Late Devonian paleontology and paleoenvironments at Red Hill and other fossil sites in the Catskill Formation of north-central Pennsylvania

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Late Devonian paleontology and paleoenvironments at Red Hill and other fossil sites in the Catskill Formation of north-central Pennsylvania

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ABSTRACT

The stratified red beds of the Catskill Formation are conspicuous in road cut exposures on the Allegheny Plateau of north-central Pennsylvania. During this field trip we will visit and explore several fossil localities within the Catskill Formation. These sites have been central to recent investigations into the nature of Late Devonian continental ecosystems. By the Late Devonian, forests were widespread within seasonally well-watered depositional basins and the spread of plants on land from the late Silurian through the Devonian set the stage for the radiation of animals in both freshwater and terrestrial settings. A diverse assemblage of flora and fauna has been recovered from the Catskill Formation including progymnosperms, lycopsids, spermatophytes, zygopterid and stauripterid ferns, barinophytes, invertebrates and invertebrate traces, and vertebrates such as placoderms, acanthodians, chondrichthyans, actinopterygians, and a variety of sarcopterygians including early tetrapods. Since the early 1990s, highway construction projects along the Route 15 (Interstate 99) have provided a new opportunity for exploration of the Catskill Formation in Lycoming and Tioga counties. The faunas along Route 15 are dominated by *Bothriolepis* sp. and *Holoptychius* sp. and also include *Sauripterus taylori* and an assortment of other interesting records. The most productive Catskill site, and the source of early tetrapod remains, is Red Hill in Clinton County. Red Hill presents a diverse and unique flora and fauna that is distinct from Route 15 sites, and also provides a spectacular section of the alluvial plain deposits of the Duncannon Member of the Catskill Formation.

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OVERVIEW

The earliest paleontological investigations of the Catskill Formation in Pennsylvania date to the 1830s and 1840s, when James Hall described the pectoral fin of the rhizodontid sarcopterygian *Sauripterus taylori* from a fossil discovered during construction of a railroad line near Blossburg, Tioga County (Hall, 1843). Charles Lyell passed through Blossburg in 1840 and examined the Catskill Formation during one of his two North American tours (Leviton and Aldrich, 1992; Davis et al., 2004). Additional fossil material from the Upper Devonian red beds of Pennsylvania was described by Leidy, Newberry and Eastman during the nineteenth century and early twentieth century. During the 1960s, Keith S. Thomson described the tristichopterid sarcopterygian *Hyneria lindae* (Thomson, 1968) from material found in the vicinity of North Bend, Clinton County, and *Sterropterygion brandei* (Thomson, 1972; Rackoff, 1980) from Tioga County. Thomson became aware of Catskill Formation localities from Donald Baird and Alfred Sherwood Romer of Harvard University who had done prospecting and collecting in the region during the 1950s. Paleobotanical investigations in the Catskill Formation began with Leo Lesquereux, who described two species of *Archaeopteris* from Meshoppen, Wyoming County (Lesquereux, 1884) in his pioneering report on Pennsylvania's coal flora for the state's Second Geological Survey. Chester Arnold figured and further described these specimens (Arnold, 1936), as well as other plants from the Oswayo Formation in northern Pennsylvania (Arnold, 1939), a lateral marine equivalent of the Catskill. The most productive sites in this unit were near Port Allegany in McKean County, and when John Pettitt and Charles Beck reinvestigated Arnold's material, they were able to describe the first confirmed seed from the Late Devonian, *Archaeosperma arnoldii* (Pettitt and Beck, 1968). Recent paleobiological investigations into the Catskill Formation were initiated in 1993 as field crews from the Academy of Natural Sciences of Philadelphia–University of Pennsylvania began systematic exploration of exposures of the Catskill Formation principally in Clinton, Lycoming, and Tioga Counties.

Natural, unweathered exposures of the Catskill Formation are rare in Pennsylvania, so paleontological investigations have been closely linked with the construction of the railway system in the nineteenth century and the highway system in the twentieth and twenty-first centuries. We are indebted to the Pennsylvania Department of Transportation and its contractors for access to the sites where most of our fossil discoveries have been made.

The Catskill Formation is composed of sand, silt, and mud deposited in a series of prograding deltas, known as the Catskill Delta Complex (Sevon, 1985) (Fig. 1). This clastic wedge was derived from the middle to late Devonian Acadian Mountains shedding sediment westward and northwestward toward a shallow epicontinental sea in the foreland basin of the orogenic zone (Faill, 1985). The Acadian Orogeny was part of the Middle to Late Paleozoic assembly of the Euramerican landmass (a.k.a. Laurussia or the Old Red Sandstone Continent) and subsequent assembly of the supercontinent Pangea. The deposits of the Catskill Delta Complex grade upward from basinal black shales to nearshore marine facies through transitional facies and into delta plain and alluvial plain depositional settings.

Our paleontological studies have focused on the deltaic and alluvial plain facies at the top of the Catskill Formation. Palynological analysis has placed all but one of the productive field sites visited on this trip within the Fa2c part of the Fammenian Stage (Traverse, 2003). This corresponds to the poorly calibrated VH palynozone and is perhaps less ambiguously attributed to the

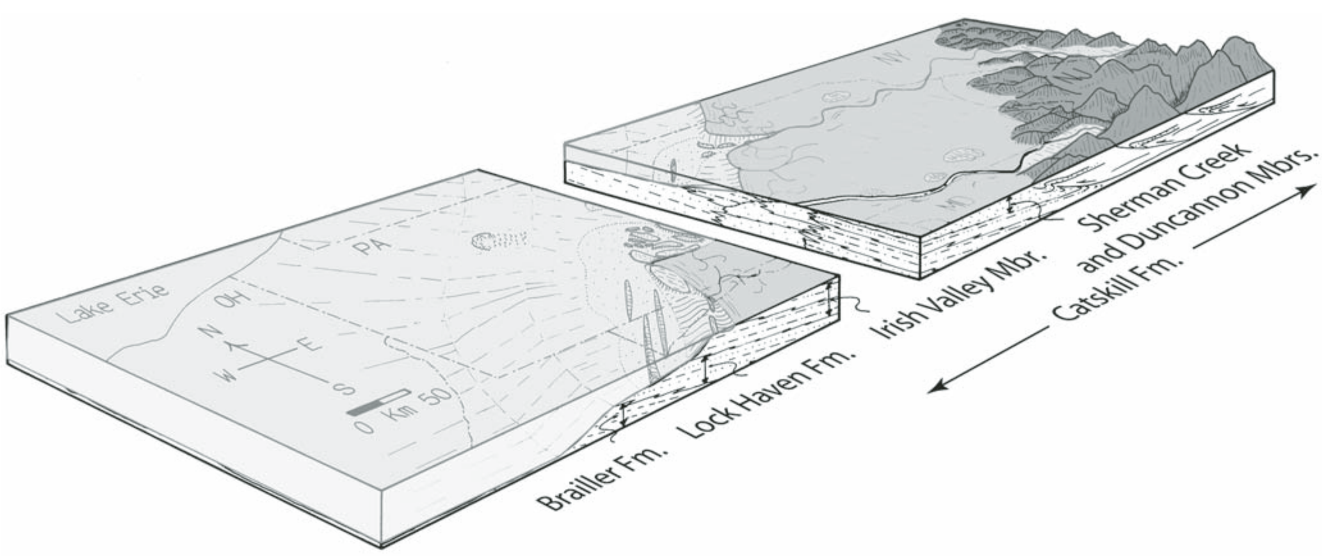

Figure 1. Block diagram of depositional systems of the Catskill Delta Complex during the Late Devonian in Pennsylvania. Reprinted from Cressler et al. (2010a).

VCO palynozone (sensu Streel et al., 1987). The Tioga Welcome Center locality in Tioga County (Stop 4) is slightly older. Where differentiated, the uppermost subdivisions of the Catskill Formation are the Sherman Creek Member and the overlying Duncannon Member (Fig. 2).

At Powys Curve (Stop 1) in Lycoming County, the Sherman Creek Member is well exposed. The Sherman Creek Member is typically composed of fining-upward cycles on the order of two to three meters thick. These cycles are often laterally continuous and are dominated by fine to medium sandstones and siltstones. Poorly developed paleosols and root traces are seen in the fine sandstones and siltstones in the upper part of each cycle (Harvey, 1998). The lithology suggests that the Sherman Creek Member formed in a delta plain setting characterized by low-gradient, high-sinuosity, shallow channels near the coastline (Sevon, 1985).

