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VERTEBRATE TAPHONOMY, PALEONTOLOGY, SEDIMENTOLOGY, AND PALYNOLOGY OF A FOSSILIFEROUS LATE DEVONIAN FLUVIAL SUCCESSION, CATSKILL FORMATION, NORTH-CENTRAL PENNSYLVANIA, USA

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ABSTRACT: **The fluvial facies of the Catskill Formation record important ecological events that occurred during Late Devonian time. A well-exposed section between the towns of Blossburg and Covington, in north-central Pennsylvania, contains abundant macrofossils and sedimentary features, making it well-suited for linking Upper Devonian fossil occurrences with depositional environments and sedimentary processes. Strata consist of two distinct fluvial facies: floodplain lithofacies consist of mudrocks, with evidence of pedogenic overprinting and sharp-based sandstones interpreted as crevasse splays; channel-bar lithofacies consist of single- and multi-storied cross-stratified lenticular sandstone bodies interpreted as fluvial channel-bar complexes. Macrofossils occur in 22 discrete horizons spanning > 240 m of stratigraphic succession that include *Archanodon* bivalve shell impressions, two genera of "placoderms" (*Bothriolepis*, *Phyllolepis*), an unidentified acanthodian, and several taxa of sarcopterygian fishes, including lungfish (Dipnoi indet.), *Holoptychius*, *Langlieria*, and *Sauripterus*. Most vertebrate macrofossils are preserved as disarticulated, abraded plates, scales, and bone fragments in sandstone channel-bar deposits. Articulated, unabraded remains are preserved in proximal floodplain deposits. Miospores recovered from Catskill Formation fossil sites in the Blossburg-Covington section belong to the COR subzone of the VCo (*Diducites versabilis-Grandispora cornuta)* palynological zone, indicating deposition ca. 362 to 361.8 Ma during the late Famennian stage of the Late Devonian. Catskill Formation fluvial strata exposed tens of kilometers to the south and west yield latest Famennian palynomorphs. These broadly contemporaneous continental depositional environments supported Late Devonian vertebrate evolution, including the fin-to-limb transition in tetrapodomorphs, and the possible euryhalinity of vertebrates occupying marine-to-nonmarine transitional habitats.**

INTRODUCTION

The Late Devonian period (383–359 Ma) witnessed increased diversity of terrestrial ecosystems, freshwater fishes, and the dispersal of major vertebrate groups (e.g., "placoderms", cartilaginous fishes, ray-finned fishes, and lobe-finned fishes including early tetrapods). The Upper Devonian Catskill Formation in north-central Pennsylvania provides abundant, well-exposed evidence of these important environmental and biological changes by preserving diverse assemblages of Upper Devonian fossil plants, invertebrates, and vertebrates (Cressler et al. 2010; Daeschler and Cressler 2011; Broussard et al. 2018). Fossil flora include species of the progymnosperm *Archaeopteris*, early ferns, and early seed-bearing plants (Driese et al. 1997; Cressler 2006; Cressler et al. 2010). Fossil invertebrates are represented by *Archanodon catskillensis* bivalves (Chamberlain et al. 2004; Broussard et al. 2018), millipedes (Wilson et al. 2005), scorpions, a trigonotarbid arachnid (Shear 2000), a eurypterid (Tetlie 2008), and invertebrate trace fossils (Jones 2011). Vertebrate remains consist of "placoderms", acanthodians, chondrichthyans, early actinopterygians, and sarcopterygians including early tetrapods (Cressler et al. 2010; Daeschler and Cressler 2011; Broussard et al. 2018). Collectively, these studies provide insight on Late Devonian terrestrial ecosystems but details of the paleoenvironmental transition from terrestrial to nearshore marine environments has not been well-documented in the Catskill Formation.

Recent studies suggest that diversification of Late Devonian and Early Mississippian vertebrates occurred in nearshore environments and lower reaches of adjacent river systems (Carpenter et al. 2015; Goedert et al. 2018; Sallan et al. 2018; Ahlberg 2019; Gess and Whitfield 2020). Fossil-bearing Catskill Formation strata in Tioga County in north-central Pennsylvania range from marginal marine nearshore to terrestrial fluvial environments, making the location suitable for integrated paleontological-sedimentological studies elucidating the coastal environments and ecological conditions in which Late Devonian vertebrate diversification occurred (Daeschler and Cressler 2011; Broussard et al. 2018).

Much of our understanding of Late Devonian fluvial ecosystems represented by the Catskill Formation stems from detailed studies of a single roadcut, Red Hill, located in Clinton County, Pennsylvania, over the past two decades (Woodrow et al. 1995; Cressler 2006; Cressler et al. 2010; Daeschler and Cressler 2011). However, Red Hill represents a single

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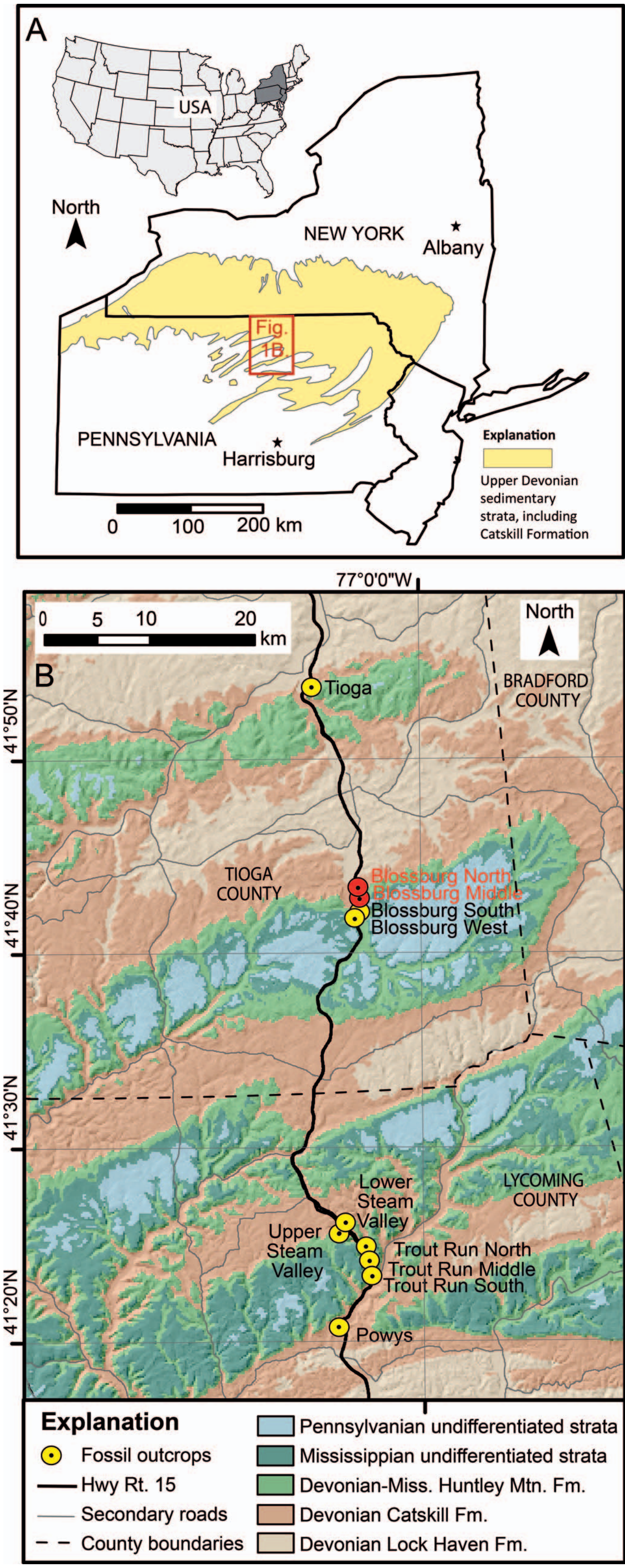

FIG. 1.—Map of Upper Devonian strata and fossil sites of north-central Pennsylvania. **A**) Distribution of Upper Devonian sedimentary strata (yellow) in north-central Pennsylvania and adjacent areas. **B**) Inset (red rectangle) from A showing bedrock geology and key outcrops that have previously yielded vertebrate, invertebrate, and/or plant fossil remains in Upper Devonian fluvial strata (yellow circles). This study focuses on two fossiliferous outcrops spanning almost the entirety of the Upper Devonian Catskill Formation: Blossburg North and Blossburg Middle (red circles and red text). References for previous sites are summarized in Daeschler and Cressler (2011) and Broussard et al. (2018). Geology from Berg and Dodge (1981).

"snapshot" in time and space from a several-meter-thick stratigraphic horizon. Recent work by Broussard et al. (2018) shows that similar Late Devonian faunas occupied fluvial habitats ~ 50 km east of Red Hill in Lycoming County, Pennsylvania (Steam Valley and Trout Run sites on Fig. 1). The current study focuses on two outcrops of the Catskill Formation created during highway construction completed in 2004 on PA Route 15 (Interstate 99) between the towns of Blossburg and Covington, in Tioga County, Pennsylvania. These Catskill Formation outcrops yield abundant vertebrate fossils and diverse sedimentary features preserved in a variety of terrestrial depositional settings, making them well-suited for linking Upper Devonian fossil assemblages and their associated taphonomy with sedimentary processes. Here we document the fossil taxa, taphonomy, sedimentology, and palynology of these previously unstudied, closely spaced outcrops that span a nearly complete and continuous stratigraphic section through the Catskill Formation, and integrate these new data with previous studies throughout the Catskill depositional system.

GEOLOGIC SETTING

The Catskill Formation (Upper Devonian) is a thick succession of chiefly mudstones, siltstones, and sandstones occupying the uppermost portion of the Acadian clastic wedge in Pennsylvania (Figs. 1, 2). It is thickest in central and eastern Pennsylvania (> 2000 m) and thins and interfingers with marine facies to the west (Berg et al. 1983). Convergent tectonics and sediment influx from the east coupled with marine regression in the west in the Appalachian foreland basin prompted westward progradation of alluvial-fluvial systems (Fig. 2) (Faill et al. 1985). Previous paleogeographic and paleomagnetic data place the study area under warm and seasonally wet and dry conditions at tropical to subtropical paleolatitudes during Late Devonian time (Fig. 2) (Kent 1985; Sevon 1985; Miller and Kent 1988; Blakey 2008; Scotese 2008).

The Upper Devonian stratigraphy of north-central Pennsylvania is characterized by a coarsening-upward succession of siliciclastic sedimentary strata interpreted as shallow marine, coastal plain, and alluvial plain deposits (Sevon 1985; Harper 1999; Slingerland et al. 2009). The Lock Haven Formation and lower part of the Catskill Formation reflect deposition in shallow marine and coastal plain paleoenvironments (e.g., Beard et al. 2017), whereas the middle to upper Catskill Formation record deposition chiefly in meandering fluvial systems that locally contain diverse fossil vertebrates and plants (e.g., Berg and Edmunds 1979; Daeschler and Cressler 2011; Broussard et al. 2018) (Fig. 3). The Upper Devonian–Lower Mississippian Huntley Mountain Formation preserves the transition from meandering fluvial paleoenvironments of the Upper Devonian Catskill Formation to braided fluvial paleoenvironments of the Lower Mississippian Burgoon Sandstone Formation (Berg and Edmunds 1979; Berg 1999).

Prior to this study, palynological analysis of Catskill Formation strata in north-central Pennsylvania was confined to upper portions of the formation (Warg and Traverse 1973; Streel and Traverse 1978; Traverse 2003). Traverse (2003) collected and analyzed spore-bearing samples from Catskill Formation sites in north-central Pennsylvania and concluded that early tetrapod-bearing samples from the Red Hill outcrop near Hyner, PA were restricted to upper Famennian palynozone VH (*Apiculiretusispora verrucosa-Vallatisporites hystricosus*) and equivalent to the upper part of the European palyzone Fa2c. Palynological analyses from the lower part of

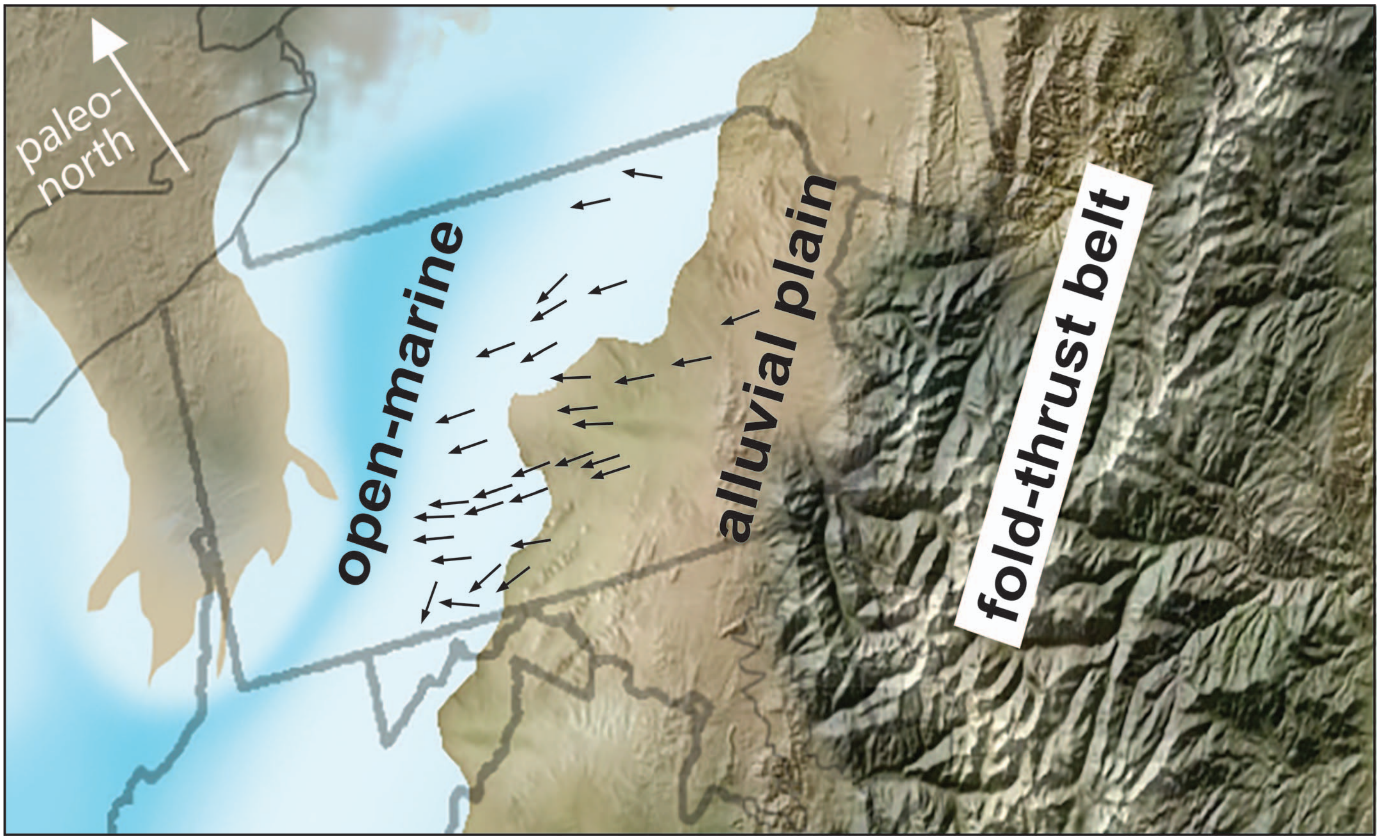

FIG. 2.—Late Devonian (~ 375 Ma, Frasnian) depositional setting of the Appalachian foreland basin inboard (west) of fold-thrust belt during the Acadian orogeny. Arrows depict paleocurrent measurements from Upper Devonian outcrops (Harper 1999). Westward to northwestward progradation of alluvial environments and sea-level regression shifted the shoreline westward. By late Famennian time, when the strata at Blossburg-Covington were deposited, the shoreline had prograded further west and the locality lay in the lower coastal plain © 2013 Colorado Plateau Geosystems Inc.

