soils (inceptisol) that were subjected to tidally driven brackish and fully marine waters.

Sedimentological evidence indicates that the outcrop of claystone and quartz arenites at Homewood represents a siliciclastic-dominated nearshore marine setting characterized as a barrier island with back-barrier deposits (e.g., Walker, 1984; Boggs, 1995). A basal, moderately well-sorted quartz arenite is overlain by a poorly developed silty, clay-rich, deeply rooted paleosol in which the herbaceous lycopsid *Hartsellea* and other plants grew. The erect isoetaleans and their soil-litter (O) horizon were covered by a well-sorted, massive quartz arenite exhibiting a lobate surface geometry deposited in a single event. Death and subsequent decay of the erect axes resulted in an arenite infill by the overlying entombing sediment, indicating shifting sands across the top of the deposit following void development. This sequence was repeated at the site with the overlying thicker inceptisol in which the same plant assemblage is preserved as the result of the emplacement of another fine-grained, well-sorted, quartz-rich sand body. Hence, a repetitive process was responsible for organic matter preservation in this regime, overtopping a herbaceous wetland community that is, by definition, a marsh.

Laterally adjacent lenticular assemblages within the silty claystone preserve macroinvertebrates that were co-opted as part of the inceptisol, the result of channel accretion and fill to where the sediment surface was raised sufficiently to allow for plant colonization. The Homewood assemblage is very low diversity when compared with other Late Mississippian coastal, deltaic, and shallow-marine faunas, such as the bivalve-rich Redoak Hollow (e.g., Elias, 1957), the Greenbrier Limestone, and Mauch Chunk Formations (Kammer and Lake, 2000). The near predominance of *Edmondia*, the butterflied and disarticulated nature of the shell occurrences, and the localized distribution restricted to pockets of claystone within low swale areas of the quartz arenite are consistent with a transported thanatocenosis rather than an in situ biocenosis.

A fully marine habitat for the Homewood invertebrates is well established in the literature by authors using a combination of shell morphology, faunal associations, and lithologic characteristics. The absence of brachiopods restricts the assemblage to shallower-water settings (e.g., Bretsky, 1969), and although Kammer and Lake (2000) concluded that *Edmondia* and *Streblochondria* were euryhaline taxa, *Edmondia* generally is interpreted as a shallow-burrowing marine form (e.g., Craig, 1956; Calver, 1968; Runnegar and Newell, 1974; Hoare, Sturgeon, and Kindt, 1979; Gibson and Gastaldo, 1987). This interpretation is based upon association with other known marine invertebrates and such morphological characteristics as the elongate, oval shell form, nearly equilateral valve shapes, position and nature of external ornamentation, and internal anatomy (e.g., Stanley, 1970, 1972). Stanley (1970) notes that many of the analodesmatids, to which *Edmondia* belongs, were likely endobyssate, a life-habit adaptation for substrate stabilization. Such adaptations in bivalves are indicative of life that is just below the sediment-water interface or, perhaps, semi-infaunal (Stanley, 1972). *Streblopteria* and *Streblochondria* usually are interpreted as epibyssate shallow-nearshore to deeper-water offshore epifauna (e.g., Watkins, 1975; Hoare et al., 1979; Kammer and Lake, 2000), with *Strebolopteria* perhaps restricted to lower oxygen conditions as indicated by its occurrence in black shale facies. Considering the depositional setting and the relationship of in situ plants to the mollusc-dominated macroinvertebrates, the invertebrate assemblage represents a localized, reworked marine fauna trapped within peritidal clastics (tidal channels, tidal flats, or the marsh, proper).

The absence of invertebrate trace fossils within both the quartz arenites and claystones, as compared with other Hartselle occurrences (Rindsberg, 1994) or other Mississippian units such as the Pennington (e.g., Sheehan, 1988) or Borden (e.g., Chaplin, 1982) Formations, indicates that either burrowing organisms were not common in the Homewood substrates or evidence for burrowing was not preserved. In the case of the sandstone, this is due probably to mobility of the substrate and/or subaerial exposure.

The presence of rooted *H. dowensis* in micritic limestones of the Greenbrier Group expands the habitat range of this plant from strictly siliciclastic muddy, back-barrier environments to a carbonate mud substrate. Muddy carbonate depositional environments are indicative of settings surrounded by fully marine conditions, away from significant siliciclastic influence (e.g., Walker, 1984). The Greenbrier is considered to be the equivalent of the Newman Limestone (Big Lime) in Kentucky (Harris and Sparks, 2000), a shallow-marine carbonate sequence that overlies the deeper marine carbonates of the Fort Payne Formation. The oolites of the Big Lime were deposited in shoals or tidal channels (MacQuown and Pear, 1983) in a more offshore position than time-equivalent lithologies in West Virginia where peritidal lime mudstone, peloidal, ooid and skeletal grainstones formed (Smosna, 1996; Wynn and Read, 2002). Hence, the preservation of *Hartsellea* in these peritidal environments indicates that it was a colonizer of wetlands throughout the transitional to marine regime.