In contrast, the Duncannon Member generally consists of 5–10-m-thick fining-upward cycles dominated by thick, cross-bedded, basal sandstones. The contact between the channel sandstone and the mudstone at the top of the underlying cycle is sharp and irregular. Mature paleosols and root traces are often recognized in the mudstones. The Duncannon Member formed in meandering stream channels and overbank deposition on an alluvial plain and is very well exposed at Red Hill (Stop 5), the source of abundant fossil material including plants, arthropods, and a diverse vertebrate fauna including early tetrapods.

As recorded in the rocks observed on this field trip, the Late Devonian was a time of major transitions in flora, fauna, and the geobiological system. By the Late Devonian, forests were widespread within the seasonally well-watered depositional basins. The dominant tree was the progymnosperm *Archaeopteris*, growing up to 18 m tall. This was the first plant known with a bifacial cambium as in modern wood, but it reproduced through spores (Meyer-Berthaud et al., 1999). Seed plants are first known from the Late Devonian (Rothwell, et al., 1989). Evidence at Red Hill indicates that opportunistic seed plants, growing in areas disturbed by fire, took advantage of the destruction of the widespread fern *Rhacophyton* (Cressler, 2006; Cressler et al., 2010a). Lycopsids were important swamp plants in the Late Devonian, attaining the stature of small trees and, along with *Rhacophyton*, contributing to the thin coal seams known from this time. These small Late Devonian lycopsids are the precursors of the immense lycopsids that were the primary components of Carboniferous coal swamps (Cressler and Pfefferkorn, 2005). The increased stature of the plants in the Late Devonian was accompanied by a concomitant increase in root zone depth, which led to increased paleosol development (Driese and Mora, 1993). The development of paleosols has been linked to increased nutrient flow to the adjacent marine basins, a factor that may also explain increased anoxia, black shale formation, and marine extinctions (Algeo and Scheckler, 1998).

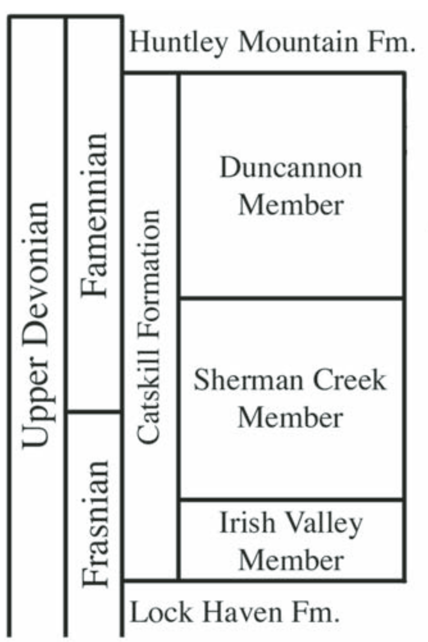

Figure 2. Stratigraphic relationships of the Catskill Formation in north-central Pennsylvania.

The spread of plants on land from late Silurian through the Devonian set the stage for the radiation of animals in both freshwater and terrestrial settings. Large, suspension-feeding bivalves, *Archanodon catskillensis*, are recorded sporadically from throughout the Catskill Formation. Fossil terrestrial arthropods (first known from the Silurian) include millipedes (Wilson et al., 2005), scorpions, and a trigonotarbid arachnid (Shear, 2000) from the Catskill Formation. All of these are either detritivores or predators, and there is no evidence of herbivory on living plant tissue during the Late Devonian. It appears that the increased contribution of organic detritus by land plants to terrestrial and freshwater ecosystems during this time provided the primary productivity for these increasingly complex and diverse ecosystems.

A diverse vertebrate assemblage, including placoderms, acanthodians, chondrichthyans, actinopterygians, and a range of sarcopterygians including at least three species of tetrapods (Daeschler et al., 1994, 2009; Daeschler, 2000b; Shubin et al., 2004) is known from the Catskill Formation. There are two distinct faunas that characterize the vertebrates from the Catskill Formation. The fauna dominated by the porolepiform sarcopterygian *Holoptychius* sp. and antiarch placoderm *Bothriolepis* sp. is characteristic of the Sherman Creek Member and much of the undifferentiated Catskill. This assemblage also includes rare occurrences of the rhizodont sarcopterygian *Sauripterus taylori*. These appear to be organisms mainly restricted to lower alluvial plain–deltaic habitats. Red Hill is characteristic of the other distinct fauna, which includes groenlandaspidid placoderms, a gyracanthid acanthodian, megalichthyid and tristochopterid sarcopterygians, and tetrapods, all from alluvial plain depositional facies. Some of the sarcopterygians (particularly the tetrapods) are lineages adapted for mobility in stream channels and shallow, obstructed waters, a habitat that the well-vegetated alluvial plains of the Catskill Delta Complex seem to have provided. Red Hill has been the subject of recent analyses of plant distribution in a Late Devonian landscape (Cressler, 2006) and the paleoecological conditions associated with terrestrialization during the Late Devonian (Cressler et al., 2010a).

DAY 1

Road Log

Cumulative miles	*(km)*	*Directions and notes*
0.0	(0.0)	Take Exit 178 off Interstate 80 onto Route 220 North towards Lock Haven. The first few miles on Route 220 cross an anticlinal valley of Ordovician units. The ridges to north and south are composed of resistant sandstones of the Reedsville, Bald Eagle and Juniata formations.
3.5	(5.6)	Crossing through the Ordovician sandstones of Bald Eagle Mountain into Silurian units flanking the north side of the ridge (Tuscarora Formation). Route 220 continues to the northeast with Bald Eagle Mountain to the southeast (this is the last ridge of the Valley and Ridge Province) and the Allegheny Plateau to the northwest.
30.8	(49.6)	Take Exit 29 for Route 15 North (also called Interstate 99). Route 15 North cuts into the Allegheny Plateau along Lycoming Creek. Between road log miles 34.5 and 40.5, a series of road cuts begin with Middle Devonian near-shore marine sediments of the Lock Haven Formation and after crossing the structural boundary of the Allegheny Front (Beautys Fault in this region) begins to move up-section.
39.4	(63.4)	to
40.4	(65.0)	Excellent section exposed in road cuts through the lower part of the Catskill Formation (Irish Valley and Sherman Creek Members).
43.6	(70.2)	Take Exit for Route 14 North (Trout Run).
44.1	(71.0)	Sharp U-turn onto access road (SR-17). Follow access road south, parallel to Route 15.
47.8	(76.9)	Pull over onto right shoulder of road to examine blocks along roadbed.

Stop 1. Powys Curve

Coordinates: N41°20.840′ W77°05.614′

Construction along this stretch of Route 15 (Interstate 99) was completed in 1994. We will spend time looking at rocks and fossils along the debris slope between the highway road bed and the access road that runs adjacent to the highway along the bend in Lycoming Creek. At this stop, we can observe the Sherman Creek Member of the Catskill Formation exposed in the large vertical cut on the west side of Route 15. The Sherman Creek Member at this site is composed of laterally continuous siltstones and fine sandstones in 2–3-m-thick fining-upward cycles. The depositional setting for this section is a delta plain with low-gradient, shallow channels.

Since 1994, vertebrate material has been collected from the debris slopes all along the raised portion of the highway roadbed. The fauna is dominated by the antiarch placoderm *Bothriolepis* sp. and the porolepiform sarcopterygian *Holoptychius* sp. A single pectoral fin and shoulder girdle of *Sauripterus taylori* was recovered from this site in 1995 (Fig. 3). The new specimen of *Sauripterus taylori* is quite informative and, remarkably, preserves the same portion of the skeleton, a right pectoral girdle and fin in ventral view, as the classic specimen described by Hall in 1843 (AMNH 3341) from ~40 km north of Powys Curve. The new specimen is described and discussed by Daeschler and Shubin (1998) and Davis et al. (2004).