the Catskill Formation and the Huntley Mountain Formation of north-central Pennsylvania are absent from the literature.

MATERIALS AND METHODS

Upper Devonian stratigraphy is well exposed in roadcuts along US Rt. 15 (Interstate 99) between the towns of Blossburg and Covington in Tioga County north-central Pennsylvania. Four closely spaced roadcuts expose a > 450 m thick stratigraphic section of gently dipping strata that conformably grade from marine strata of the uppermost Lock Haven Formation through diverse non-marine strata of the overlying Catskill and Huntley Mountain formations (Fig. 3). This study focuses on two Catskill Formation outcrops: Blossburg North, which exposes the lower ~ 115 m of the Catskill Formation, and Blossburg Middle, which exposes the upper ~ 60 m of the Catskill Formation (Fig. 1).

Fossiliferous horizons at Blossburg North and Blossburg Middle (Figs. 1, 3) were first reported by Slane and Rygel (2009). As part of the current research, those fossil horizons were re-located and excavated from 2017–2019 to characterize the taxa and taphonomy of fossils present (Table 1). For the present study we also incorporated fossil material that was previously collected *in situ* and from talus by the Academy of Natural Sciences of Drexel University (ANSP) during road construction from 2004 to the present. Additional sedimentologic information was collected from the fossiliferous zones to provide depositional interpretations of each fossil horizon (Table 2). Lithologies were denoted in terms of grain size, sedimentary structures, fossil condition, bed geometry, bed thickness, and the nature of the bed contacts. The lithofacies documented in the field and as discussed herein have been widely reported in the literature; a detailed review of the literature is thus not provided. Key sedimentological features are shown within the measured stratigraphic section in Figure 4 and photographs in Figure 5. Table 2 summarizes the sedimentology and paleontology of each fossil horizon. Not all sedimentologic details can be depicted on the measured stratigraphic section (Fig. 4) for reasons of scale. Taphonomic attributes of macrofossils within each horizon include the degree of articulation, fragmentation, and abrasion (e.g., Behrensmeyer 1988). Degree of articulation ranges from imbricated scales and bony elements arranged in proper anatomical configuration (articulated) to isolated scales and bony elements (disarticulated). Degree of fragmentation ranges from complete scales and bony elements (entire) to partially complete scales and bony elements (fragmentary). Degree of abrasion ranges from fossils that show no rounding of edges with no surface scour (unabraded), to slight rounding of edges with minimal surface scour (abraded), to significant edge rounding and surface scour (highly abraded).

Macrofossils were prepared mechanically with a pin vise and air scribe by C F. Mullison at the ANSP and are reposited there. Photographs were taken with Nikon cameras. Illustrations were assembled in Adobe Photoshop and Illustrator. Images were corrected only for brightness and contrast.

Mudrocks were sampled for palynology to provide improved age constraints and additional paleoenvironmental insight. Special care was taken to choose mudrocks lacking visible evidence of pedogenesis, including rootlets, desiccation cracks, caliche, and pedogenic slickensides. From a suite of twenty samples spanning the entire Catskill Formation and the lower part of the Huntley Mountain Formation from the Blossburg-

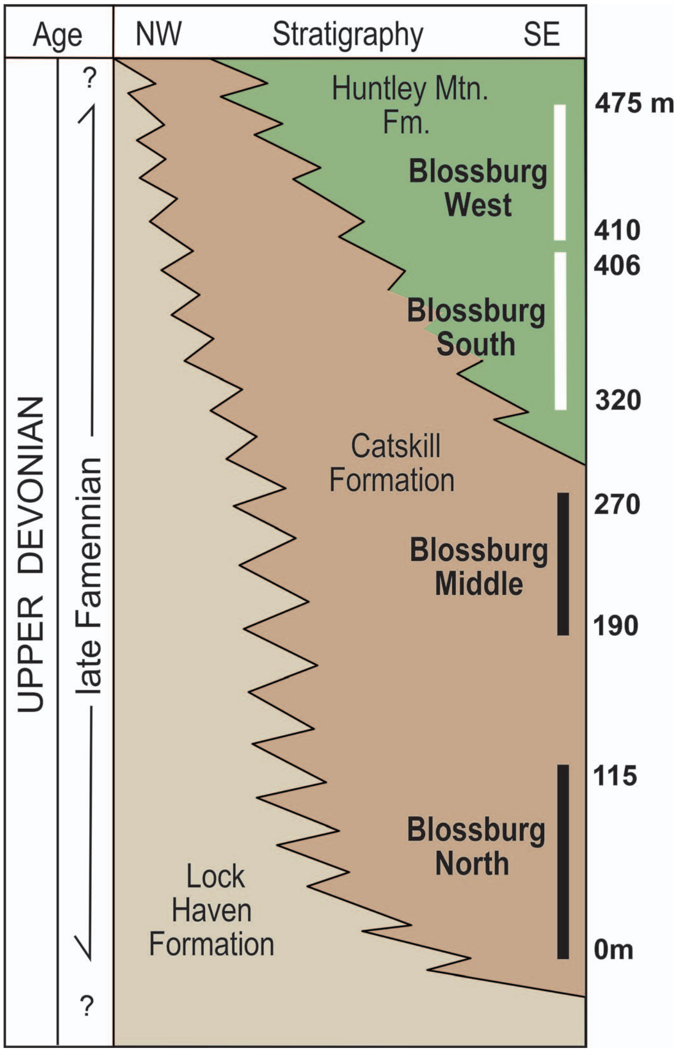

FIG. 3.—Generalized stratigraphy of Upper Devonian sedimentary strata in north-central Pennsylvania. Stratigraphy adapted from Berg et al. (1983) and Broussard et al. (2018). Area spans 105 km from western Potter County (northwest) to Easternmost Tioga County (southeast). Time scale from Walker et al. (2012). Vertical lines on right depict generalized stratigraphic position of the Blossburg-Covington section discussed herein. Black bars indicate strata included in present study (Blossburg North and Blossburg Middle). White bars indicate strata not included in present study (Blossburg South and Blossburg West). Abbreviations: mtn. = mountain; fm. = formation.

Covington section, ten samples were selected for palynological analysis (solid circles on Fig. 4). For GPS locations of palynological samples see Online Supplemental File. Selections were made from lithologies most likely to yield palynomorphs and throughout the stratigraphy in order to provide biostratigraphic coverage of the upper, middle and lower portions of the stratigraphy. The ten samples were prepared for palynology (spores, algae, and acritarchs) and one of the authors (PZ) performed palynological and organic residue analyses (for detailed preparation methods see full palynology report in the Online Supplemental File). Table 3 summarizes the raw counts of palynomorphs recovered from individual samples.

SEDIMENTOLOGIC RESULTS

The > 240-m thick Blossburg-Covington measured section shown in Figure 4 provides reference for the sedimentological descriptions and interpretations provided below. The section consists of two facies associations that are summarized below.

Channel-Bar Facies Association

Description.—Channel-bar sandstones have lenticular geometries with channels exhibiting a basal erosional scour surface that cuts into underlying strata. (Fig. 5A, 5B). Lenticular sandstone bodies are composed of a single isolated sandstone body (i.e., single story bodies) or multiple stacked sandstone bodies (i.e., multi-story bodies) bounded by scours and, in some examples, thin (< 0.30 m thick) mudrock deposits. Single-story bodies ~ 2–3 m thick occur in the lower part of the section, whereas ~ 5–7 m thick multi-storied bodies occur in the upper part of the section (Fig. 4). Low-angle convex-up surfaces occur in single- and multi-story bodies; these surfaces dip oblique to paleocurrent orientations derived from cross-stratification (Fig. 4). Sandstone bodies generally fine upward and are encased within red mudrock deposits of the Floodplain Facies Association (described below). Internally, sandstones are very fine- to fine-grained; most sandstones are reddish gray but light grayish green sandstones are increasingly common upsection. Sandstones exhibit dune- to ripple-scale planar and trough cross-stratification (Fig. 5C) and horizontal stratification. Erosional surfaces (scours) are common (Fig. 5C) and many are lined by conglomeratic lags composed of granule- to pebble-sized intraformational clasts (mud chips and concentrically laminated caliche nodules) and in some examples, vertebrate macrofossil fragments (Fig. 6A–6D). Sparse floral remains, mainly unidentifiable stems, are locally concentrated along erosional scours. Clay-lined rootlets overprint many channel-bar sandstones (Fig. 5D). The tops of some channel-bar sandstones contain abundant examples of the trace fossil *Beaconites antarcticus*.

Less common muddy channel bodies are composed of inclined heterolithic packages of sandstone, siltstone, and mudstone (Fig. 5E, 5F). Individual beds are < 0.25 m thick and commonly pinch out along the inclined surface. Ripple-scale cross-laminae occur within sandstones; roots and burrows occur near the tops of heterolithic channel bodies.

Interpretation.—These sandstone-dominated lithofacies represent sandy bars and bedforms, laminated sand sheets, and downstream- and lateral-accretion macroforms in sandy fluvial channels. The presence of low-angle cross-stratification and convex-up bar surfaces indicates lateral or downslope transport of bar macroforms (e.g., Miall 1985; Bridge 2003). Lenticular upward-fining sandstone bodies are characteristic of deposition within sinuous channels or bars and lateral channel migration across finer-grained floodplain regions (e.g., Miall 1985; Cotter and Driese 1998). Subordinate muddy channel bodies filled with inclined heterolithic strata record lateral migration of point bars within sinuous channels. Locally pervasive rooting indicates colonization by plants during protracted dry periods or following lateral migration or avulsion of channels (e.g., Driese et al. 1997). Similar sandstone facies interpreted as sinuous fluvial channel-bar deposits are reported from Upper Devonian strata in central Pennsylvania (e.g., Sevon 1985; Diemer 1992; Cotter and Driese 1998) and adjacent parts of New York (Bridge and Gordon 1985; Gordon and Bridge 1987; Willis and Bridge 1988; Bridge 1988).

Floodplain Facies Association

Description.—Mudrock and sheet sandstone deposits comprise successions < 5 m thick to > 25 m thick. The majority of red mudrocks are red mudstone and siltstone that extend laterally across the outcrop extent for tens to > 100 m. Most individual beds have even thicknesses with non-erosive basal contacts (Fig. 7A). Mudrocks include horizons with distinct relict bedding as well as massive units with mudstone aggregates composed of subangular blocky peds. Mudrocks exhibit downward bifurcating reduction halos that are locally micritic (rhizoliths) (Fig. 5H),

TABLE 1.—*Macrofossil fauna identified from Upper Devonian Catskill Formation strata in the Blossburg-Covington section*

- Animalia
  - Mollusca
    - Bivalvia
      - Unionida
        - Archanodontidae
          - *Archanodon catskillensis* (Vanuxem)
  - Vertebrata
    - Placodermi
      - Antiarcha
        - Bothriolepididae
          - *Bothriolepis* sp. (Leidy)
      - Arthrodira
        - Phyllolepididae
          - *Phyllolepis thomsoni* (Long and Daeschler)
    - Acanthodii
      - Climatiiformes
        - Indet
    - Sarcopterygii
      - Dipnomorpha
        - Dipnoi
          - Indet.
          - Porolepiformes
            - *Holoptychius* sp.(Agassiz)
      - Tetrapodomorpha
        - 'Osteolepiformes'
          - Tristichopteridae
            - *Langlieria radiatus* (Newberry)
          - Rhizodontidae
            - *Sauripterus taylori* (Hall)

TABLE 2.—*Macrofossil assemblages, fossil taphonomy, and sedimentology of fossil-bearing Upper Devonian Catskill Formation strata in the Blossburg-Covington section.*