Herbaceous wetland plants possess shallow rooting structures within the upper few decimeters of poorly developed soils (inceptisols). In modern marshes, shallow rooting is due to several factors. These include periodically saturated near-surface or surficial pore waters following rainfall or incursion of daily tides; the availability of only a shallow freshwater lens, derived from meteoric waters, overlying saline pore water at some depth; and changing redox potentials at depth in response to organic accumulation, methanogenesis, and the activity of sulfur-reducing bacteria. Autochthonous *Harstellea* in both siliciclastic and carbonate peritidal settings indicates that this plant may have been tolerant of brackish, if not fully marine waters during times when storm washover events and/or high (King) tides brought saline waters into this wetland setting. The presence of fully marine macroinvertebrates in the paleosol is evidence that these bivalves were transported into this setting before plant colonization. These animals represent both dead and living bivalves, as indicated by disarticulated valves and articulated specimens, respectively. This indicates that the bivalves lived in close proximity to the marshland, were transported into a channel feature (the lenticular geometry of the assemblage in an otherwise nondescript claystone), and subsequently buried. The energy required to move these benthic, infaunal bivalves is associated with hurricane-style storm events during which salt spray and inundation of fully ocean waters are common in back-barrier settings. Hence, it is parsimonious to propose that *Hartsellea* was tolerant of some saline influence in its habitat.

Hartsellea probably was not the only Carboniferous lycopsid tolerant of at least brackish waters. Gastaldo (1986) noted that the presence of in situ, autochthonous *Stigmaria* preserved in Mississippian bioclastic carbonates of the Battleship Wash Formation, Arizona, (Pfefferkorn, 1972), was evidence for brackish and/or salt-water tolerance of arborescent lycopsids in the Early Carboniferous. Hence, it appears that the lycopsid clade had evolved this physiological tolerance by at least the late Paleozoic.

The modern Gulf Coast barrier island system off Alabama, as well as the coastal barrier-island chain along the eastern seaboard, paralleling the coasts of Georgia to New Jersey, may serve as a modern environmental and process analogue for the wetland vegetation and associated macroinvertebrate assemblages (Dardeau et al., 1992; Kopaska-Merkel et al., 2000; see discussion of modern nearshore and primary-to-tertiary bay faunas and their ecologies in Britton and Morton, 1989; Fig. 10). Wetland marshes are composed primarily of herbaceous plants growing in back-barrier settings on the more protected, restricted marine side of these islands. These wetlands are the result of colonization of peritidal deposits that have accreted to near the air-water interface. A low-diversity bivalve community colonizes the sediment-water interface within tidal channels that cross the back-barrier marshes, although individuals may be found within the marshes byssally attached to the roots of grasses (e.g., *Spartina*; Prezant et al., 2002). Within the tidal channels of St. Catherines Island,