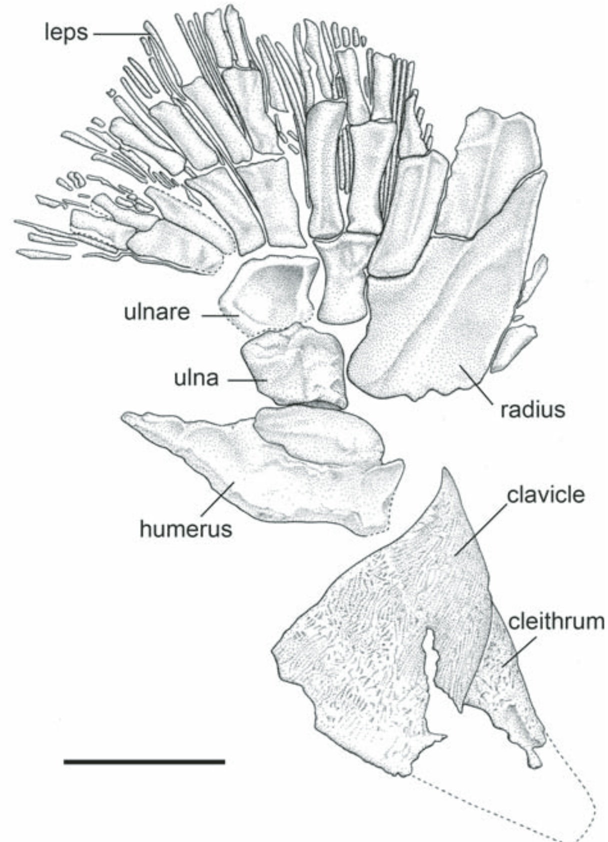

Figure 3. Ventral view of right pectoral fin of *Sauripterus taylori* discovered at Powys Curve, Lycoming County, Pennsylvania, in 1995. Note that the distal fin rays (lepidotrichia) are not preserved. Abbreviation: leps—lepidotrichia. Scale bar equals 5 cm.

During construction of the roadway between Powys Curve and Trout Run, partially articulated skull material of a large tristichopterid, cf. *Eusthenodon* sp. was recovered. This material is easily distinguished from *Hyneria lindae*, the large tristichopterid common at the Red Hill site in Clinton County (Stop 5). Both are derived members of the tristichopterid clade and typical of late Famennian large tristichopterids with cosmopolitan distribution. The cf. *Eusthenodon* sp. material from Powys Curve–Trout Run includes derived features such as no contact between the posterior supraorbital and intertemporal, a long parietal shield with the pineal foramen located in the posterior portion of the shield (well behind the orbits), and a lacrimal with a postorbital bar excluding the jugal from the orbital margin.

***The* "Bothriolepis *Problem*"**

Thomson and Thomas (2001) and Weems (2004) reviewed the taxonomic status of *Bothriolepis* from the Catskill Formation. It is clear from these papers that the diagnosis of species-level features in *Bothriolepis* from the Catskill Formation is a microcosm of the issues concerning species-level taxonomy of this cosmopolitan Late Devonian genus more broadly. *Bothriolepis* material from the Catskill Formation was first described by Leidy (1856) as *Stenacanthus nitidus* based on a distal portion of a pectoral appendage from Blossburg, Tioga County, Pennsylvania. Newberry (1889) described a new bothriolepid species from the Catskill Formation, *Bothriolepis leidyi*, from Mansfield, Tioga County, Pennsylvania, acknowledging a synonymy with *Stenacanthus nitidus*. Newberry (1889) also described a new species, *Bothriolepis minor* from the Upper Devonian of Bradford County, Pennsylvania, that is distinguished by smaller size and finer ornament than *Bothriolepis leidyi.* Several authors have questioned or rejected the validity of *Bothriolepis minor* (e.g., Stensiö, 1948; Weems et al., 1981; Thomson and Thomas, 2001). Cope (1892) recognized the priority of *Bothriolepis nitidus* as a senior synonym of *Bothriolepis leidyi*, although Eastman (1907) changed the name to *Bothriolepis nitida* to correct the gender disagreement of the binomen. Weems et al. (1981) described *Bothriolepis virginiensis* from a Catskill Formation equivalent in Virginia. Thomson and Thomas (2001) suggested that *Bothriolepis nitida* be used to refer to all *Bothriolepis* material from the United States, mostly due to poor material and lack of diagnostic characters, although Weems (2004) maintained that *B. virginiensis* is a distinct species. The situation regarding the species-level taxonomy of Catskill Formation *Bothriolepis* suggests the need for further work, especially in light of the large sample of well-preserved *Bothriolepis* sp. material collected recently along the Route 15 corridor (Interstate 99) in Lycoming and Tioga counties (see Figure 6D for an example of recently collected material).

Cumulative miles	*(km)*	*Directions and notes*
47.8	(76.9)	Carefully make U-turn to head north on access road.
48.8	(78.5)	Stay left and follow short ramp onto Route 15 North. After passing Trout Run, Route 15 North climbs into Steam Valley and moves up section into the Duncannon Member of the Catskill Formation.
55.9	(90.0)	Pull over onto shoulder just before guardrail and sign for the Cogan House Exit.

Stop 2. Steam Valley

Coordinates: N41°26.421″ W77°05.994′

Road work that was completed in 2010 created significant new exposures of the upper part of the Catskill Formation in the southbound lanes of Route 15 in Steam Valley, and in the area where Steam Valley Road / Green Valley Road intersects the northbound lanes of Route 15. Scattered vertebrate remains, particularly *Bothriolepis* sp. and *Holoptychius* sp., have been found in rock fall from the series of older exposures along the previously improved northbound lanes. An interesting horizon with freshwater bivalves (*Archanodon catskillensis*) can be observed in situ at this site. The dense packing of these infaunal suspension feeders speaks to the productivity of the Late Devonian continental ecosystem. Chamberlain et al. (2004) reviewed the paleoecological and biogeographic implications of archanodonts, suggesting that they inhabited freshwater floodplain and brackish estuarine environments of the Old Red Continent. Remington et al. (2008) studied the *Archanodon*-bearing sediments at this exposure and indicated that the *Archanodon* horizon occurs in the point bar facies within an incised channel body. Palynomorphs from near the base of the exposure suggest a Famennian 2c age (Traverse, 2003) for the strata at this site. Vertebrate collections from the recent construction work on the southbound lanes of Route 15 in Steam Valley include the typical *Holoptychius* sp. material, as well as a small phyllolepid placoderm trunk plate.

Cumulative miles	*(km)*	*Directions and notes*
55.9	(90.0)	Continue north on Route 15.
58.3	(93.8)	Take Exit for Route 184 (Steam Valley). Go left at top of ramp. Follow across overpass and to entrance for the Turkey Ranch Restaurant. Lunch stop. Return to overpass and get back on Route 15 North.
63.3	(101.9)	to
65.3	(105.1)	A series of low road cuts on west side of the highway expose upper parts of the Catskill Formation. These cuts have produced a skull roof of the cosmopolitan rhynchodipterid lungfish *Soederberghia groenlandica* (discussed in Ahlberg et al., 2001), and an articulated body of the megalichthyid osteolepiform *Sterropterygion brandei*, which as described by Thomson (1972) and

endochondral fin anatomy discussed by Rackoff (1980).

71.3 (114.7) Cresting Bloss Mountain, southern limb of the Blossburg Syncline.

75.0 (120.7) Exposures of Carboniferous units Burgoon Sandstone and Pottsville Group in center of syncline.

77.0 (123.9) Beginning to move down-section through the northern limb of the Blossburg Syncline.

78.0 (125.5) to

80.0 (128.7) Huntley Mountain Formation grading downward into persistent red beds of the Catskill Formation. The Devonian-Carboniferous boundary is within Huntley Mountain Formation.

81.2 (130.7) Exposure of grey silty sands of the Lock Haven Formation.

83.0 (133.6) Take Exit for Covington/Canoe Camp. Go left at bottom of ramp, continue under overpass, and take immediate left onto ramp for Route 15 South.

87.8 (141.3) Pull over onto right shoulder just before guardrail. Please be very careful and aware of traffic, as the shoulder of the road is quite narrow.

Stop 3. Blossburg-Covington Section

Coordinates: N41°42.872′ W77°04.732′

This section of Route 15 bypassing the town of Covington was built in 2003 and 2004. The entire Catskill Formation is relatively thin at this location and is undifferentiated with regard to member designations. The contact between the Catskill and the overlying Huntley Mountain Formation is gradational (Berg and Edmunds, 1979). Sandstone bodies become increasing common upsection and take on a gray color in this transition zone from the meandering river facies of the Catskill Formation to predominantly braided river facies. The Devonian-Carboniferous boundary is within the lower part of the Huntley Mountain Formation. We will examine rocks and fossil material that are found in the large debris slope off the western shoulder of the highway.