Meters above base of section	Fossil assemblage	Fossil taphonomy	Mean bed thickness	Maximum outsized clast size	Mean sediment grain size	Sediment grading	Outsized mudstone/caliche clasts	Rootlets cross-cutting deposit	Additional observations	Inferred depositional setting
240 m	*Bothriolepis, Holoptychius*	Disarticulated, highly abraded, fragmentary	6 cm	1.5 cm	Fine sand	Normal	Present	Not evident	Cross-stratified sandstone	Fluvial channel/bar
236 m	*Bothriolepis, Holoptychius*	Disarticulated, highly abraded, fragmentary	15 cm	2 cm	Upper fine sand	Normal	Present	Not evident	Lag above scour grading into upward fining succession	Fluvial channel/bar
230.5 m	*Bothriolepis, Holoptychius*	Disarticulated, highly abraded, fragmentary	30 cm	2 cm	Upper fine sand	None	Present	Not evident	Sandstone grading into upward fining succession	Fluvial channel/bar
230 m	*Bothriolepis, Phyllolepis, Holoptychius*	Disarticulated, abraded, fragmentary	12 cm	7 cm	Upper fine sand	None	Present	Not evident	Abundant plant fragments	Fluvial channel/bar
111m	*Bothriolepis, Holoptychius*	Disarticulated, highly abraded, fragmentary	3.5 cm	<1 cm	Fine sand	None	Present	Present	Sharp base and top, mudstone drape	Floodplain crevasse splay
110 m	*Bothriolepis, Holoptychius*	Disarticulated, abraded, fragmentary	7 cm	6 cm	Fine sand	None	Present	Present	Sharp base and top, mudstone drape	Floodplain crevasse splay
106 m	*Bothriolepis, Holoptychius, Langlieria*	Disarticulated, abraded, fragmentary	8 cm	6 cm	Fine sand	None	Present	Present	Sharp base and top, mudstone drape	Channel-margin levee
90 m	*Bothriolepis, Holoptychius*	Disarticulated, highly abraded, fragmentary	15 cm	<1 cm	Fine sand	None	Present	Not evident	Inclined heterolithic succession	Fluvial channel/bar
80 m	*Bothriolepis, Holoptychius*	Disarticulated to articulated, unabraded, entire plates and scales	8 cm	9 cm	Very fine to lower fine sand and silt	None	Not evident	Present	Discrete <5 cm thick bedding plane; siltstone overlies fine grained sandstone	Floodplain crevasse splay
75 m	*Bothriolepis, Holoptychius, Phyllolepis*	Disarticulated, highly abraded, fragmentary	7 cm	<1 cm	Upper fine sand	Normal	Present	Not evident	Sandstone grading into upward fining succession	Fluvial channel/bar
70 m	*Bothriolepis, Holoptychius*	Disarticulated, highly abraded, fragmentary	5 cm	<1 cm	Very fine sand and silt	None	Present	Not evident	Lag above scour grading into upward fining succession	Fluvial channel/bar
53 m	*Bothriolepis, Phyllolepis*	Disarticulated, highly abraded, fragmentary	31 cm	3 cm	Fine sand	None	Present	Not evident	Sandstone grading up into upward fining succession	Fluvial channel/bar
47 m	*Bothriolepis, Phyllolepis, Holoptychius, Sauripterus*	Disarticulated, highly abraded, fragmentary	80 cm	4 cm	Fine sand	Normal	Present	Not evident	Sandstone grades up into upward fining succession	Fluvial channel/bar
45.5 m	*Bothriolepis, Holoptychius*	Disarticulated, highly abraded, fragmentary	21 m	2 cm	Very fine sand and silt	None	Present	Not evident	Lag above scour grading into upward fining succession	Fluvial channel/bar
44 m	*Archanodon, Bothriolepis, Holoptychius, Langlieria*	Disarticulated, highly abraded to abraded, fragmentary	150 cm	10 cm	Very fine sand	Normal	Present	Not evident	Four distinct fossiliferous sandstones	Fluvial channel/bar
35 m	*Bothriolepis, Phyllolepis, Holoptychius, Langlieria*	Disarticulated, highly abraded, fragmentary	11 cm	3 cm	Very fine to lower fine sand	None	Present	Not evident	Sharp base and top, mudstone drape	Floodplain crevasse splay
30 m	*Bothriolepis, Holoptychius, Langlieria*	Disarticulated, highly abraded, fragmentary	9 cm	3 cm	Very fine to lower fine sand	None	Present	Present	Sharp base and top, mudstone drape	Floodplain crevasse splay
24 m	*Bothriolepis, Holoptychius*	Disarticulated, highly abraded, fragmentary	3-9 cm	2 cm	Very fine sand	None	Present	Not evident	Sharp base and top, mudstone drape	Floodplain crevasse splay
22 m	*Bothriolepis, Holoptychius*	Disarticulated, highly abraded, fragmentary	1.5-2 cm	2 cm	Very fine to lower fine sand	None	Present	Present	Lag above scour grading into upward fining succession	Channel/bar
14b m*	*Holoptychius*	Articulated, unabraded, entire scales	1.5-2 cm	10 cm	Mud and very fine sand	None	Not evident	Not evident	Mudstone overlies sharp-topped sandstone	Muddy abandoned channel fill
14a m*	*Bothriolepis, Holoptychius*	Disarticulated, highly abraded, fragmentary	1.5-2 cm	<1 cm	Very fine sand	None	Abundant	Present	Mudstone drape	Fluvial channel-margin levee
13 m	*Bothriolepis, Holoptychius*, Dipnoi	Disarticulated to articulated, unabraded, entire plates and scales	0.5-1 cm	9 cm	Very fine to fine sand	None	Not evident	Present	Sharp base and top, mudstone drape	Floodplain crevasse splay

* 14a and 14b are distinct fossiliferous horizons within the same strata separated by ~ 30 m

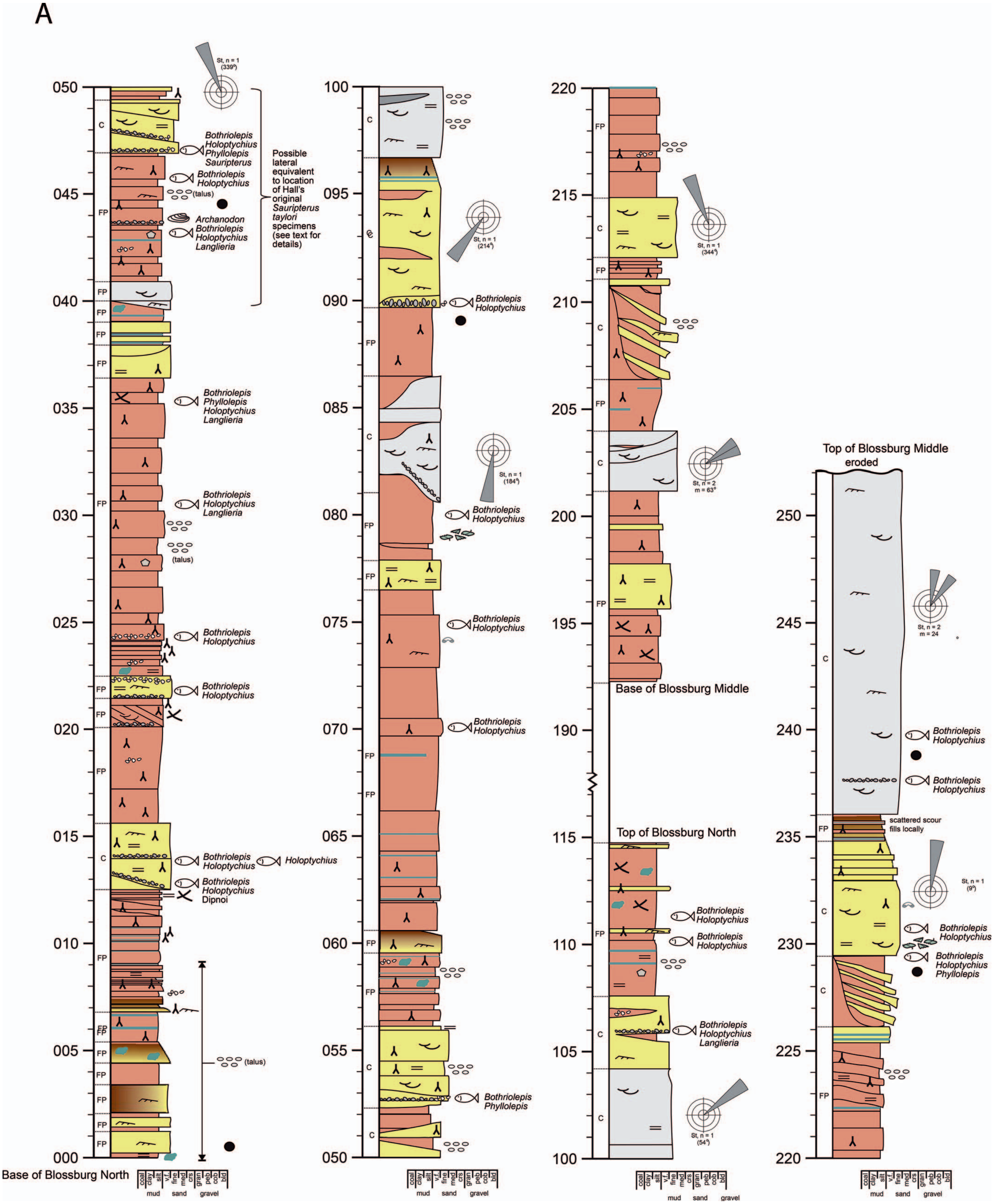

FIG. 4.—Stratigraphy of study area. **A**) Measured stratigraphic section. **B**) Stratigraphic section legend. Sedimentological features, fossil assemblages, and palynomorph samples at each horizon are shown. Adapted from Slane and Rygel (2009). Refer to Figure 1 for section location. GPS coordinates: base of Blossburg North = 41°43′37.8″N 77°04′35.8″W, top of Blossburg Middle = 41°41′29.1″N 77°04′27.1″W. Note generally north-directed paleoflow measurements that deviate from generally west-directed regional paleoflow (Fig. 2). We interpret this deviation as a local meander in the fluvial system as opposed to a north-south axial system.

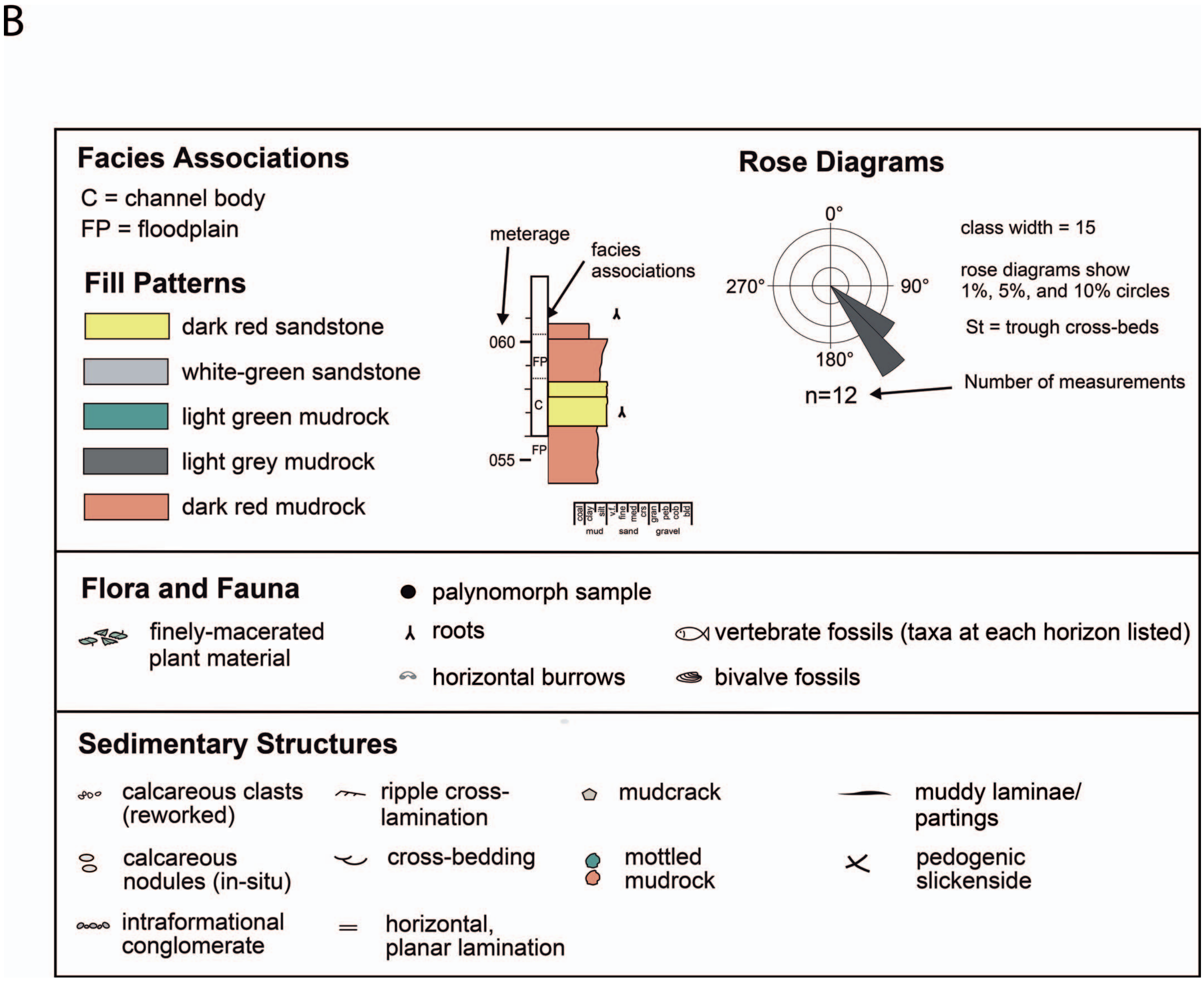

FIG. 4.—Continued.

downward bifurcating clay-lined rootlets (Fig. 5I), desiccation cracks (Fig. 5J), *in situ* carbonate nodules, and smooth curving slickenside surfaces oriented $> 20°$ from bedding. Drab, irregular-shaped mottles, including patches of oxidized (red-yellow) or reduced (gray-green) colors, occur locally. Mudrocks show abundant bioturbation locally, including abundant traces of *Beaconites antarcticus*, rare traces of *Hyperoeuthys teichonomos*, and many unidentified invertebrate traces. Scattered organic remains, sparse green to greenish gray mudstone and claystone horizons less than 0.2 m thick (top of Fig. 5H), and diffuse, irregular mottles (Fig. 5H) occur among the red mudrocks.