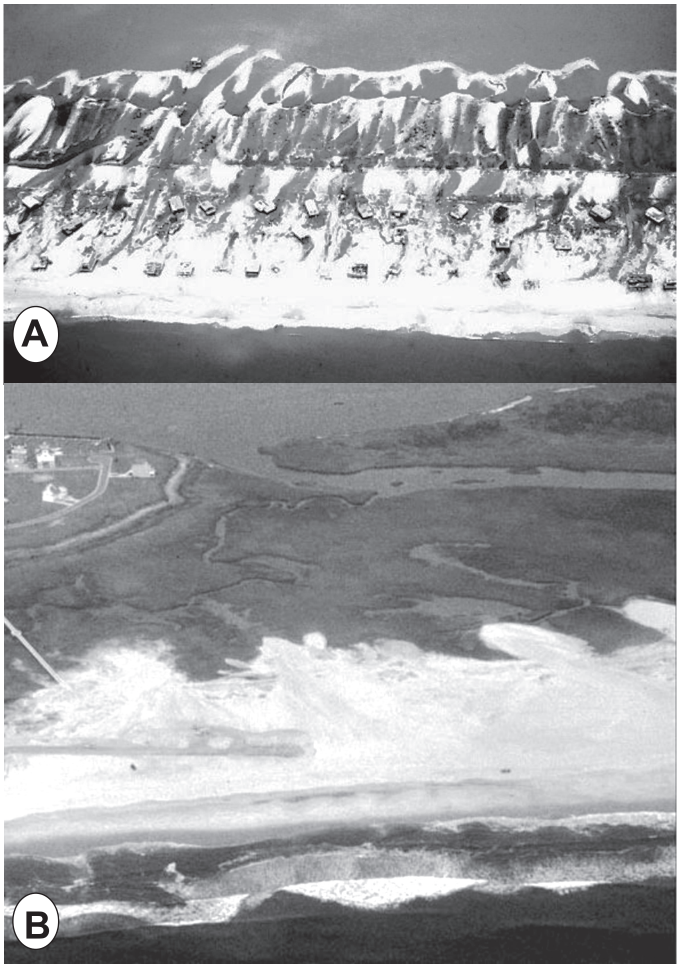

Figure 10. Oblique aerial photographs of recent overwash-fan deposits on the Atlantic and Gulf Coasts. (A) Overwash fan on Dauphin Island photographed the day after Hurricane Frederick, 1979, with wind speeds of 143 mph recorded on the island (photograph by J. Dindo, Dauphin Island Sea Lab, Alabama). (B) Overwash fan deposits on Carolina Beach, south of Wilmington, North Carolina, deposited during Hurricane Bonnie in 1998. Note how the overwash sand was deposited over the back-barrier marsh vegetation (photograph by J. Buie)

Georgia, larger bivalves tend to burrow in muddy point bars within tidal creeks, and small to large oyster bars occasionally are found to occupy creek banks (Prezant et al., 2002). Reworking of such assemblages during intense storm activity (e.g., hurricane-force winds) results in shell concentrations within the tidal channels or within the marshes (Donnelly et al., 2001); vertical accretion of tidally transported mud within the channels results in their infill and subsequent colonization by marsh plants. Storm surges associated with hurricanes also are responsible for the redistribution of foreshore and upper shoreface sands up and over dunes into the back-barrier wetlands (Fig. 10B; Donnelly et al., 2001) . Such overwash sands interbedded with back-barrier marsh-and-lake deposits are considered to be formed in response to the most intense hurricane strikes (Liu and Fearn, 1993, 2000; Donnelly et al., 2001). The contact between the underlying marsh mud or peat and the overlying well-sorted quartz sand is abrupt and often displays soft-sediment deformation. The overwash sand may be up to several decimeters closest to the barrier, thinning to less than 1 cm in distal sites. Depending upon the stem diameter and structural rigidity of the marsh plants in the path of the overwash sediments, these may be entombed either in an erect, standing orientation or in a prostrate position at the upper soil horizon in contact with the overlying sand.

CONCLUSIONS

Cormose lycopods assigned to *Hartsellea dowensis* gen. and sp. nov. occur in siliciclastic- and carbonate-dominated marine settings of the Mississippian within the eastern United States. These isoetaleans are preserved in peritidal environments in back-barrier wetlands that provide evidence for the first unequivocal marshes in the stratigraphic record. This interpretation is based on the herbaceous vegetational character of the assemblages, dominated by cormose lycopsids assigned to the Chaloneriaceae (Isoetales), and on leaves, seeds, and pollen organs of an unidentified pteridosperm within sedimentological context. The Homewood, Alabama, locality preserves an autochthonous assemblage of in situ plants with cormose bases rooted in a silty claystone inceptisol, and erect aerial stems entombed and cast by overlying fine-grained quartz arenite. Two stratigraphically successional marshes are preserved in the sequence, with the standing vegetation restricted to the basal paleosol. This exposure of the Hartselle Sandstone records barrier-island overwash deposits into back-barrier marshes during an interval of sea-level rise (TST). Here, a depauperate, low-diversity bivalve assemblage is preserved within the paleosol, as well as in lenticular beds lateral to the soil horizon that represent tidal channel fills. Invertebrates preserved in these beds—*Edmondia*, *Streblopteria*, and *Streblochondria*—are considered to be fully marine, and their presence in this depositional setting indicates that these taxa probably were transported into the back-barrier environment and buried during high-energy storm conditions. The rooted presence of *H. dowensis* in the Greenbrier Limestone of West Virginia, preserved in a carbonate mudstone, indicates that these isoetaleans were capable of colonizing both siliciclastic and carbonate tidal-flat deposits. Hence, the herbaceous lycopsids of the Chaloneriaceae, normally found within peat-accumulating wetlands, were well adapted to other wetland settings, and were the principal component of Carboniferous marshes in North America.

ACKNOWLEDGMENTS

The authors are indebted to Doug Owen of Birmingham, Alabama, of Milo's Famous Sweet Tea, for finding and collecting the cormose lycopsids from behind the factory site in Homewood, Alabama, and contacting the University of Alabama and Auburn University in the early 1990s. We would like to thank the following individuals who helped in the collection and analysis of the samples over the subsequent decade: Todd Grant, Nikolai Pedentchouk, Alex Webster, and Jonathan Collier of Auburn University; Matthew Charles of Colby College, and Kathleen Pigg, Arizona State University. Reviews by Kathleen Pigg, Cort Eble, and Steve Greb are greatly appreciated and were used as the basis for manuscript revision.

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Manuscript Accepted by the Society 28 June 2005

Printed in the USA