A diverse fauna has been collected from this section of the highway that includes separate mass mortality layers of adult and juvenile *Bothriolepis* sp. A small area of the debris slope is the source of numerous samples that preserve the mass mortality of juvenile *Bothriolepis* sp. material. Criswell et al. (2007) reported head plus trunk shield lengths of 20 mm to 30 mm for most individuals from the mass mortality layers (Fig. 4). The morphology of these individuals matches the expectations for juvenile morphology of *Bothriolepis canadensis* as established by trends in allometric growth discussed by Werdelin and Long (1986). Of particular note is the relatively large head shield, the relative size of the orbital fenestra, and a large ventral opening in the trunk shield. The occurrence of numerous, similar-sized, articulated individuals in a closely packed taphocoenosis may provide clues about the nature of the earliest life history of *Bothriolepis*.

Other material recovered from this section includes adult *Bothriolepis* sp. (Fig. 6D), a phyllolepid placoderm, a single specimen of a palaeoniscid actinopterygian, *Holoptychius* sp., and informative skull material of a tristichopterid sarcopterygian. The skull material of the tristichopterid is associated with scales (Fig. 6B) that are identical to *Holoptychius radiatus* Newberry 1889 and discussed below (Stop 4).

Alongside the Tioga River, which runs northward on the valley floor, is an old railroad grade that was built to transport coal from Blossburg, an early source of high quality coal called "bloss." This was the Blossburg-Corning Railroad and was traveled by James Hall in July of 1839 as he sought to clarify some New York geological boundary issues in Pennsylvania (Leviton and Aldrich, 1992). Just below the newly made highway exposures is a substantial man-made exposure of Catskill Formation along the railroad bed between Blossburg and Covington. The lithology at the railroad cut is very similar to the red-brown, medium sandstone matrix of the original *Sauripterus taylori*

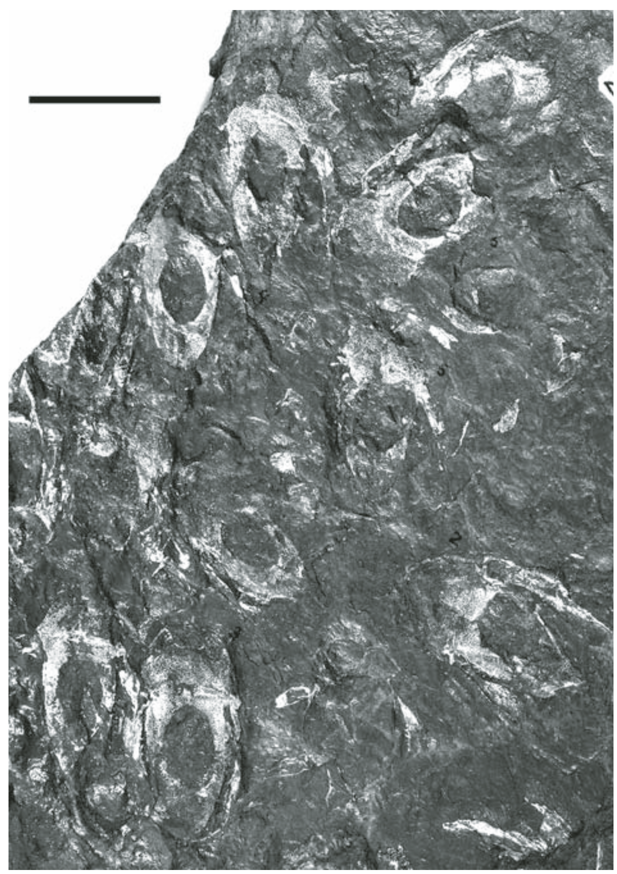

Figure 4. Bedding plane with multiple articulated juvenile individuals (in ventral view) of *Bothriolepis* sp. from the Catskill Formation near Blossburg, Tioga County, Pennsylvania. Scale bar equals 2 cm.

specimen (AMNH 3341) (Fig. 5). The fossiliferous nature of the rocks along the railroad bed is confirmed by specimens from Hall at the American Museum of Natural History identified as cf. *Eusthenodon* and with labels indicating that they were collected "at the railroad cut between Blossburg and Covington." The Late Devonian fossils from this section induced Charles Lyell to take a trip to Blossburg (along this rail line) to investigate the similarity between the fossil fauna from Blossburg and that of the Old Red Sandstone in the British Isles (Leviton and Aldrich 1992).

Cumulative miles	*(km)*	*Directions and notes*
87.8	(141.3)	Continue on Route 15 southbound.
90.9	(146.3)	Take Exit for Blossburg. Go left at bottom of ramp, continue under overpass, and take immediate left onto ramp for Route 15 North.
108.5	(174.6)	Catskill Formation grading downward into Lock Haven Formation
110.3	(177.5)	Take Exit for Route 287 / Tioga. Go left at bottom of ramp, continue under overpass, and take immediate left onto ramp for Route 15 South.
112.8	(181.5)	Enter and park at Tioga Welcome Center Rest Stop.

Stop 4. Tioga Welcome Center Rest Stop

Coordinates: N41°54.026′ W77°07.542′

This highway facility has restrooms and vending machines and offers nice views to the west. To the north of the welcome center you can observe the gradational contact of the Catskill Formation (undifferentiated) with the underlying Lock Haven Formation. The contact zone between the gray sands and muds of the marine Lock Haven Formation and the red beds of the Catskill Formation is characterized by the presence of articulate brachiopods, *Lingula* and vertical burrows, and may represent a muddy tidal flat at the marine-terrestrial interface (Slane and Rygel, 2009). South of the welcome center the gradational contact between the Catskill Formation and the overlying Huntley Mountain Formation is mapped half way up the wooded hillside. The Catskill is thus relatively thin in this location (~100 m thick).

The welcome center was built as part of a project to upgrade this section of the highway in 2001–2002. At that time, a section of the Catskill Formation was removed at the

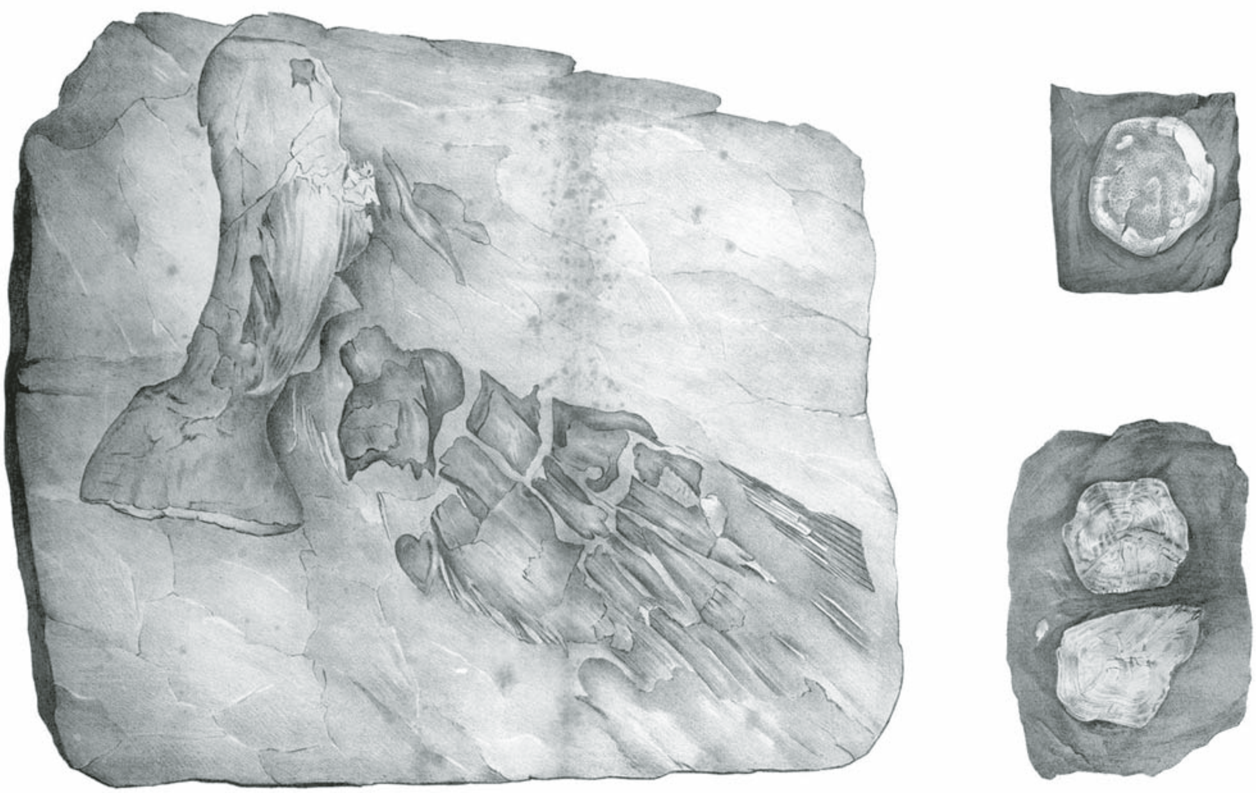

Figure 5. Original illustration from Hall (1843) of *Sauripterus taylori* pectoral fin and scales found along a railroad cut near Blossburg, Tioga County, Pennsylvania.

present site of the welcome center to create a flat building site. The excavations were examined numerous times during that phase of the work. Collected was fossil material of the placoderms *Bothriolepis* sp., *Phyllolepis* sp., a single element of a large dinichthyid, cf. *Dunkleosteus* sp., as well as the sarcopterygians *Holoptychius* sp., a tristichopterid, and the recently described lungfish *Apatorhynchus opistheretmus* (Friedman and Daeschler, 2006) (Fig. 6E). A palynomorph sample collected near road level across the highway from the welcome center suggests a Famennian 2b age for the lower part of this section (A. Traverse, 2004, personal commun.).