Commonly interbedded with the red mudrocks are sandstone sheets. These beds typically extend laterally for several tens of meters; their complete extent is typically unclear due to limited outcrop exposure. Individual sheets range from < 0.25 m to > 2 m thick. Bases are sharp and flat to locally undulating bases; tops are flat to locally convex-upward. Most individual beds fine upwards from fine-grained sandstone to siltstone. Normal grading is common; some beds grade upward from intraformational conglomerate with granule- to pebble-sized reworked carbonate nodules and mud-chip rip-ups, and in some cases, vertebrate macrofossil fragments. Internally, most sheet sandstones are massive but horizontal laminae and ripple cross-stratification occur locally. The upper portion of many beds are overlain by mud drapes and cross-cut by desiccation cracks and/or rootlets. Sheet sandstones range from isolated occurrences to clusters of numerous closely spaced beds that form sandstone-rich successions separated by thin mudrock horizons. Subordinate lenticular sandstones with irregular erosive bases occur in association with the sheet sandstone and mudrock facies; internally, these sandstones are massive but horizontal laminae occur locally.

Interpretation.—Mudrocks and associated sheet sandstones are interpreted to represent repeated episodes of floodplain aggradation via overbank deposition from overtopped or breached channels alternating with nondeposition and pedogenesis. Mudrocks are interpreted to reflect deposition via weak traction currents and suspension fallout during waning flow of overbank flooding. Infilled desiccation cracks and subangular blocky peds indicate repeated wetting and drying of previously deposited muds (e.g., Retallack 1988; Driese et al. 1992). Abundant clay-lined rootlets and less common root-like rhizoliths traces record plant

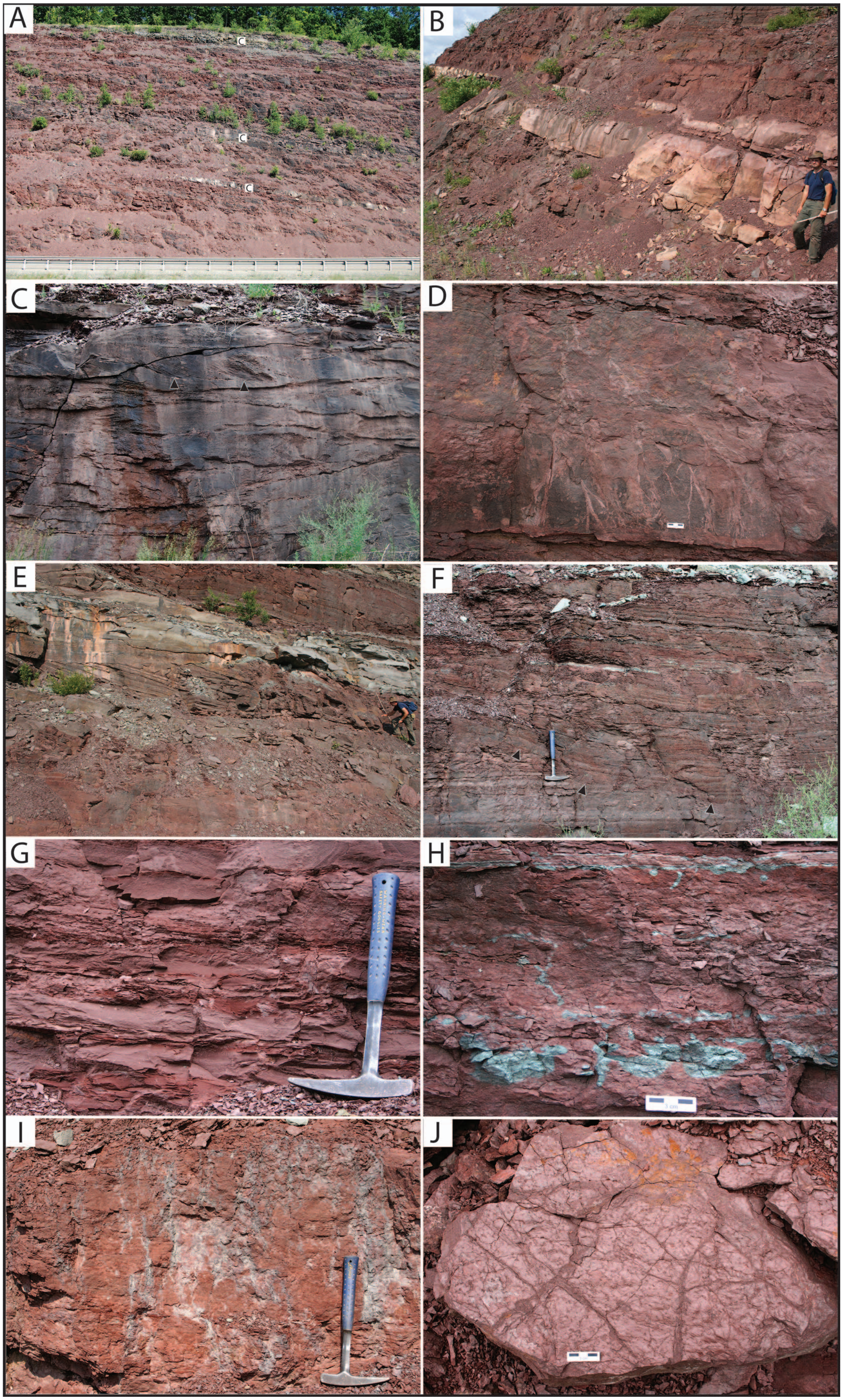

FIG. 5.—Key lithofacies and sedimentary structures in channel-bar and floodplain lithofacies. **A**) Interbedded red floodplain mudrocks and broadly lenticular channel-bar sandstone packages (C) from the lower ~ 110 m the measured section. **B**) Channel-bar sandstone encased in red floodplain mudrock. **C**–**F**) Lithofacies and

TABLE 3.—*Distribution data for palynomorphs from the Catskill and Huntley Mountain formations by sample with associated palynozone of each sample.*

Palynology sample number	Outcrop name	Formation	Meters above base of Catskill Fm.	*Ancyrospora? sp*	*Aneurospora greggsii?*	*Apiculiretusispora fructicosa?*	*Auroraspora macra*	*Grandispora cornuta?*	*Knoxisporites literatus/triangularis*	*Retispora flexuosa*	*Rugospora flexuosa*	*Small thin 32 um echinate-verrucate*	*Spore indeterminate*	*Vallatisporites hystricosus*	*Verrucosisporites nitidus*	*Calamospora? sp*	*Cyclogranisporites?*	*Grandispora echinata*	*Retusotriletes sp*	*Apiculiretusispora? sp indet*	*Auroraspora sp?*	*Geminospora? sp indet*	*Grandispora cornuta? very dark opaque*	*Knoxisporites? sp indet*	*Punctatisporites spp*	*Retusotriletes crassus*	*Vallatisporites? sp indet*	*Verrucosisporites sp*	*Grandispora echinata?*	*Retispora? sp indet fragment*	*Rugospora flexuosa?*	*Vallatisporites pusillites?*	*Punctatisporites cf hannibalensis*	*Dibolisporites cf aritarchus*	*Grandispora cornuta*	*Hystricosporites cf multifurcatus? opaque*	*Aneurospora? sp indet opaque*	*Diducites versabilis*	*Geminspora-Aneurospora Traverse 2003*	*Hystrichosporites cf porcatus?*	*Retusotriletes? tetrad*	*Rugospora cf minuta*	*Retusotriletes incohatus*	**Palynozone**
20	Bloss West	Huntley Mtn.	470	1	20	3	1	1	2	25	27	3	9	8	1																													LN
19	Bloss West	Huntley Mtn.	470		8	8	1	1	2	8	49	1	9	3	2	1	1	1	7																									LN
17	Bloss South	Huntley Mtn.	405		1						28		38	1			1	1	9	3	3	2	2	1	6	2	3	1																VH
16	Bloss South	Huntley Mtn.	382		2	1	4	1					33						7		1			1	1	2			1	1	1	1												VH
15	Bloss Middle	Catskill	240		2		6	1			17		14					3	9		3				17	24							5											in COR
14	Bloss Middle	Catskill	230			3	2	1					64						7		1	1	5	1	2	7		1	2					1	2	2								in COR
9	Bloss North	Catskill	90																																									⇅
6	Bloss North	Catskill	44																																									⇅
2	Bloss North	Catskill	1		2								42						6	3			1			1										2	3	3	5	1	1	1		Base COR
1	Bloss North	Catskill	1		1		2						62						8	8	1		1			4										2		3		3			1	Base COR

Note: Refer to Figure 1 for outcrop locations and Figure 11 for explanation of palynozone abbreviations.

colonization following mud deposition (Driese and Mora 1993; Driese et al. 1997). Curved slickenside surfaces are interpreted to have formed in paleosols by repeated movements along shear planes associated with shrinking and swelling of clay-rich deposits during episodic water infiltration and evaporation (e.g., Yaalon and Kalmar 1978; Gray and Nickelsen 1989). The presence of micritic rhizoliths and carbonate nodules reflect pedogenic carbonate accumulation (Driese and Mora 1993; Daniels 2003). The presence of scattered organic remains, green mottles, and laminated mudstone deposits that lack evidence for pedogenic alteration is consistent with subaqueous deposition in ponded water or episodic rises in the water table rise during wet periods (e.g., Calder et al. 2005). Palynomorph taxa recovered from sampled floodplain mudrocks indicate the presence of ponded water swamp/wetland environments (discussed below in Paleoenvironmental Variation), although palynomorphs may have been transported from those environments.

Thin sheet sandstones are interpreted as crevasse-splays deposited adjacent to fluvial channels/bars. Individual deposits formed when floodwaters breached the levee of a channel and deposited lobate sand-silt sheets on the adjacent floodplain (e.g., Tooth 2005; Arnaud-Fassetta 2013; Colombera et al. 2013). The tabular bedding of horizontally stratified and ripple cross-stratified sandstone sheets and overlying mudstone suggest crevasse-splay deposition as a result of distal, waning flow (e.g., Miall 1996; Bridge 2006). The sharp and locally erosional bed bases indicate relatively high-velocity flow immediately following crevassing when sediment-laden waters entered the floodplain, whereas the diffuse tops suggest a transition to deposition from suspension when the floodplain was inundated and suspended-load sediment formed conformable drapes of mud (e.g., Hampton and Horton 2007; Jones and Hajek 2007; Nichols and Fisher 2007; Gulliford et al. 2014; van Toorenenburg et al. 2016; Burns et al. 2017). Minor lenticular sandstone bodies within the sandstone sheet successions are interpreted as crevasse-splay feeder channels that focused flow near channel breaches (e.g., Arnaud-Fassetta 2013; Ford and Pyles 2014) or distributary channels that formed when fluvial systems debouched into floodplains during avulsions (e.g., Smith et al. 1989; Slingerland and Smith 2004). Similar mudstone and sheet sandstone facies interpreted as fluvial floodplain deposits are reported from Upper Devonian strata in central Pennsylvania (e.g., Sevon 1985; Driese et al. 1997; Cotter and Driese 1998) and adjacent parts of New York (e.g., Bridge and Gordon 1985; Gordon and Bridge 1987; Willis and Bridge 1988).

PALEONTOLOGIC RESULTS

Macrofauna

A total of 22 separate fossiliferous horizons spanning ~ 240 m of stratigraphic thickness of the Catskill Formation (Fig. 4A) yielded invertebrate and vertebrate taxa listed in Table 1 and Figure 4. Table 2 summarizes the taphonomic and sedimentologic features of each fossil horizon. Body fossils of invertebrate taxa are limited to clusters of post-mortem, hydrodynamically transported *Archanodon catskillensis* bivalve shell impressions (Figs. 4, 6, 7). Most vertebrate macrofossils are preserved as disarticulated and abraded plates, scales, and bone fragments that accumulated at or near the base of sandy channel-bar facies (Table 2). Articulated, unabraded remains of vertebrates are less common and occur in siltstone and very fine-grained sandstones preserved in floodplain facies and muddy, abandoned channel-fills (Table 2, Fig. 6). Vertebrate taxa collected as part of this project include at least two genera of "placoderms" (*Bothriolepis* and *Phyllolepis*), isolated spines and scales of an unidentified acanthodian, several taxa of sarcopterygian fishes, including an isolated tooth plate of a lungfish (Dipnoi indet.), isolated and articulated scales of *Holoptychius* sp., an isolated scale of *Sauripterus taylori,* and isolated scales and dermal skeletal elements of *Langlieria radiatus*. Fossil prospecting in overlying Huntley Mountain Formation strata yielded a few

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sedimentary structures in channel-bar lithofacies: **C**) Cross-stratification (triangles) and in channel-bar sandstone; **D**) Rootlets cross-cutting channel-bar sandstone; **E**) Inclined heterolithic strata (center) between gray channel-bar sandstone (above) and red mudrock (below); and **F**) Muddy channel fill comprised of heterolithic strata above a scour (triangles). **G**–**J**) Key lithofacies and sedimentary structures in floodplain lithofacies: **G**) Platy red siltstone and mudstone; **H**) Diffuse green drab halos/mottling in red blocky mudrock; **I**) Clay-lined rootlets bifurcating downward through red mudrock; **J**) Desiccation cracks in red mudrock.

