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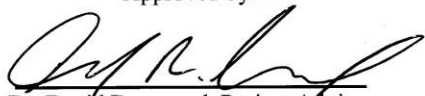
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Paleoecological Analysis of a Late Devonian Catskill formation
Using Vertebrate Microfossils

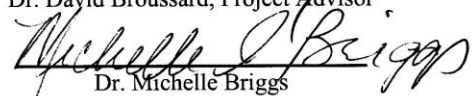
Presented to the faculty of Lycoming College in partial fulfillment of
the requirements for Departmental Honors in Biology

By
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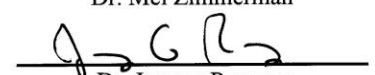
Dr. David Broussard, Project Advisor



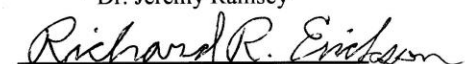
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Abstract

The Red Hill site located along a road cut near Hyner in Clinton County, Pennsylvania, represents a floodplain ecosystem during the late Famennian Stage of the Upper Devonian Period. Fossil vertebrates from the Red Hill site include those of sarcopterygian fish, placoderms, acanthodians, actinopterygian fish, freshwater sharks, and early tetrapods. Vertebrate microfossils are often used to assess the paleoecology of extinct ecosystems. Differences in species richness in similar geological sediments can indicate differences in the paleoecology between locations. Fossils were collected from two distinct strata: an oxidized stratum representing the sediments from the main river channel margins and a reduced stratum representing sediment from highly vegetated floodplain ponds. Four quarries were excavated at the Red Hill site with two quarries in each strata. Vertebrate fossils were identified and counted from each quarry. A total of 293 vertebrate fossils were recorded. These fossils included teeth and scales of *Hyneria lindae*, dermal bony plates of *Groenlandaspis* placoderms, scales of Megalichthyid sarcopterygian fish, *Gyracanthus* sp. spines, teeth of *Ageleodus pectinatus* (freshwater shark), and body impressions of *Limnomis delaneyi*. A total of 17 *H. lindae* scales, 3 *H. lindae* teeth, 12 placoderm plates, 5 megalichthyid scales, 2 *Gyracanthus* spines, and 2 *Limnomis* partials were found in the reduced strata. A total of 128 *H. lindae* scales, 33 *H. lindae* teeth, 72 placoderm plates, 37 megalichthyid scales, 11 *Gyracanthus* spines, and 10 *Ageleodus pectinatus* teeth were collected from the oxidized strata. From these data, I concluded that the main river channel habitats contain higher densities of vertebrates than the still water ponded environments. My findings also possibly indicate that the flowing water and ponded water types of habitats preserved at Red Hill supported different types of vertebrate communities.

Introduction

Paleoecology is the study of the network of relationships between organisms and their environment in the geologic past (Lawrence 1971). Paleoecological analysis can use vertebrate fossils to reconstruction past environments, elucidate population structures, and determine survivorship curves (Blob and Fiorillo 1996). Emphasis is placed upon taphonomy, a process that leads to the conversion of organic matter into fossil deposits. Understanding taphonomic conditions is essential to correctly interpreting fossil origin within specific strata, as remains could be transferred from one location to another via fluvial events (Gifford 1981).

Microfossils, defined as fossilized remnants of teeth, bone fragments, and scales, are often used to estimate species density, diversity, and taxa richness in extinct ecosystems. These differences in species richness in similar geological sediments can indicate differences in the paleoecology between locations (Blob and Fiorillo 1996). Additionally, the sizes of microfossils can be directly related to the overall body size of the individual: the larger the scale, tooth, or plate, the larger the fish. Collecting significant numbers of microfossils, identifying the species present, and measuring the size of selected fossils can provide additional insight into the paleoecology of an area (Blob and Fiorello 1996). The presence or absence of certain species can indicate the presence of either physical or chemical barriers between different bodies of water (Griffiths 2006).