Although fragmentary, the tristichopterid material from this site (also seen at Stop 3) is consistently associated with the same distinctive scale morphology (Fig. 6B). These distinct scales were named *Holoptychius radiatus* from specimens collected in the Blossburg area in the late nineteenth century (Newberry 1889). The type material of *H. radiatus* consists of distinctive scales with the characteristic tristichopterid feature of a raised, tear-drop shaped boss on the internal surface. With the suite of new specimens, this scale morphology can now be associated with lower jaw and skull material (e.g., Fig. 6C). A more complete description of this tristichopterid sarcopterygian (with a new generic attribution) is in order.

Cumulative miles	*(km)*	*Directions and notes*
112.8	(181.5)	Continue southbound on Route 15.
120.3	(193.6)	Take Exit for Route 6, Mansfield/Wellsboro. Take a right at the bottom of the ramp following Route 6 West (towards Wellsboro).
132.7	(213.6)	In Wellsboro, turn left at light (intersection of Route 6 and Route 660) onto Main Street.
132.8	(213.7)	Turn right into parking lot for Penn Wells Hotel. End of Day 1.

DAY 2

Road Log

Cumulative miles	*(km)*	*Directions and notes*
132.8	(213.7)	Turn right on Main Street and continue for one block.
132.9	(213.8)	Left onto Route 287 South.
144.5	(232.5)	Bear right to follow 287 South.
145.2	(233.8)	Right on to Route 414 West.
175.3	(282.1)	Right on to Route 44 North.
180.5	(290.5)	Bear right to follow Route 44 North.
185.8	(299)	Left on to Hyner Mountain Road (look for signs for Hyner Run State Park).
192.7	(310.1)	Right on Route 120 West.
194.7	(313.3)	Pull over on to wide shoulder at outcrop on right.

Stop 5. Red Hill

Coordinates: N41°20.645′ W77°40.800′

Introduction to Red Hill

The Red Hill road cut is a kilometer-long exposure of slightly western-dipping alluvial sandstones, siltstones and paleosols of the Duncannon Member of the Catskill Formation. The western part of the exposure is dominated by channel sandstones. The face of the road cut is quite steep here and reaches a height of 30 m, thus fossil prospecting has been restricted to examination of the frequent rock falls. A few fossil discoveries have been made in the finer-grained rocks that have fallen, but collecting has been minimal in this part of the outcrop due to taphonomic and logistical factors. The lack of collecting, however, is compensated for by the considerable sequence of fluvial strata that can be observed here, indicative of a dynamic Late Devonian alluvial plain.

The eastern portion of the road cut is dominated by finer-grained channel margin and inter-channel siltstones and paleosols. A vertically thin (3 m) but laterally broad (~200 m exposed) sequence of fossiliferous strata in this portion of the outcrop is the source of the abundant fossil remains from Red Hill. The fossiliferous lenses reflect several different styles of deposition from low energy standing water to higher energy lags. The slope of the outcrop is not cut as steeply in these fine-grained layers. The presence of talus and the creation of terraces during fossil prospecting allow more access to the strata for close observation and continued collecting. The talus slopes are good for collecting fragmentary specimens of fish teeth and scales, and plant compressions. Please USE CAUTION when climbing the rock face, and always be aware of traffic at this roadside location.

Red Hill has produced one of the most diverse and abundant samples of life from a Late Devonian continental ecosystem. At least thirteen species of plants have been identified, representing an ecological patchwork of progymnosperm forests, lycopsid wetlands, zygopterid fern glades, and patches of early spermatophytes that occupied sites disturbed by fires. Two newly discovered terrestrial arthropods have been described from Red Hill, a trigonotarbid arachnid and a myriapod. The remains of at least fifteen species of vertebrate have been recovered, including placoderms, an acanthodian, chondrichthyans, palaeoniscid actinopterygians, finned sarcopterygians, and three early tetrapod species. A variety of inter-channel depositional settings formed a wide range of aquatic and terrestrial habitats as a result of the periodic avulsion of meandering rivers across the alluvial plain. These habitats formed a crucible of evolution for plants and animals, including innovations critical to the further development of life on land.

Red Hill Sedimentology

Traditionally, sedimentation in upper alluvial and coastal plain settings has been envisioned as being produced by single-thread meandering rivers. However, the pattern of sedimentological structures at Red Hill conforms to a model of periodic avulsion

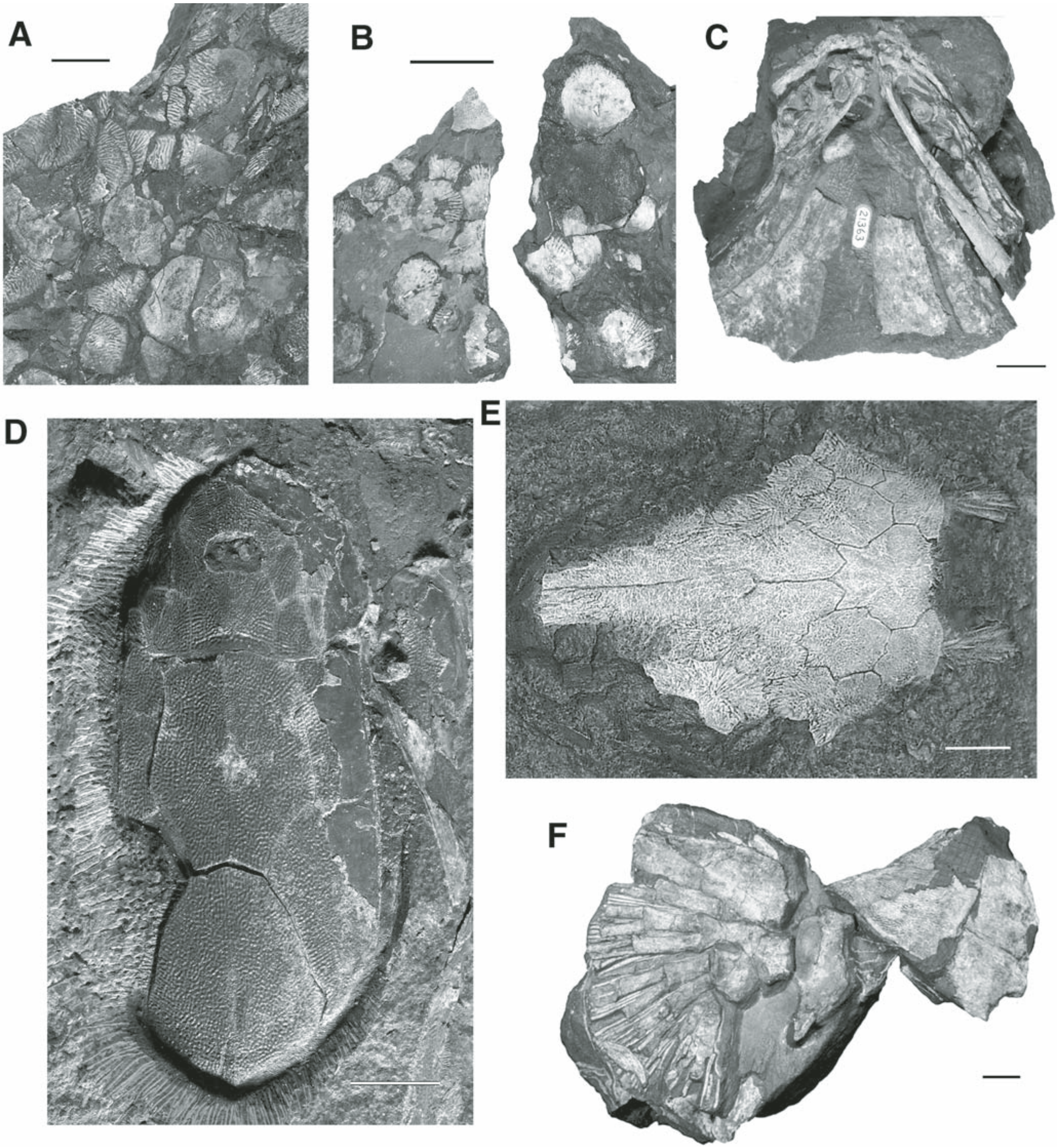

Figure 6. Typical vertebrate fauna from the Catskill Formation along U.S. 15 (Interstate 99) in Lycoming and Tioga counties, Pennsylvania. (A) Scales of porolepiform, *Holoptychius* sp. (B) Scales of tristichopterid, *Holoptychius radiatus*. (C) Rostral portion of lower jaws of *H. radiatus* with submandibulars and gulars. (D) Dorsal view of adult antiarch placoderm *Bothriolepis* sp. from mass mortality zone (E) Partial skull in dorsal view of lungfish, *Apatorhynchus opistheretmus*. (F) Pectoral fin of rhizodontid, *Sauripterus taylori*. Scale bars equal 2 cm.