FIG. 6.—Photographs of taphofacies preserving vertebrate fossils in Catskill Formation strata in the Blossburg-Covington section. **A**–**D**)Disarticulated, abraded and fragmentary *Bothriolepis* sp. fossils (outsized white clasts including concave and convex clasts) deposited as streamflow bedload along channel bottoms and bars. Fossils

TABLE 4.—*Faunal assemblage variation within the Upper Devonian Catskill Formation in the Blossburg-Covington section and other locations.*

Blossburg	Powys	Mill Creek	Tioga	Trout Run North	Lower Steam Valley	Upper Steam Valley	Red Hill
Archanodon	*Archanodon*	*Archanodon*	*Lingula*	Arthrodire	*Archanodon*	*Phyllolepis*	*Phyllolepis*
Bothriolepis	*Bothriolepis*	*Bothriolepis*	*Bothriolepis*	*Gyracanthus*	*Bothriolepis*	*Groenlandaspis*	*Groenlandaspis*
Phyllolepis	*Phyllolepis*	*Groenlandaspis*	*Phyllolepis*	*Holoptychius*	*Phyllolepis*	*Turrisaspis*	*Turrisaspis*
Acanthodii	Acanthodii	*Holoptychius*	Arthrodire	Megalicthyid	*Holoptychius*	*Gyracanthus*	*Ctenacanthus*
Dipnoi	Dipnoi		*Dunkleosteus*	whatcheerid	tristichopterid	*Holoptychius*	*Ageleodus*
Holoptychius	*Holoptychius*		*Apatorhynchus*	like-tetrapod		Megalicthyid	*Limnomis*
Langlieria	*Langlieria*		*Holoptychius*			*Eusthenodon*	Dipnoi
Sauripterus	Megalicthyid		*Langlieria*				Rhizodontid
	Sauripterus						Megalicthyid
							Hyneria
							Hynerpeton
							Densignathus
							whatcheerid
							like-tetrapod
Number of fossil horizons							
22	unknown	1	7	1	5	1	1

Note: faunal lists and number of fossil horizons derived from present study at Blossburg, Broussard et al. (2018) (Mill Creek, Trout Run North, Lower and Upper Steam Valley), Friedman and Daeschler (2006) (Powys and Tioga), Cressler et al. (2010) (Red Hill), and Downs and Daeschler (2020) (Powys and Red Hill).

unidentifiable vertebrate bony fragments. However, one isolated scale of a megalicthyid sarcopterygian was identified.

A dense accumulation of *A. catskillensis* decalcified shell impressions of various lengths and orientations occur at the base of a channel-bar sandstone at 44 m in Blossburg North (Fig. 4), suggesting individual shells were transported as post-mortem bedload and subsequently buried. Similar types of preservational modes of *A. catskillensis* occur at other Catskill Formation sites in Pennsylvania and Upper Devonian terrestrial and marginal marine units in New York (Bridge et al. 1986; Chamberlain et al. 2004; Remington et al. 2008; Broussard et al. 2018).

Two taxa of "placoderms" were identified in the Blossburg-Covington outcrops during this study. Remains of the antiarch *Bothriolepis* sp. were present within 21 of 22 fossiliferous horizons. *Bothriolepis* is commonly recorded from Catskill Formation outcrops in Pennsylvania (Table 4) and other Upper Devonian marginal marine and freshwater sites in North America and Europe (Cloutier et al. 2011; Daeschler and Cressler 2011; Downs et al. 2011; Lukševičs et al. 2012). At the Blossburg-Covington outcrops, most *Bothriolepis* are preserved as disarticulated, abraded fragments. However, several siltstone slabs were recovered from the Blossburg-Covington section that contain fully articulated, unabraded adult *Bothriolepis* sp. (Fig. 8). A total of 31 adult individuals were identified on ten different siltstone slabs collected from a single horizon at ~ 80 m (Fig. 4) during initial road construction in 2004. The lithology of these slabs and the taphonomy of the individuals that comprise this *Bothriolepis* death assemblage indicate floodplain deposition of these *Bothriolepis* individuals (Table 2) that were likely living near their final site of deposition. The lack of strong preferred orientation of individuals on two of these death assemblage blocks and the dominance of mud-sized grains indicates a low-energy depositional environment (Fig. 8). Additionally, numerous siltstone blocks containing articulated juvenile *Bothriolepis* were collected from talus slopes created during initial road construction. Based on lithology of these siltstone blocks, orientation of the bodies, and the preservation (articulated, unabraded) of the fragile juvenile *Bothriolepis*, these individuals were probably living in floodplain ponds before gentle burial by sediments (Downs et al. 2011).

Isolated, fragmentary, plates of phyllolepid "placoderms" were also observed during this study. Long and Daeschler (2013) described *Phyllolepis thomsoni* from a siltstone block collected in talus during road construction at the Blossburg-Covington outcrops. According to Long and Daeschler (2013), the lithology and location of the specimen indicates that it came from low in the section where several isolated phyllolepid plates were identified during the present study.

A fine-grained sandstone block containing isolated scales and several spines of an unidentified acanthodian was collected from the lower part of the Catskill Formation at the Blossburg North outcrop prior to our study. These specimens are similar in appearance to isolated spines and scales collected at the Powys site (Table 4) (Davis et al. 2004) located ~ 50 km south of the Blossburg-Covington section. The Blossburg-Covington and

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occur in sandstone and conglomerate that range from thick, ungraded to normal graded beds (A, B) to thin, normal graded beds (C, D). **E**–**J**) Taphofacies deposited by overbank flooding on levees and proximal floodplains consist of mixed sandstone and conglomerate that exhibit sharp bed bases and poorly (E) to well-developed normal grading (F). Fossils are preserved throughout individual beds (E, F) or along thin, discrete layers (G–J) and range from disarticulated (E, F) to articulated (H, I) and abraded (E, F) to unabraded (G–J).

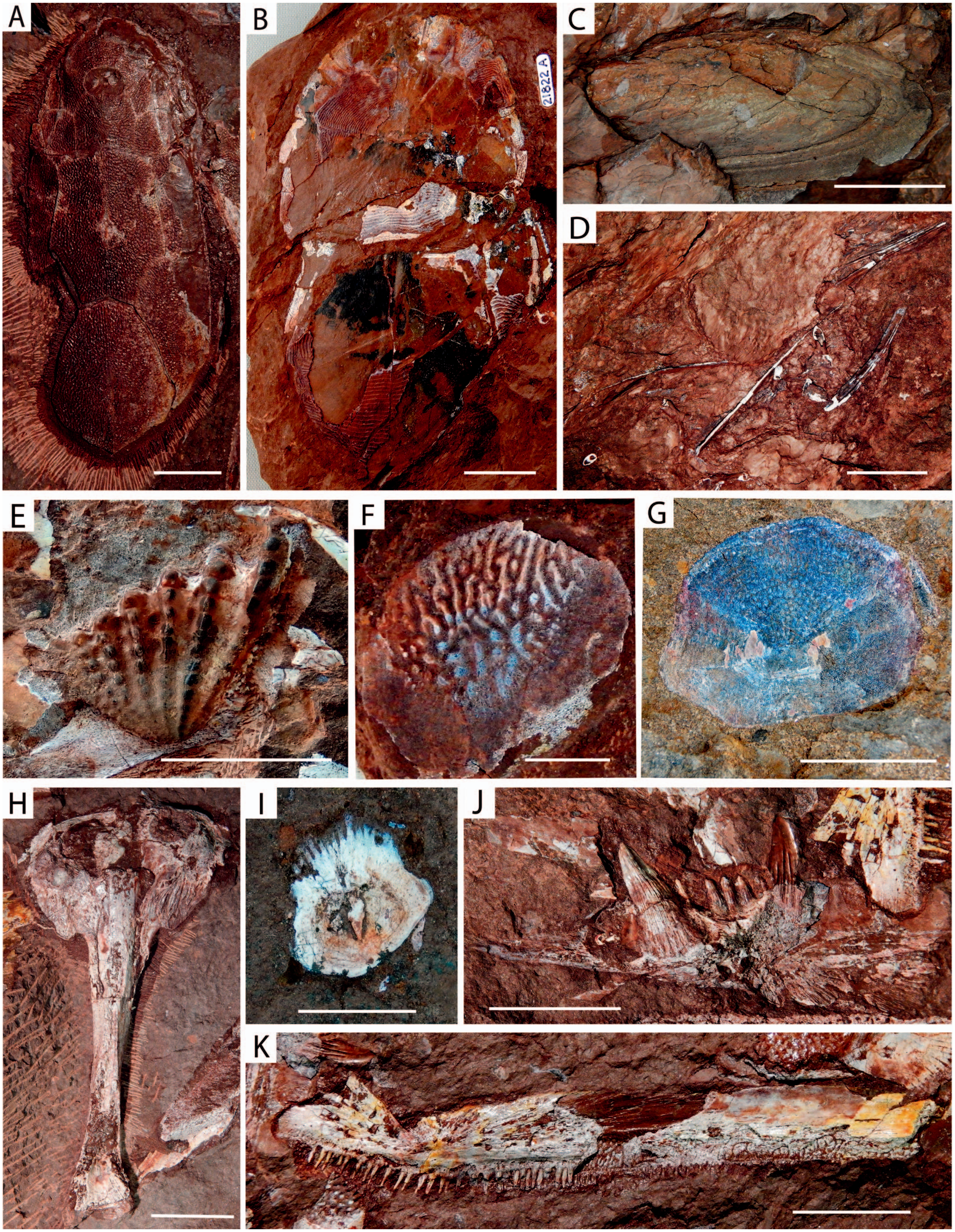

FIG. 7.—Representative fossil elements from the Blossburg-Covington section. **A**) Dorsal view of an adult *Bothriolepis* sp. from ~ 80 m (ANSP 21818). **B**) Dorsal view of *Phyllolepis thomsoni* (ANSP 21822); stratigraphic position low in section. **C**) Internal mold of decalcified shell of *Archanodon catskillensis* from 44 m. **D**) Fin spines of

Powys spines are broadly comparable to marine taxa such as *Howittacanthus* (Long 1986) and *Homalocanthus* (Cloutier et al. 2011). However, with such limited material, it is not possible to diagnose the acanthodian spines and scales at this time.

Remains of four sarcopterygian taxa were identified from Catskill Formation strata in the Blossburg-Covington section (Fig. 7, Table 1), including an isolated dipnoan tooth plate from 13 m that is similar in appearance to other isolated dipnoan tooth plates collected in the Catskill Formation (Friedman and Daeschler 2006). Isolated and articulated scales of the porolepiform *Holoptychius* sp. were identified in all 22 fossil horizons in the section. *Holoptychius* sp. are reported from many other Catskill outcrops except Red Hill (Table 4; Cressler et al. 2010; Daeschler and Cressler 2011; Broussard et al. 2018). Isolated scales of *Langlieria radiatus* were identified in several horizons during this study (Fig. 4). Daeschler et al. (2019) assigned isolated scales and well-preserved skull material of the tristichopterid sarcopterygian collected previously from ~ 35 m to *L. radiatus*. One isolated scale of the rhizodontid *Sauripterus taylori* was identified during the present study at 46 m. Hall (1843) described *S. taylori* from isolated scales and an articulated right pectoral fin including pectoral girdle elements in a fine- to medium-grained red-gray sandstone block from a railroad cut near Blossburg (Leviton and Aldrich 1992). Specimens of *Bothriolepis*, *Holoptychius*, and cf. *Eusthenodon* were also collected at or very near this railroad cut along with the original *S. taylori* specimens (Davis et al. 2004). Davis et al. (2004) located the site that produced Hall's *S. taylori* and other vertebrate specimens less than 1 km west of the Blossburg North and Middle outcrops. Based on the orientation of strata and satellite imagery of the Blossburg-Covington section, it is likely that Hall's original site is stratigraphically equivalent to ~ 40–50 m in the Blossburg North outcrop (Fig. 4). This 10 m thick interval of the Blossburg North outcrop shares lithological as well as paleontological similarities to the original block containing *S. taylori*, which is deposited at the American Museum of Natural History (AMNH 3341).

Trace Fossils

Catskill Formation strata at the Blossburg-Covington section have yielded several different types of trace fossils. Invertebrate burrows include *Beaconites antarcticus* (Fig. 9A, 9B) which were most commonly found low in the Blossburg-Covington section (Fig. 4). *Beaconites antarcticus* has also been identified from several Catskill Formation outcrops in the study region, including Powys and Steam Valley (Fig. 1) (Jones 2011). Burrow casts include horizontal branching invertebrate burrows interpreted as feeding traces (Fig. 9C, 9D). Putative "lungfish estivation" burrows (*Hyperoeuthys teichonomos*) were also identified from float blocks and at several locations in the Blossburg-Covington section (Fig. 9F) adding to the list of outcrops known to yield such traces (Woodrow and Fletcher 1968; Jones 2011).

An arthropod trace fossil collected during this study as float at ~ 14 m in the Blossburg-Covington section represents a type of arthropod trackway that has been previously unreported from the Catskill Formation. The single trackway occurs on a small slab of mudrock ~ 6 cm long and ~ 3 cm wide (Fig. 9E; ANSP IP 81679), and comprises a series of irregular, slightly oblong or chevron-shaped tracks oriented along a continuous medial impression. The general track pattern is most suggestive of a chelicerate maker (Braddy 1995). Upper Devonian chelicerate ichnotaxa in this region include *Kouphichnium* (Caster 1938), typically ascribed to xiphosurans, and *Palmichnium* (Richter 1954), usually ascribed to a scorpion or eurypterid trackmaker. The new trackway more closely resembles *Palmichnium*, which is characterized by an en échelon track pattern comprising bifid-shaped tracks and a continuous medial dragline (Richter 1954; Braddy and Milner 1998), and we assign the trackway to that ichnogenus. Eurypterid body fossils (*Hallipterus excelsior*; Tetlie 2008) and putative scorpion fragments (Shear 2000) have been found previously in the Catskill Formation of Pennsylvania and Upper Devonian fluvial strata of New York. In the new example of *Palmichnium* sp., the medial dragline could represent telson drag and thus a eurypterid maker. In this case, the absence of paddle traces would suggest that the trackway was made by a walking-legged stylonurid; for example, *Hallipterus*.