One of the most productive sites for vertebrate fossils in north-central Pennsylvania is Red Hill, lying along Route 120, just west of the village of Hyner, in Clinton County, Pennsylvania (Figure 1). A thirty meter high vertical exposure of a red bed formation dated to the Famennian Stage of the Late Devonian (approximately 365 million years ago) was exposed when a large road cut was excavated along the West Branch of the Susquehanna River during the

1970's. This site represents sediment deposited along river channel margins and within flood plain ponds along the ancient Catskill River Delta (Cressler 2006; Daeschler 2009; and Cressler 2010).

The Devonian Period is often known as the “age of fishes” due to the rapid growth in the number of gnathostome species (Dahl et al. 2010). The average size of marine vertebrates also increased significantly during this time period, and the first large “high energy” vertebrate predators began to emerge. The fossil record indicates that average fish body size increased gradually from a few centimeters in the Cambrian Era to tens of centimeters during the Silurian. But by the end of the Devonian, large predatory fish several meters long had evolved, and fish species diversity had increased dramatically (Dahl et al. 2010).

The Late Devonian was distinguished by the development of ecosystems with modern characteristics (DiMichele and Hook 1992).

Land plant diversity increased significantly to include numerous terrestrial seed bearing plants, including ground cover, shrubs, vines, and woody progymnosperm trees, the predecessors of modern day conifers (Cressler 2006). Rapid land plant expansion during the Devonian



Figure 1: Location of the Red Hill Site in Clinton County, Pennsylvania, USA. Image Credit: Cressler 2006.

significantly altered the composition of the earth's atmosphere and drastically influenced the global climate. The rise of land plants significantly contributed to the growth and increase in aquatic vertebrate populations and the radiation of new species throughout the globe (Dahl et al. 2010, Bambach 2002)

Prior studies found that vertebrate microfossils help estimate faunal abundance, determine habitat partitioning, and reconstruct paleoecology from Cretaceous aged strata (Larson and Currie 2006; Lyson and Longrich 2010; Wilson 2008). The current study is the first to use vertebrate microfossil analysis to determine Devonian paleoecology. Cressler (2006) first described the paleoecology of Red Hill. He excavated a total of 12 quarries along a 65 meter transect within the reduced strata to reconstruct the layout of floodplain ponds by studying the distribution of Late Devonian plant species. Cressler et al. (2010) created a comprehensive list of the vertebrate and invertebrate fauna found and identified at Red Hill over the past twenty years (Table 1). To my knowledge, no prior study has attempted to describe the paleoecology of a Late Devonian aged site using variation in vertebrate microfossils. This goal of my study was to quantify variation in vertebrate microfossils between two different strata at the Red Hill site in Clinton County. Based on previous descriptive studies of the vertebrate fauna at Red Hill, I predicted that vertebrate microfossil density would be greater in strata representing river channel margins than in strata representing floodplain ponds. The findings from my research could offer insight into the habitat partitioning of Late Devonian vertebrates during the rise of early tetrapods.

Animalia	
Chelicerata	
Arachnida	
Trigonotarbida	
Palaeocharinidae	
Gigantocharinus szatmaryi Shear	
Myriapoda	
Diplopoda	
Archidesmida	
Zancloidesmidae	
Orsa desmus rubecillus Wilson	
Vertebrata	
Placodermi	
Phyllolepida	
Phyllolepididae	
Phyllolepis rosimontina Lane and Cuffey	
Arthrodira	
Groenlandaspidae	
Groenlandaspis pennsylvanica Daeschler	
Turrisaspis elector Daeschler	
Incertae Sedis Acanthodii	
Climatiiformes	
Gyracanthidae	
Gyracanthus cf. G. sherwoodi Newberry	
Chondrichthyes	
Ctenacanthiformes	
Ctenacanthidae	
Ctenacanthus sp.	
Insertae Sedis	
Ageleodus pectinatus (Agassiz)	
Osteichthyes	
Actinopterygii	
Palaeonisciformes	
Limnomis delaneyi Daeschler	
Sarcopterygii	
Dipnoi	
Indet.	
Crossopterygii	
Rhizodontidae	
cf. Sauripterus sp. Indet.	
Megalichthyidae	
Indet.	
Tristichopteridae	
Hyneria lindae Thomson	
Amphibia	
Ichthyostegalia	
Hynierpeton bassetti Daeschler	
Densignathus rowei Daeschler	