like that described in recent studies of modern fine-grained fluvial systems that show these systems cycling through two stages with a typical period on the order of 1000 years (Smith et al., 1989; Soong and Zhao, 1994; Slingerland and Smith, 2004). Stage I begins when a channel changes course by permanently breaching its levee. A sediment wedge progrades down-current from the avulsion site resulting in intense alluviation of the floodplain as the system changes from a single channelized flow into rapidly evolving distributary channels. These channels split and coalesce in a complex network while scouring the floodplain to create transient ponds and lakes as they encounter preexisting channel levees and floodplain vegetation. Commonly observed deposits of this stage are: (1) coarser-grained crevasse splays of a variety of lobate, elliptical, or elongate shapes (Smith, 1986; O'Brien and Wells, 1986; Bristow, 1999); and (2) finer-grained lake and distal splay deposits in which rapid burial has preserved organic debris from oxidation. The former are observed at Red Hill in the variety of sandstone bodies ranging in morphology from wedge-shaped lenticular, to flat-bottomed and convex-upward. The latter comprise the main fossiliferous strata at Red Hill, further described below as comprising four taphofacies.

Stage II of the avulsion cycle begins when distributary channels once again follow the regional slope and start flowing subparallel to the parent channel where they are eventually abandoned as flow is captured into a new trunk channel similar in scale to the parent channel that initially avulsed (Smith et al., 1989). Sedimentation rates are low, allowing soil formation to resume on the floodplain. The new trunk channel incises into its earlier avulsion deposits, creating a new meander belt that is relatively narrow and only reworks a small fraction of the Stage I avulsion fill floodplain deposits into meander belt deposits. Evidence at Red Hill for Stage II of the avulsion cycle consists of the extensive paleosols easily observed at the eastern end of the outcrop and the massive channel sandstone bodies observable at the western end of the outcrop.

The considerable lateral and vertical variation within the strata at Red Hill reflects the heterogeneity of depositional facies of the avulsion model. This variation in depositional facies, in turn, results in the uncommon circumstance of a range of taphonomic modes preserving both plant and animal remains at the same site. Four different taphofacies preserve fossil material: sorted microfossil horizons, basal lags, channel-margin and standing-water deposits. Well-sorted microfossil accumulations and basal lag deposits contain abundant, but fragmentary, vertebrate material that may be allochthonous and thus have poor time and ecological fidelity. The channel-margin taphofacies contains isolated and associated vertebrate material, often in discrete lenses. The character of the entombing sediments indicates that the fossils accumulated along the strandline of the aggrading margins of temporary channels in overbank areas after avulsion episodes. Deposits of this sort have the potential to accumulate relatively quickly, and the fact that the taphofacies shows little or no abrasion or pre-depositional weathering of accumulated material indicates that the associated taxa were living penecontemporaneously in the areas near the site of deposition. The standing-water taphofacies is represented by green-gray siltstones with abundant plant material and an occasional occurrence of arthropod and vertebrate remains. The vertebrate remains from this setting are black and "carbonized" suggesting different water chemistry (perhaps more acidic) and diagenetic conditions than other taphofacies at Red Hill. These deposits represent low energy, reducing environments, such as floodplain ponds and distal splay settings that can provide excellent temporal and ecological fidelity.

Red Hill Flora (Table 1)

All the of the well-preserved plant fossils from Red Hill have come from a single gray green siltstone pond deposit at the eastern end of the outcrop, with the exception of a few significant specimens found in a rock that had fallen from the western end. The floral characteristics of Red Hill are typical of a Late Devonian plant assemblage, specifically a subtropical *Archaeopteris* forest. Four *Archaeopteris* leaf morphospecies are dominated by *A. macilenta* and *A. hibernica* (Fig. 7C). This progymnosperm tree is an index fossil for the Late Devonian (Banks, 1980), as is the second most abundant set of plant remains at Red Hill, the zygopterid fern assigned to *Rhacophyton ceratangium*. The early diversification of arborescent lycopsids are represented by numerous decorticated stems (Fig. 7B), some identifiable as *Lepidodendropsis*. Also, well-preserved remains of cormose isoetalean bases and stems have been described as *Otzinachsonia beerboweri* (Cressler and Pfefferkorn, 2005). Two species of spermatophytes are present, including the newly described species *Duodimidia pfefferkornii* (Fig. 7A; Cressler et al., 2010b) characterized by fused symmetric cupule pairs, and *Aglosperma quadrapartita* (Cressler, 2006). The palynological age of the strata make it coeval with other sites preserving the earliest recorded spermatophytes in Belgium and West Virginia (Fairon-Demaret and Scheckler, 1987; Rothwell et al., 1989). Other minor floral elements include the stauripterid fern *Gillespiea* and a variety of barinophytes (Cressler, 2006). Major plant groups found at other Late Devonian sites, but not yet discovered at Red Hill, are the sphenopsids and cladoxylaleans.

Red Hill Fauna (Table 1)

The arthropod fauna discovered at Red Hill is likely only a very limited subset of the invertebrate community present in the floodplain ecosystem. A trigonotarbid arachnid (Fig. 7M; Shear, 2000) and archidesmid myriapod (Fig. 7L; Wilson et al., 2005) have been described from the standing-water taphofacies, but greater diversity is evidenced by enigmatic body impressions, burrow traces and walking traces. The vertebrate assemblage represents a diverse community that was living in aquatic habitats within the alluvial plain of the Catskill Delta Complex. These include bottom feeders, durophages, filter feeders and a wide range of predators. The placoderm assemblage is dominated by the small groenlandaspidid, *Turrisaspis elektor* (Fig. 7D), one of the most common taxa from the site (Daeschler et al., 2003). Lane and Cuffey (2005) recognize a new species of

TABLE 1. RED HILL FAUNA AND FLORA

RED HILL FAUNA

- Chelicerata
  - Arachnida
    - Trigonotarbida
    - Palaeocharinidae
      - ***Gigantocharinus szatmaryi*** Shear
- Myriapoda
  - Diplopoda
    - Archidesmida
      - Zanclodesmidae
        - ***Orsadesmus rubecollus*** Wilson
- Vertebrata
  - Placodermi
    - Phyllolepida
      - Phyllolepididae
        - ***Phyllolepis rossimontina*** Lane and Cuffey
    - Arthrodira
      - Groenlandaspididae
        - ***Groenlandaspis pennsylvanica*** Daeschler
        - ***Turrisaspis elektor*** Daeschler
  - Acanthodii
    - Climatiiformes
      - Gyracanthidae
        - ***Gyracanthus*** cf. ***G. sherwoodi*** Newberry
  - Chondrichthyes
    - Ctenacanthiformes
      - Ctenacanthidae
        - ***Ctenacanthus*** sp.
    - Xenacanthiformes
      - Indet.
    - Insertae Sedis
      - ***Ageleodus pectinatus*** (Agassiz)
  - Osteichthyes
    - Actinopterygii
      - Palaeonisciformes
        - ***Limnomis delaneyi*** Daeschler
        - Indet.
    - Sarcopterygii
      - Dipnoi
        - Indet.
    - Crossopterygii
      - Rhizodontidae
        - cf. ***Sauripterus*** sp.
        - Indet.
      - Megalichthyidae
        - Indet.
      - Tristichopteridae
        - ***Hyneria lindae*** Thomson
  - Amphibia
    - Ichthyostegalia
      - ***Hynerpeton bassetti*** Daeschler
      - ***Densignathus rowei*** Daeschler
      - cf. Whatcheeridae
        - Indet.