Palynomorphs and Macroflora

Plant macrofossils recovered from Catskill Formation strata in the Blossburg-Covington section include abundant rootlets low in the section and abundant macerated stems at 80 m and 230 m (Fig. 4). Although well-preserved plant remains of several taxa are commonly found elsewhere in Catskill Formation strata (Daeschler and Cressler 2011), no identifiable plant macrofossils were recovered from the Blossburg-Covington section during this study. However, palynomorphs were recovered from eight of 10 mudstones sampled between 1 m and 240 m in the section (solid circles on Fig. 4). Organic residues recovered from the samples consist of sparse to abundant spores and angular woody fragments; no marine palynomorphs (acritarchs or chitinozoans) were observed in the sampled mudrocks. Eight samples yielded sufficient palynomorphs to determine a succession of late to latest Famennian (Late Devonian) ages. Table 3 summarizes the palynomorph taxa recovered from each sample. Figure 10 depicts representative images of age-diagnostic palynomorph taxa.

Four samples from the Catskill Formation in the Blossburg-Covington section yielded palynomorphs that are restricted to the COR subzone of the *Diducites versabilis-Grandispora cornuta* (VCo) palynomorph (Fig. 11, Table 3). Based on the co-occurrence of *Diducites versabilis* and *Grandispora cornuta,* Catskill Formation strata exposed ~ 1 m above the base of the section are restricted to the COR subzone. Higgs et al. (2013) show an acme zone of *Diducites versabilis* at the base of COR subzone (mid-late Famennian). Catskill Formation strata exposed 230–240 m above the base of the section also represent subzone COR judging from the presence of *Grandispora cornuta* and the absence of *Retispora lepidophyta* and *Knoxisporites literatus/triangularis* and *Vallatisporites hystricosus*.

Four samples from the overlying Huntley Mountain Formation in the Blossburg-Covington section (Blossburg South and Blossburg West on Fig. 1B) yielded palynomorphs restricted to the VH (*Apiculiretusispora verrucosa-Vallatisporites hystricosus)* and LL (*Retispora lepidophyta-Knoxisporites literatus)* palynozones (Fig. 11, Table 3). Samples from 382 and 485 m above the base of the section represent palynomorph zone VH based on the presence of *Vallatisporites hystricosus, Vallatisporites pusillites*?, *Grandispora cornuta*?, and *Rugospora flexuosa* and the absence of *Retispora lepidophyta* and *Knoxisporites literatus/triangularis*. Samples from ~ 470 m above the base of the section are diagnostic of palynomorph zone LL based on the co-occurrence of *Retispora lepidophyta* and *Knoxisporites literatus/triangularis*.

Collectively, these palynological data indicate that Catskill Formation strata in the Blossburg-Covington section accumulated ca. 362 to 361.8 Ma during the late Famennian stage of the Late Devonian, whereas the overlying Huntley Mountain Formation was deposited ca. 361.8 to 359.8 Ma during the late to latest Famennian stage of the Late Devonian (Fig. 11).

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Acanthodii indet.; stratigraphic position low in section (ANSP 23542). **E**) Isolated tooth plate of *Dipnoi* indet. from 13 m (ANSP 25029). **F**) Partial scale of a *Holoptychius* sp. from 22 m (ANSP 25031). **G**) Isolated scale of *Sauripterus taylori* from 46 m (ANSP 25030). **H–K)** Elements of *Langlieria radiatus* from ~ 35 m including articulated vomers and parasphenoid (H, ANSP 21886), isolated scale (I, ANSP 25032), ectopterygoid (J; ANSP 21886), and a right maxilla (K; ANSP 21886). Scale bars = 2 cm except for I = 1 cm.

FIG. 8.—Siltstone slabs that contain multiple articulated adult *Bothriolepis* sp. individuals numbered separately on each slab. **A**) ANSP 21804. **B**) ANSP 21805. Rose diagrams (in increments of 30°) depict orientations of individual bodies on each slab. Note lack of preferred alignment of individual *Bothriolepis*, indicating preservation under low-energy conditions. Scale bars = 5cm. Slabs are from approximately 80 m in the Blossburg-Covington section of the Catskill Formation (see Fig. 4).

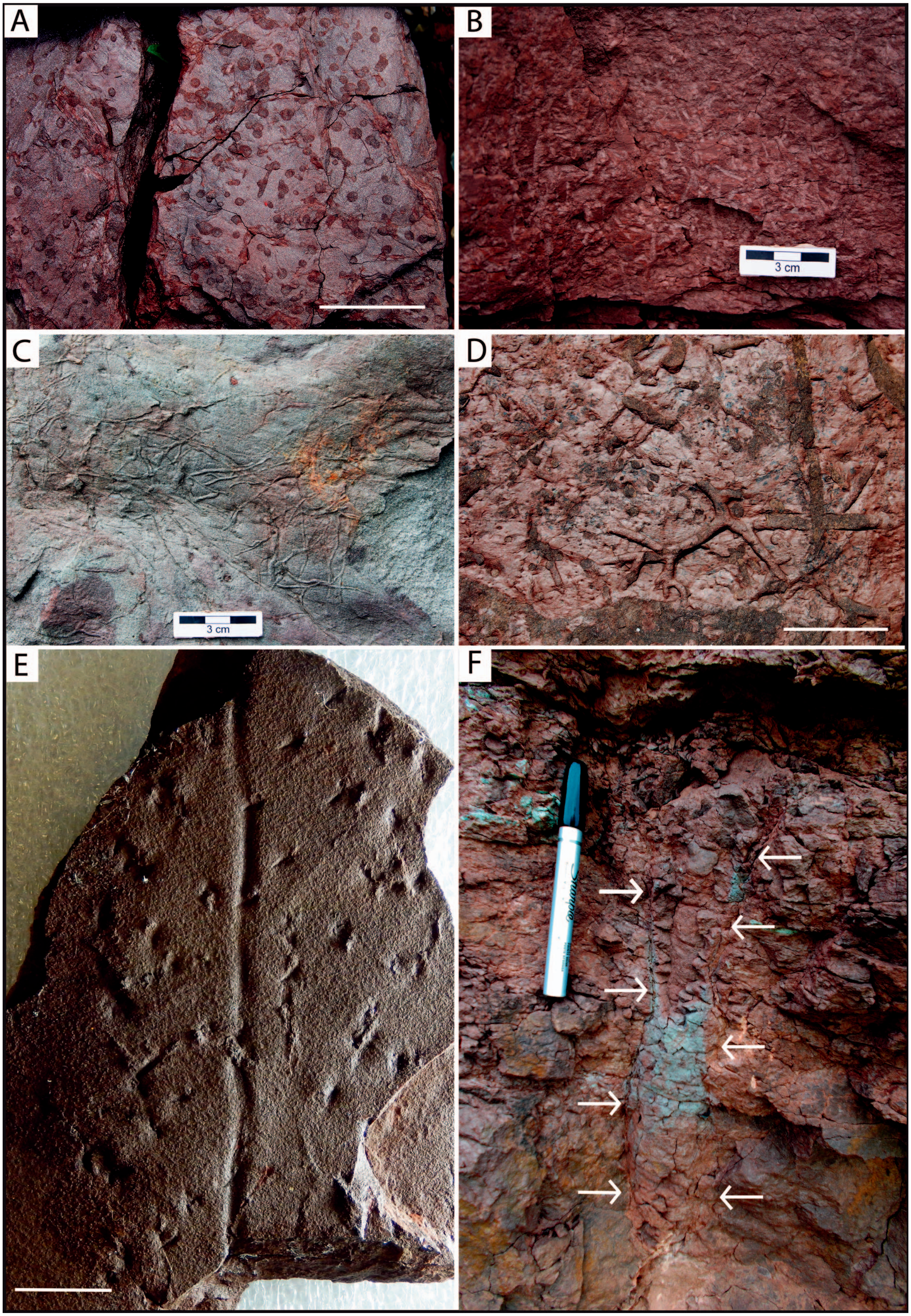

FIG. 9.—Biogenic structures in Catskill Formation strata in the Blossburg-Covington section. **A**, **B**) *Beaconites antarcticus*. **C**, **D**) Unidentified invertebrate horizontal burrows. **E**) Trackway of *Palmichnium* sp. from ~ 14 m (ANSP IP 81679). **F**) Burrow of *Hyperoeuthys teichonomos* with arrows indicating burrow edges. Scale bars = 2 cm.

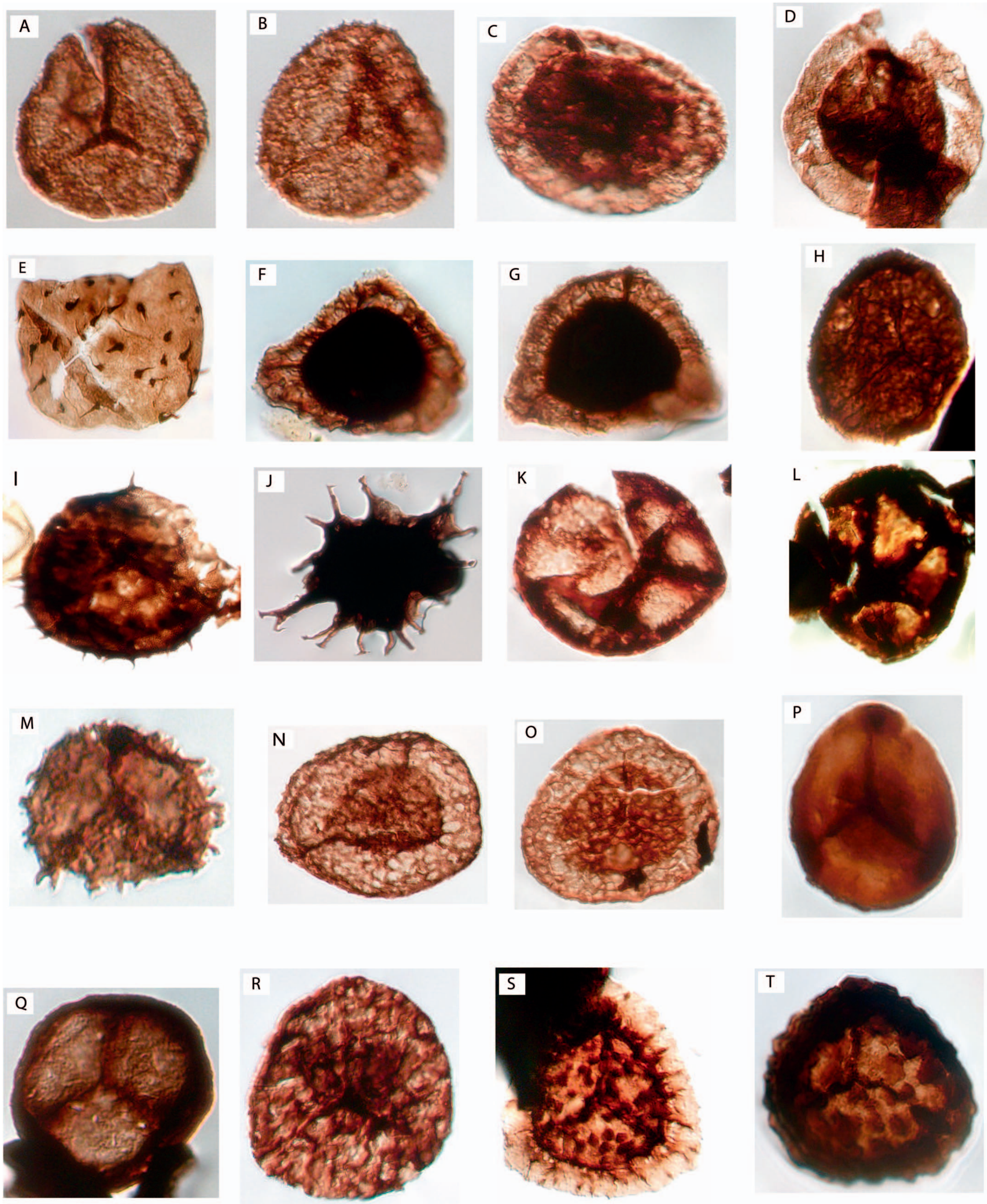

FIG. 10.—Photomicrographs of selected plant palynomorphs from Upper Devonian Catskill Formation (CF) and overlying Huntley Mountain Formation (HMF) at the Blossburg-Covington section. Refer to Figure 3 for stratigraphy, Figure 4A for stratigraphic positions of Catskill Formation samples, and Table 3 for a summary of all

DISCUSSION

Depositional Age

New palynological analyses indicate that samples spanning the exposed stratigraphic thickness of the Catskill Formation in the Blossburg-Covington section accumulated during mid-late Famennian time, ca. 362–361.8 Ma (COR subzone of the VCo palynozone on Fig. 11). Samples from the lower ~ 130 m of the Huntley Mountain Formation indicate deposition during latest Famennian time, ca. 361.8–359.8 Ma (VH and LL palynozones on Fig. 11). Traverse (2003) collected and analyzed eight palynomorph samples from Red Hill, Cammal, and Lower Steam Valley which are located tens of kilometers to the west and south of the Blossburg-Covington section and represent the upper part of the Catskill Formation. Six of the eight samples presented in Traverse (2003) can be restricted to the late Famennian subzone HYS of palynozone VH (Fig. 11) based on the presence of *Vallatisporites hystricosus* and absence of *Retispora lepidophyta* and *Knoxisporites literatus*. The other two samples are broadly palynozone VCo or younger based on the presence of *Rugospora flexuosa*. Catskill Formation outcrops at Cammal and Red Hill are re-interpreted in an updated palynozonation to be restricted to subzone HYS of palynozone VH, (361.0–360.5 ma) and equivalent in age to samples 17-Bloss South HMF 85 and 16-Bloss South HMF 62 from the current study (Fig. 11). The only sample collected from Lower Steam Valley is within palynozone VCo or younger based on the presence of *Rugospora flexuosa*. It also contained a questionable specimen of ?*Knoxisporites literatus,* so the age is possibly as young as palynozone LL. Thus, the limited palynological data suggests that Red Hill and Cammal overlap in age with fluvial strata exposed at Blossburg South mapped as lowermost Huntley Mountain Formation (Figs. 1, 11). Unfortunately, previous palynological samples are not reported within the context of measured stratigraphic sections, preventing regional stratigraphic correlation.