RED HILL FLORA

- Zosterophyllopsida
  - Barinophytales
    - **cf. *Protobarinophyton*** sp.
    - ***Barinophyton obscurum*** (Dun) White
    - ***Barinophyton sibericum*** Petrosian
- Lycopsida
  - Isoetales
    - ***Otzinachsonia beerboweri*** Cressler and Pfefferkorn
    - **cf. *Lepidodendropsis*** Lutz
- Filicopsida
  - Zygopteridales
    - ***Rhacophyton ceratangium*** Andrews and Phillips
  - Stauropteridales
    - ***Gillespiea randolphensis*** Erwin and Rothwell
- Progymnospermopsida
  - Archaeopteridales
    - ***Archaeopteris macilenta*** (Lesq.) Carluccio et al.
    - ***Archaeopteris hibernica*** (Forbes) Dawson
    - ***Archaeopteris obtusa*** Lesquereaux
    - ***Archaeopteris halliana*** (Göppert) Dawson
- Gymnospermopsida
  - Pteridospermales
    - **cf. *Aglosperma quadrapartita*** Hilton and Edwards
    - ***Duodimidia pfefferkornii*** Cressler et. al.

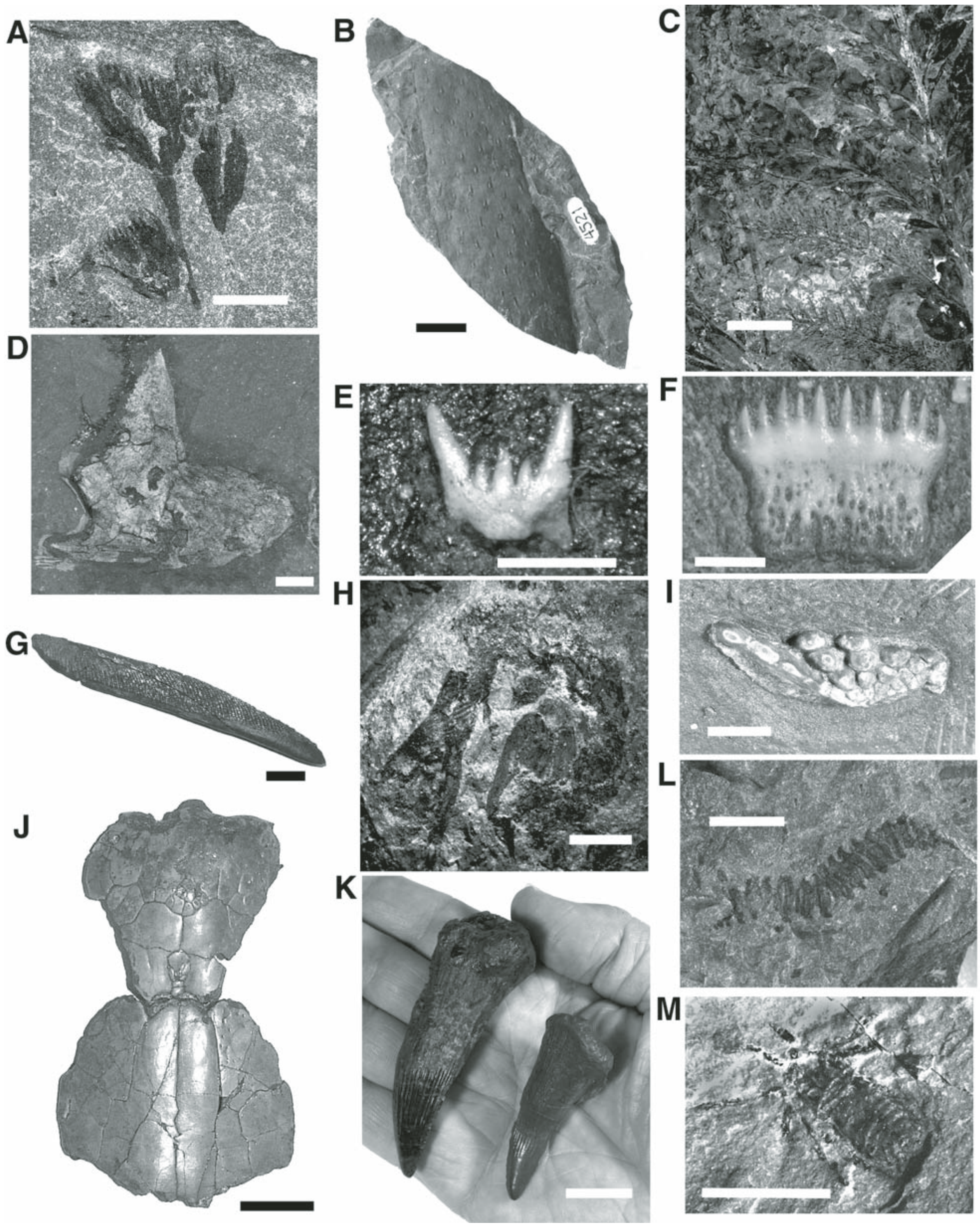

Figure 7. Typical fauna and flora from the Catskill Formation at Red Hill, Clinton County, Pennsylvania. (A) Early spermatophyte, *Duodimidia pfefferkornii*. (B) Lycopod stem, cf. *Lepidodendropsis*. (C) Progymnosperm, *Archaeopteris* sp. (D) Head and truck shields in oblique lateral view of groenlandaspidid placoderm, *Turrisaspis elektor*. (E) Tooth of xenacanthiform chondrichthyan. (F) Tooth of chondrichthyan, *Ageleodus pectinatus*. (G) Pectoral fin spine of gyracanthid acanthodian, *Gyracanthus* cf. *G. sherwoodi*. (H) Body of small actinopterygian, *Limnomis delaneyi*. (I) Small lungfish tooth plate. (J) Skull roof of megalichthyid osteolepidid, gen. et sp. indet. (K) Isolated vomerine teeth of large tristichopterid, *Hyneria lindae*. (L) Millipede, *Orsadesmus rubecollus*. (M) Palaeocharinid arachnid, *Gigantocharinus szatmaryi*. Scale bars equal 2 cm (B, C, D, G, J, K), 5 mm (A, H, I, L, M), and 1 mm (E, F).

Phyllolepis, a cosmopolitan placoderm reaching the Euramerica landmass in the Famennian. Fin spines and pectoral girdle elements of the acanthodian *Gyracanthus* (cf. *G. sherwoodi*) (Fig. 7G) are common, as are small isolated teeth of the chondichthyan *Ageleodus* (Fig. 7F; Downs and Daeschler, 2001). Rare xenacanthiform chondrichthyan teeth have been recognized (Fig. 7E). Among the bony fish, the small palaeoniscid actinopterygian, *Limnomis delaneyi* (Fig. 7H; Daeschler 2000a), and the large tristichopterid sarcopterygian, *Hyneria lindae* (Fig. 7K; Thomson, 1968), are the dominant components. Other sarcopterygians include rhizodontid and megalichthyid (Fig. 7J) forms. Early tetrapod remains are rare and are represented by isolated skeletal elements, although recent analysis suggests that at least three penecontemporaneous taxa are present: *Hynerpeton bassetti* (Fig. 8A), *Densignathus rowei* (Fig. 8B), and a whatcheerid-like form (Fig. 8F, 8I) (Daeschler et al., 2009). Interestingly, taxa such as *Bothriolepis* and *Holoptychius* that are common at most other late Famennian sites in the Catskill Formation are absent at Red Hill, except for *Holoptychius* sp. scales from a rock fall from high in the Red Hill section.

Red Hill Paleoecology

A paleoecological analysis of the Red Hill plant community (Cressler, 2006) characterized the vegetation as a subtropical *Archaeopteris* floodplain forest interspersed with lycopsid wetlands and widespread stands of *Rhacophyton* on the floodplain and along water margins (Figs. 9 and 10). Taphonomic and fossil-distribution evidence was derived from systematic sampling of the floodplain pond deposit. The plant fossils had undergone little or no transport. The evidence provided in that study was interpreted to support a model of habitat partitioning of the landscape by the plants at a high phylogenetic level, a characteristic of mid-

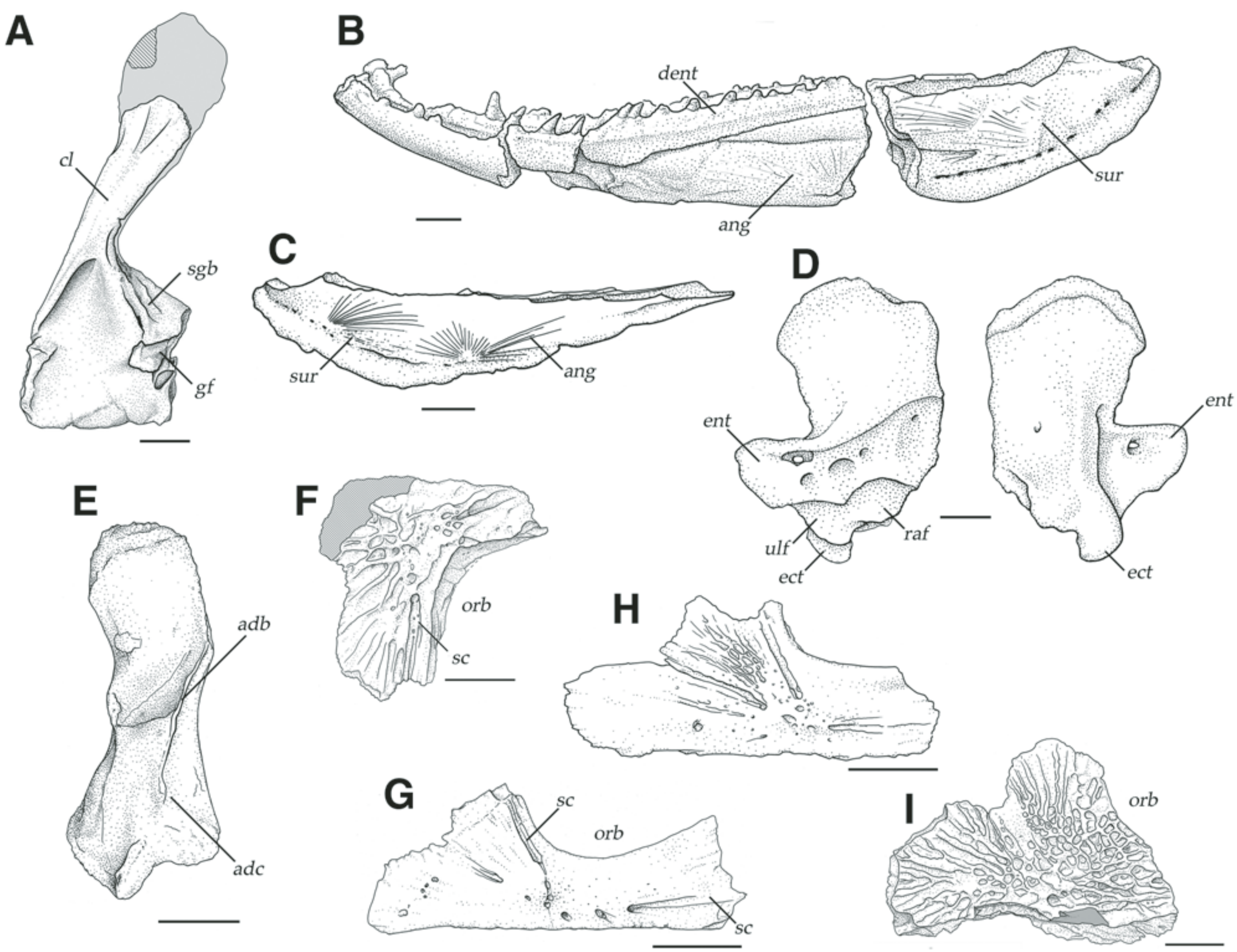

Figure 8. Isolated remains of early tetrapods from Red Hill, Clinton County, Pennsylvania. (A) Left shoulder girdle of *Hynerpeton bassetti*. (B) Left lower jaw of *Densignathus rowei*. (C) Partial right lower jaw. (D) Ventral and dorsal views of humerus (ANSP 21350). (E) Ventral view of femur. (F) Postorbital. (G) Jugal. (H) Jugal. (I) Lacrimal. Abbreviations: adb—adductor blade; adc—adductor crest; ang—angular; art—articular; cl—cleithrum; dent—dentary; ect—ectepicondyle; ent—entepicondyle; gf—glenoid fossa; it—internal trochanter; orb—orbit; raf—radial facet; sc—sensory canal; sgb—supraglenoid buttress; sur—surangular; tf—tibial facet; ulf—ulnar facet. Scale bars equal 1 cm except in F and I, where scale bars equal 0.5 cm.

Paleozoic plant communities (DiMichele and Bateman, 1996). The pattern of plant distribution at Red Hill is similar to that seen in other Late Devonian paleoecological studies (Scheckler, 1986a, 1986b; Rothwell and Scheckler, 1988; Scheckler et al., 1999). Lycopsids dominated the wettest portions of the floodplain, whereas *Rhacophyton* dominated the poorly drained floodplain margins. *Archaeopteris* grew in the better-drained areas of the landscape and seed plants grew opportunistically. At Red Hill the seed plants apparently flourished following fires that cleared the *Rhacophyton* groundcover (Cressler, 2001). This is indicated by a succession of *Rhacophyton*-to-charcoal-to-spermatophyte remains within the small-scale stratigraphic profile (Cressler, 2001; 2006). Fires presumably were associated with the wet and dry seasonal cycle that prevailed in the Late Devonian Catskill Delta system, as also indicated by the calcretes and vertic structures in the paleosols.

The floodplain habitats at Red Hill provided a range of conditions for the cohabitation of plants and animals (Cressler et al., 2010a). Plant communities were partitioned on the floodplain across a range of environments from elevated and better-drained levees to low, wetland habitats (Cressler, 2006). The aquatic settings include open river channels, shallow channel margins, anastomosing temporary channels, and floodplain ponds in interfluves that were subject to periodic flooding. This heterogeneity is expressed even on the local scale at the Red Hill site, as might be expected with the avulsion model of floodplain aggradation. Seasonal flooding and drying probably had a significant role in the annual cycles of plants and animals and their evolution.

Cumulative *miles*	*(km)*	*Directions and notes*
194.7	(313.3)	Continue on Route 120 West.
195.7	(314.9)	After crossing over bridge at Young Woman's Creek, turn right onto School House Road.
196.0	315.4)	Turn left into rear parking area of the Chapman Township Municipal Building (white building with maintenance yard in rear). Park in the rear parking area.

Figure 9. The progymnosperm *Archaeopteris* and understory fern *Rhacophyton* growing on the edge of a Devonian floodplain pond. Illustration courtesy of Stephen Greb.

Figure 10. *Rhacophyton*-dominated Devonian swamps, but arborescent lycopsids became increasingly common in the Carboniferous. Illustration courtesy of Stephen Greb.

Stop 6. Red Hill Field Station

The people of Chapman Township have allowed us to renovate the second floor of their municipal building to use as our "Red Hill Field Station and Museum." Mr. Doug Rowe is the driving force behind this facility. The Field Station serves as an important educational tool for visitors to the Red Hill site, including local school groups, fossil clubs, and casual visitors. It also provides a place for our research group to get out of the hot, cold, or wet weather while working at Red Hill. Please take some time to explore in the Field Station. Examples of most of the taxa from the Red Hill site are on display. Most are original fossil material. Almost 1,000 specimens from Red Hill are catalogued in the collections at the Academy of Natural Sciences in Philadelphia. Some of those specimens are presented as casts and photographs at the Field Station.

Cumulative miles	*(km)*	*Directions and notes*
196.0	(315.4)	Turn right out of Municipal Building parking area.
196.3	(315.9)	Turn left onto Route 120 East.
197.3	(317.5)	Passing Red Hill exposure.
219.7	(353.8)	Turn left at light to stay on Route 120 East in to Lock Haven.
220.8	(355.3)	Turn right to stay on Route 120 East.
221.4	(356.3)	Stay in right lane, and follow signs for Milesburg/Route 220 South
228.7	(368.1)	Take exit for Route 80. End of Road Log.

ACKNOWLEDGMENTS

There have been a large number of participants in our ongoing work in the Catskill Formation. We thank all for their dedicated work toward building a better understanding of the paleobiological and geological nature of the Catskill Formation in Pennsylvania. We would like to especially mention Douglas Rowe, Janice Pycha, Rudy Slingerland, Daniel Peterson, Stephen Greb, Frederick Mullison, Jason Downs, John Sime, and the Pennsylvania Department of Transportation for their invaluable contributions to this research and assistance in creating this field guide.

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