Recently reported detrital geochronological analyses support the previous and new palynological data. $^{40}Ar/^{39}Ar$ ages from detrital muscovite from Catskill Formation sandstone samples at Red Hill, Lower Steam Valley, and Trout Run North (Fig. 1) indicate maximum depositional ages of ca. 362 Ma, ca. 366 Ma, and ca. 376 Ma, respectively (Broussard et al. 2018). The detrital muscovite ages are consistent with the youngest cluster of detrital zircon U-Pb ages (~ 369 Ma) from a sandstone sample from the upper part of the Lock Haven Formation, which directly underlies the Catskill Formation (Fig. 1; Gardner et al. 2018; Gardner 2019). In summary, palynological and detrital geochronological data document late Famennian deposition of Catskill Formation vertebrate-bearing strata in north-central Pennsylvania, ca. 362 to 360.5 Ma (using Walker et al. 2012 time scale).

Paleoenvironmental Variation

This study integrates palynologic, sedimentologic, paleontologic, and taphonomic data to reconstruct the Late Devonian depositional environments preserved in the Blossburg-Covington section of the Catskill Formation in north-central Pennsylvania. Sedimentological analysis shows that macrofossil remains occur in strata interpreted as the deposits of sandy fluvial channel-bar complexes and muddy vegetated floodplains. Floodplains were prone to alternating subaqueous deposition from overbank flooding/crevassing and subaerial exposure and pedogenesis. Sedimentological features indicative of marine processes were not recognized during the present study. Palynomorphs recovered from the Catskill Formation indicate non-marine environments, possibly transitional between downstream swamp margin and swamp environments. *Diducites versabilis* has been linked to swamp environments (Maziane et al. 2002) whereas *Hystricosporites* has morphological features similar to spores of some modern-day aquatic plants (McGregor and Playford 1992). All vertebrate taxa identified during this study have been previously reported from Upper Devonian marginal marine and/or fluvial environments (Sallan and Coates 2010). The recovered invertebrate taxa including *Archanodon* bivalves (Chamberlain et al. 2004) and trace fossils of *Beaconites* and *Hyperoeuthys* are consistent with a terrestrial, fluvial habitat (Jones 2011). The presence of both *Beaconites* and *Hyperoeuthys* burrows low in the Blossburg North outcrop indicates a floodplain depositional environment prone to episodic inundation from overbank flooding (Jones 2011). Additionally, the absence of any hopping (Braddy 1995), push-off (Braddy and Milner 1998), or swimming traces (Vrazo and Ciurca 2018) associated with the new *Palmichnium* arthropod trackway suggests that the likely eurypterid trackmaker was walking in either a very shallow, low-energy sub-aqueous setting or sub-aerial environment, such as on the levee of a fluvial channel (e.g., Braddy 1995; Braddy and Milner 1998). Combined, the lithofacies, palynomorphs, vertebrate fossils, and trace fossils indicate fluvial environments with sandy sinuous channel belts bordered by floodplains that supported a diversity of flora in both subaerial and aquatic habitats prone to episodic flooding events.

Vertebrate fossils recovered from the Blossburg-Covington section exhibit a variety of taphonomic conditions. Channel-bar sandstones produce just over half of the Blossburg-Covington fossil horizons (12 of 22 fossil horizons; Table 2). Fragmentary and abraded vertebrate remains that accumulated on sandy bars and channel bottoms were most likely transported downstream as bedload and may not have been living in close proximity to their ultimate site of deposition. Previous work in terrestrial and marginal marine Upper Devonian deposits has produced similar taphonomic interpretations of fragmentary vertebrate remains. For instance, Lukševičs et al. (2012) concluded that disarticulated and highly abraded remains of vertebrates preserved in Upper Devonian strata were transported before burial in a deltaic marginal marine environment (e.g., Behrensmeyer 1988). Less fragmented, unabraded, and articulated vertebrate remains such as those of "placoderms" and lobe-finned fishes accumulated in flat-bottomed sandstones and mudrocks interpreted as muddy channel-fill as well as crevasse splays and ponds that provided aquatic floodplain habitats (ten of 22 fossil horizons; Table 2). Individual vertebrates preserved within these strata may have inhabited the floodplain during a flooding event and were stranded in these temporary aquatic floodplain environments when water levels decreased. Alternatively, these individuals may have been transported into these areas post-mortem during flooding and/or channel avulsion episodes. Strata from vertebrate fossil-bearing floodplain deposits at other localities yield broadly similar taphonomic interpretations. From Lower Mississippian strata of Scotland, Bennett et al. (2016) found more articulated, less fragmentary vertebrate fossils in floodplain deposits compared to those preserved in Catskill Formation basal lags of channel sandstones in our study. Bennett et al. (2016) interpreted floodplain deposits that preserved articulated vertebrate fossil material as ponds and lakes produced by seasonal flooding episodes.

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recovered palynomorph taxa. Maximum dimension of each figured palynomorph is listed after each taxa: **A**) *Aneurospora greggsii*? 38 μm, HMF. **B**) *Apiculiretusispora fructicosa*?, 46 μm, HMF. **C**) *Auroraspora macra*, 60 μm, HMF. **D**) *Auroraspora solisorta*, 60 μm, CF, 240 m. **E**) *Dibolisporites* cf. *acritarchus*, 53 μm, CF, 240 m. **F**) *Diducites versabilis*, 71 μm, CF, Lowermost. **G**) *Diducites versabilis*, 73 μm, CF, Lowermost. **H**. *Geminospora-Aneurospora* spp, 53 μm, CF Lowermost, **I**) *Grandispora cornuta* 75 μm, CF, 240 m. **J**) *Hystricosporites* cf. *multifurcatus*?, 160 μm, CF, Lowermost. **K**) *Knoxisporites literatus*, 75 μm, HMF. **L**) *Knoxisporites literatus*, 85 μm, HMF. **M**) *Raistrickia* cf. *minor*?, 33 μm, HMF. **N**) *Retispora lepidophyta,* 67 μm, HMF. **O**) *Retispora lepidophyta*, 71 μm, HMF. **P**) *Retusotriletes crassa*, 41 μm, CF, 240 m. **Q**) *Retusotriletes incohatus*, 60 μm, CF, Lowermost. **R**) *Rugospora flexuosa*, 65 μm, HMF. **S**) *Vallatisporites hystricosus*, 60 μm, HMF. **T**) *Verrucosisporites* sp., 50 μm, HMF.

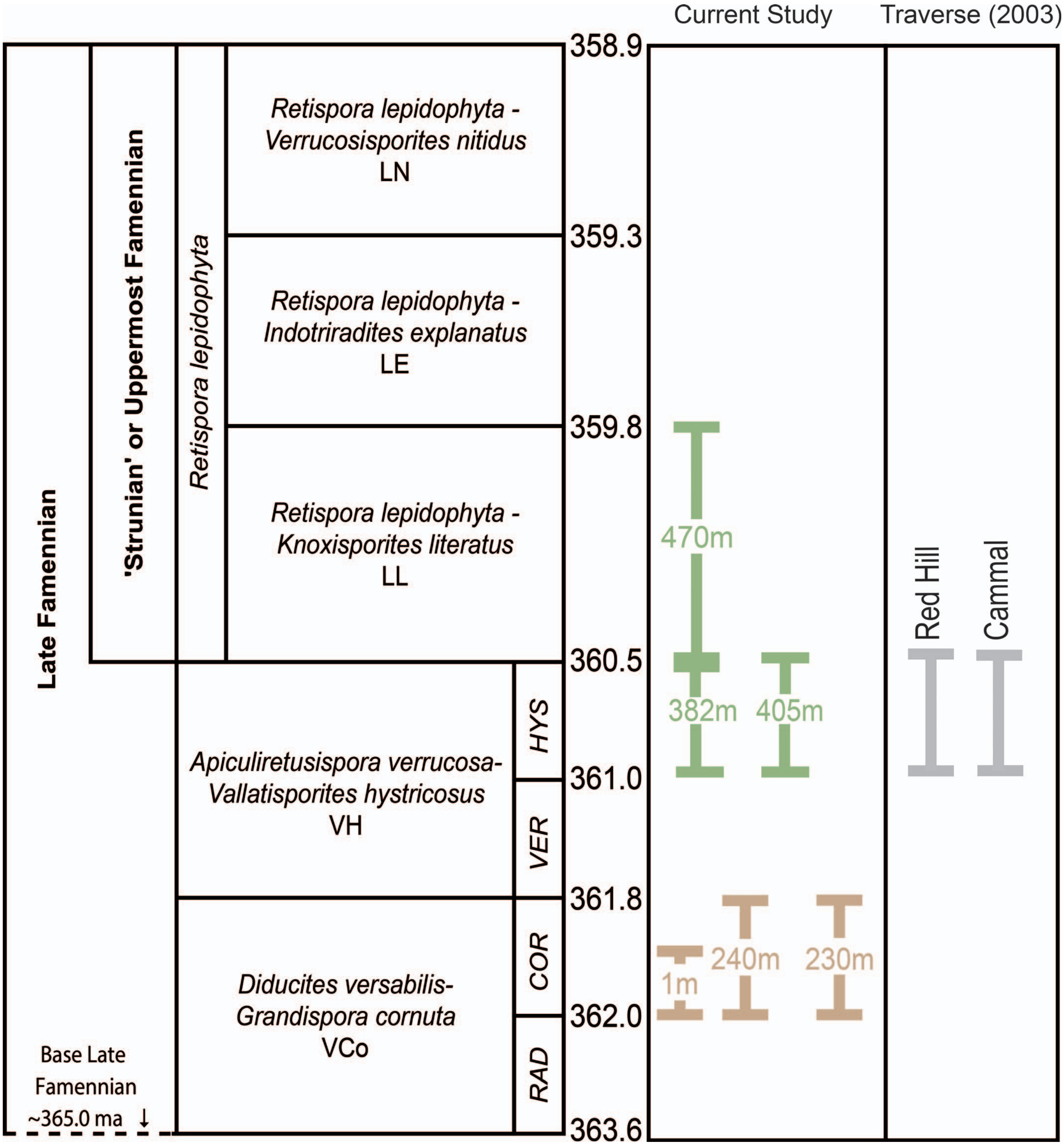

FIG. 11.—Composite palynozonation showing the range of palynomorphs recovered from Upper Devonian strata in the Blossburg-Covington section. Vertical bars show the age range of individual samples from the Catskill Formation (brown) and the overlying Huntley Mountain Formation (green) based on the most restrictive first and last occurrence age pair. Gray vertical bars indicate age ranges of palynomorphs from Catskill Formation outcrops at Red Hill and Cammal (Traverse 2003). Meters represent the stratigraphic level above the base of the measured stratigraphic section shown in Figure 4. Refer to Table 3 for a summary of recovered palynomorphs. The composite palynozonation was compiled from Richardson and Ahmed (1988), Playford and McGregor (1993), Clayton et al. (1998), Maziane et al. (1999), Maziane et al. (2002), Pereira et al. (2007), and Higgs et al. (2013). Numerical ages are estimated from Becker et al. (2012).

Animals were transported into these ponds and lakes as a result of flooding and existed before subsequent burial and preservation.

Fossils recovered from the Blossburg-Covington section provide insight into the fauna that occupied Late Devonian fluvial environments of the Appalachian Basin. Faunal assemblages in the Blossburg-Covington section are similar to previously studied Catskill Formation sites (Table 4) where *Archanodon* bivalves, "placoderms", acanthodians, and bony fishes have been documented. The fossil assemblage recovered from the Blossburg-Covington section is most similar to the fossil assemblage reported from the Powys section located ~ 50 km south of Blossburg (Fig. 1, Table 4) (Davis et al. 2004). The lower portions of the Blossburg-Covington (up to 111 m, current study) and Powys sections contain similar lithofacies including laterally persistent, several-meter-thick, fining-upward cycles of siltstones and fine to medium sandstones, with abundant root traces (Davis et al. 2004) indicating relatively low gradient, shallow sinuous fluvial channels near the coastline (Fig. 12) (Sevon 1985; Slane and Rygel 2009). These similar types of paleoenvironments supported similar faunas including suspension-feeding bivalves, arthropods (Jones 2011), and several taxa of vertebrates (Davis et al. 2004; Daeschler and Cressler 2011).

Possible Euryhalinity of Catskill Vertebrates

This study documents strata lacking sedimentological or paleontological evidence of marine influence, yet the Blossburg-Covington strata yield vertebrate taxa that may have inhabited both marginal marine and freshwater environments during the Late Devonian (Sallan and Coates 2010). Recent work suggests that some Late Devonian vertebrates were able to tolerate both freshwater and marine environments and that these transitional environments were critical for vertebrate evolution during Late Devonian time (Goedert et al. 2018; Gess and Whitfield 2020). The roadcut exposures in northern Tioga County in north-central Pennsylvania (Figs. 1, 3) record the transition from marginal marine depositional environments and ecosystems of the Lock Haven Formation to freshwater environments and ecosystems of the Catskill Formation. At Tioga, approximately 22 km to the north of the fluvial strata in the Blossburg-Covington section, the Catskill Formation records the progradation of fluvial systems across low-energy marine environments with modest tidal influence (Slane and Rygel 2009). Fossil vertebrates identified from Catskill Formation strata at Tioga include some of those that have also been identified to the south in the Blossburg-Covington section, including *Bothriolepis*, *Phyllolepis*, and the lobe-finned fishes *Holoptychius* and *Langlieria* (Table 4). At Tioga, strata spanning the gradational transition between the Catskill Formation and underlying Lock Haven Formation also yield marginal marine invertebrate taxa such as *Lingula* brachiopods (Daeschler and Cressler 2011) that have not been observed in fluvial strata in Catskill Formation outcrops to the south in the Blossburg-Covington section (Fig. 1). The Tioga section records the transition between marine and freshwater environments judging from the combination of both marginal marine and freshwater fauna and respective sedimentological features. At Tioga, gray sandstone and mudrock of the open-marine Lock Haven Formation interfingers with red beds of the Catskill Formation interpreted to represent muddy tidal flats at the marine-to-nonmarine transition zone (Slane and Rygel 2009). The Blossburg-Covington section lacks direct sedimentological and paleontological evidence of marine conditions. However, the transition from the Lock Haven Formation to the Catskill Formation is not exposed in the Blossburg-Covington section. Recent fossil prospecting by us at the Tioga section documented a partial phyllolepid plate within the Lock Haven Formation–Catskill Formation transition a few meters above and below strata that contain marine macrofossils such as crinoids and brachiopods. Collectively, these observations suggest that some Catskill Formation vertebrate taxa tolerated both marine and freshwater environments and episodically migrated between marine and freshwater environments, or that they may have possessed the ability to cope with variable salinity brought on by long-term sea-level changes similar to other Late Devonian and Early Mississippian vertebrates (Cecil et al. 2004; Brezinski et al. 2010; Carpenter et al. 2014, 2015; Gogain et al. 2016; Goedert et al. 2018). Further investigation into the potential euryhalinity of Catskill Formation vertebrate taxa is warranted, including additional fossil prospecting among lithofacies transitions between terrestrial and nearshore marine paleoenvironments (e.g., Catskill Formation–Lock Haven Formation transition) and companion stable isotope analyses (e.g., Goedert et al. 2018; Carpenter et al. 2015).

Integration of Catskill Formation Fossil Sites

The Blossburg-Covington section provides an important reference for integrating Catskill Formation fossil sites into a reconstruction of the regional Late Devonian paleoenvironmental settings (Fig. 12). Recent work at other late Famennian Catskill Formation sections in north-central Pennsylvania indicates that diverse faunal assemblages that include early tetrapods occupied vegetated fluvial environments similar to those preserved in the Blossburg-Covington section and at other coeval Catskill Formation sites in north-central Pennsylvania (Cressler et al. 2010; Daeschler and Cressler 2011; Broussard et al. 2018). In the Blossburg-Covington section the strata transition upsection from relatively thin, single-story channel-bar sandstones to thicker coarse-grained multi-storied sandstone bodies (Fig. 4, Table 2). Taphofacies also transition from thin coarse-grained coastal margins or floodplains to predominantly thick sandstone channel bodies (Table 2). Floodplain taphofacies that contain articulated macrofossils only occur in the lower portions (13 m to 111 m) of the Blossburg-Covington section (Fig. 4). Upper strata of the Blossburg-Covington section (above 111 m) preserve only abraded, disarticulated, and fragmentary macrofossil remains in coarser-grained, thicker channel-bar taphofacies. Variation in taphonomy may also be related to fossil assemblage composition in this section (Fig. 4). Higher faunal diversity (six taxa) occurs near the base of the section where floodplain deposits occur in association with relatively thin single-story channel bodies and multi-story channel belt sandstones are absent. Fewer (three) taxa occur in the upper part of the upper Catskill Formation in slightly coarser grained multi-story channel belt sandstones. This upsection decrease in diversity may reflect paleoenvironmental variation, taphonomic variation, or a combination of both. Slightly deeper, fast-moving channels upsection may have been sub-optimal habitat for a diverse fauna whereas temporary waterways on the floodplain likely may have provided more diverse habitats for vertebrates and invertebrates. Also, less accommodation may have prompted more reworking and less preservation of floodplain deposits and associated vertebrate fossils. Additionally, lower energy floodplain paleoenvironments commonly preserve identifiable fossil remains whereas fossils in channel/bar taphofacies are often difficult to identify because of their fragmentary, abraded nature (Broussard et al. 2018).

Many previous studies interpreted the Catskill Formation as the product of progradation of a tributary fluvial system that formed one or more deltas

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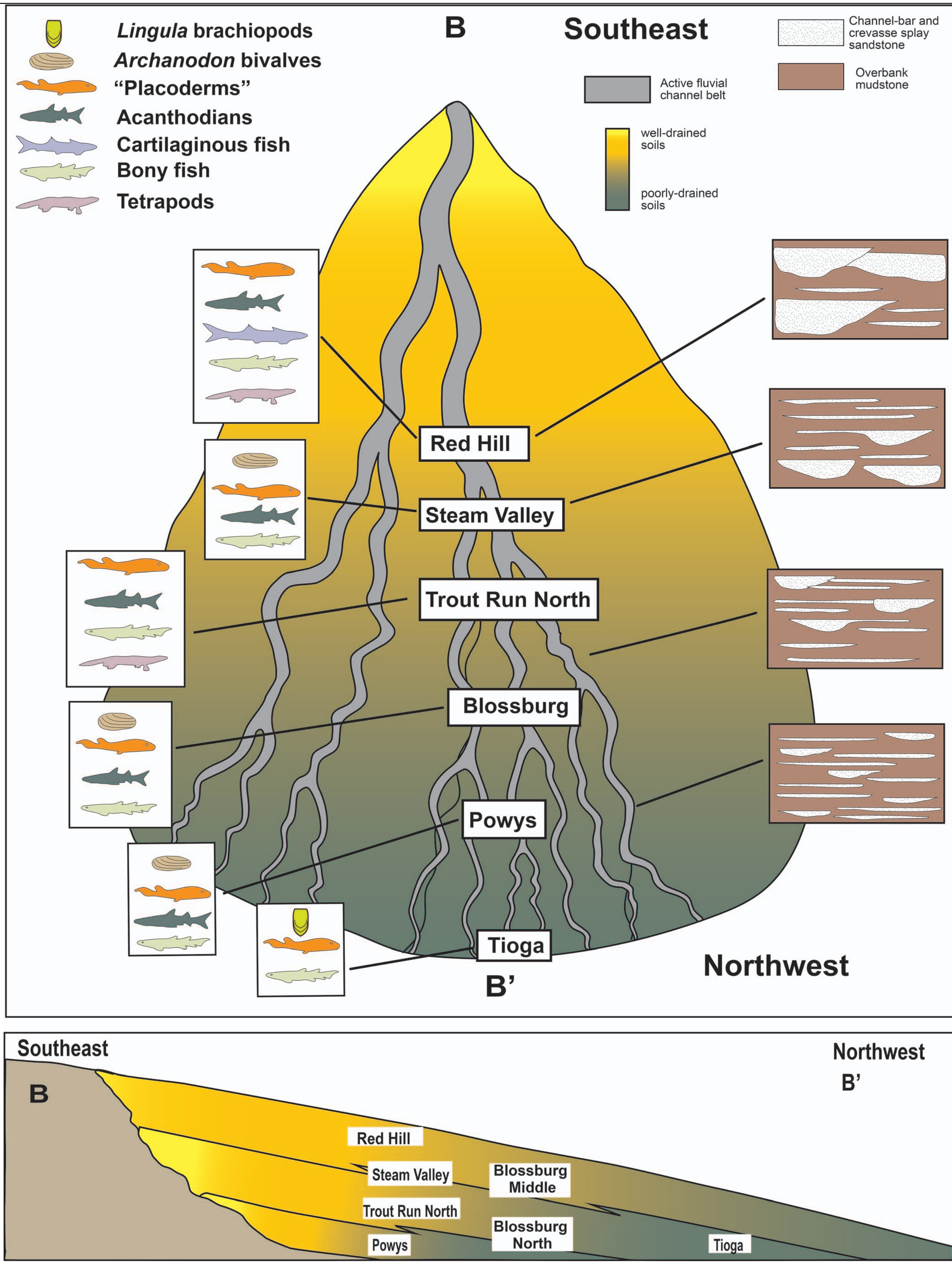
Fig. 12.—Schematic depositional model for fossiliferous Catskill Formation strata in north-central Pennsylvania showing generalized faunal assemblages at each locality. Northwestward-prograding distributive fluvial system accounts for overall upsection increases in the scale of channel-belt sandstones and paleosols indicative of better soil drainage. Distributive fluvial model adapted from Weissmann et al. (2013) and proposed for the Catskill Formation by Oest (2015), Broussard et al. (2018), and this study. Evaluation of this model will require improved chronostratigraphic constraints and quantitative fluvial architecture studies across the study region (e.g., Zaklicki et al. 2019).


Lingula brachiopods
Archanodon bivalves
"Placoderms"
Acanthodians
Cartilaginous fish
Bony fish
Tetrapods
B
Southeast
Channel-bar and crevasse splay sandstone
Overbank mudstone
Active fluvial channel belt
well-drained soils
poorly-drained soils
Red Hill
Steam Valley
Trout Run North
Blossburg
Powys
Tioga
Northwest
B'
Southeast
Northwest
B
B'
Red Hill
Steam Valley
Blossburg Middle
Trout Run North
Blossburg North
Powys
Tioga

(Catskill Delta; Ettensohn 1985; Faill 1985, 2002; Sevon 1985). However, distributary mouth bar facies and repeated coarsening-upward cycles that typify deltaic distributary channels are distinctly lacking in the Catskill Formation (Walker 1971; Walker and Harms 1971). Based on upsection trends in paleosol development, channel sandstone morphology, grain size, mineralogy, and alluvial stacking patterns, Oest (2015) attributed the Catskill Formation in Pennsylvania to a prograding distributive fluvial system. The Catskill Formation stratigraphy at Blossburg-Covington is consistent with stratigraphic patterns recognized by Oest (2015) at other outcrops in central Pennsylvania. For example, channel sandstones within the lower Catskill Formation at Blossburg North occur as single-story bodies isolated in overbank fines. The abundance of overbank fines and crevasse splay sandstones relative to channel sandstones reflects poorly channelized flow throughout much of this stratigraphic interval, consistent with medial to distal meandering feeder channels on a distributive fluvial system (Gibling 2006; Nichols and Fisher 2007; Hartley et al. 2010, 2013; Weissmann et al. 2010, 2011, 2013). Channel sandstones within the upper Catskill Formation at Blossburg Middle occur as multistory, amalgamated bodies with prominent lateral accretion sets, consistent with medial to proximal meandering feeder channels on a distributive fluvial system (e.g., Gibling 2006; Nichols and Fisher 2007; Oest 2015). The upsection shift from relatively small, isolated channels in overbank fines to larger, coarser, amalgamated channels is consistent with a prograding distributive fluvial system (Nichols and Fisher 2007; Hartley et al. 2013; Weissmann et al. 2013; Trendell et al. 2013). Variability in Catskill Formation paleosols is also consistent with progradation of a distributive fluvial system. The lower Catskill Formation at Blossburg North exhibits moderately developed paleosols, whereas paleosols higher in the section at Blossburg Middle exhibit features indicative of better drainage, including more abundant pedogenic carbonate accumulations and pedogenic slickensides. This paleosol variability may reflect variations in the proximity to active channel deposition and/or an overall increase in depth to the water table expected within increasingly source-proximal environments resulting from progradation. In summary, upsection variations in paleosols and channels documented in the Catskill Formation by Oest (2015), Broussard et al. (2018), and this study are broadly consistent with a prograding distributive fluvial system. However, criteria commonly used to distinguish prograding distributive fluvial in the modern and ancient record, such as the characteristic upward increase in grain size, amalgamation, and proportion of sandstone (e.g., Trendell et al. 2013; Weissmann et al. 2013), cannot be fully applied without detailed studies spanning broader temporal and spatial extents. Additional integrated sedimentologic-paleontologic analyses from the Catskill Formation of north-central Pennsylvania together with high-resolution age data may provide further insights into continental ecosystem evolution, environments that supported Late Devonian vertebrate evolution including the fin-to-limb transition in tetrapodomorphs, and the possible euryhalinity of Late Devonian vertebrates occupying marginal marine-to-nonmarine transitional environments.

CONCLUSIONS

Sedimentology.—Upper Devonian Catskill Formation strata in the Blossburg-Covington section consist chiefly of lenticular cross-stratified sandstone and reddish brown to red mudstone, siltstone, and shale interpreted as the deposits of sandy channel belts and vegetated muddy floodplains, respectively. Sediment accumulated in diverse terrestrial aquatic environments, including sandy channel-bar complexes, crevasse splays, and muddy floodplains that were variably overprinted by bioturbation and pedogenesis.

Paleontology.—Systematic fossil prospecting in the Blossburg-Covington section provides a census of taxa within a sedimentological and stratigraphic framework. Invertebrate taxa include post-mortem, hydrodynamically transported *Archanodon* bivalves preserved along the base of a channel-bar sandstone and other motile taxa, including large arthropods, based on trace fossil evidence. Vertebrate taxa include two genera of "placoderms" (*Bothriolepis* and *Phyllolepis*), an unidentified acanthodian, and several taxa of sarcopterygian fishes, including a lungfish (Dipnoi indet.), *Holoptychius*, *Langlieria*, and *Sauripterus*.

Depositional Age.—Catskill Formation strata in the Blossburg-Covington section yielded palynomorphs that are restricted to the COR (*Diducites versabilis-Grandispora cornuta*) palynological zone and limit deposition to ca. 362.0 to 361.8 Ma during the late Famennian stage of the Late Devonian. Palynomorphs recovered from the overlying Huntley Mountain Formation in the Blossburg-Covington section are restricted to the VH (*Apiculiretusispora verrucosa-Vallatisporites hystricosus)* and LL (*Retispora lepidophyta-Knoxisporites literatus)* and indicate deposition ca. 361.8 to 359.8 Ma during late to latest Famennian time.

Taphonomy.—Most vertebrate macrofossils in the Blossburg-Covington section consist of plates, scales, and bone fragments. Channel-bar deposits preserve disarticulated, abraded remains in mixed sandstone-conglomerate beds ranging from concentrated lags along bed bases to thicker beds. Taphonomy of fossils in channel-margins and overbank floodplain deposits range from disarticulated and abraded to articulated and unabraded indicating different taphofacies among these depositional settings.

Regional Paleoenvironments.—The Blossburg-Covington section provides a useful reference section for regionally linking Catskill Formation depositional environments and taphonomy. To the northwest, Catskill Formation outcrops record transitional marine environments with articulate brachiopods and phyllolepid "placoderms" whereas to the south, Catskill Formation strata reflect fluvial channel-floodplain environments that preserve diverse faunal assemblages.

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SUPPLEMENTAL MATERIAL

Data are available from the PALAIOS Data Archive:
https://www.sepm.org/supplemental-materials.

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