Table 1: Faunal diversity at the Red Hill site. From Cressler 2006

Site Description

Two supercontinents comprised most of the landmass during the Late Devonian. Red Hill was located along the western edge of the Acadian Mountains, running north to south across the supercontinent of Laurentia. This landmass consisted of the North American and European tectonic plates (Kent 1985). The Red Hill site represents the upper reaches of an alluvial flood plain of the Catskill River Delta Complex (Cressler 2006). The Catskill Delta complex was a

sprawling wedge that resulted from large rivers draining the massive Acadian mountains that formed during the collision of the North America, Europe, Avalon Terrane and other microcontinents during the Acadian Orogeny (Cressler 2006). Three major environmental zones existed along the western edge of the Acadian Mountains: alluvial plains, fluvial plains, and a marine shelf (Woodrow et al. 1973). The Catskill Delta represents the largest accumulation of sediment from the highlands formed during the Acadian orogeny. This large basin once covered an area from central New York through Pennsylvania and extended south to eastern Tennessee and across to eastern Ohio (Flail 1985). Increased cyclical precipitation led to significant erosion in the upper reaches of this river system, leading to large scale deposition of sediment throughout this delta. This wide delta consisted of low-gradient plains interspersed with winding streams (Cressler 2006, Figure 2).

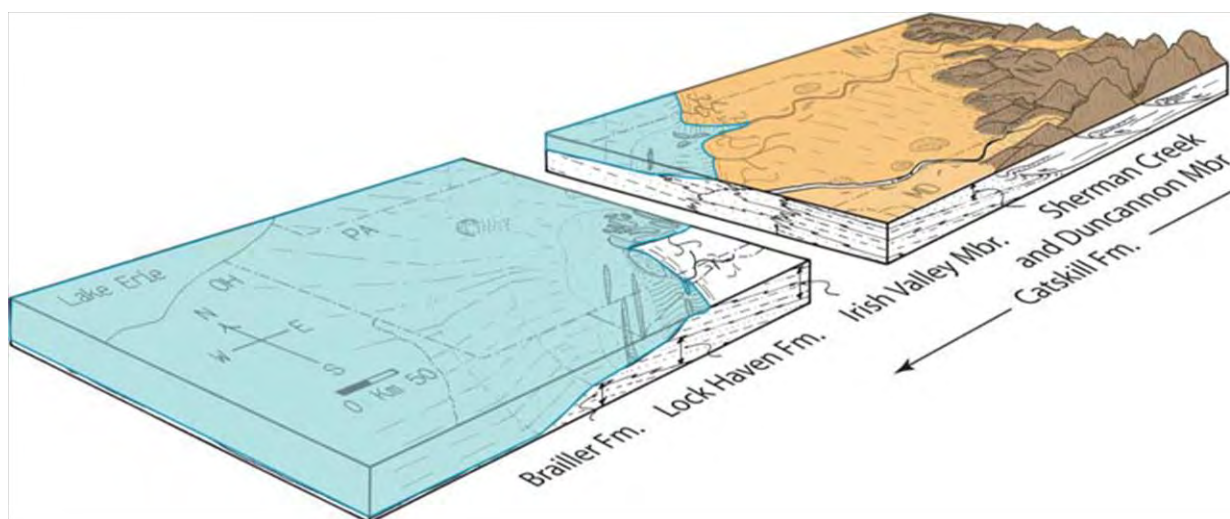


Figure 2. General depositional setting of the Appalachian basin during deposition of the strata at Red Hill. The red asterik marks the approximate location of the Red Hill Site during the late Fammenian. From Cressler et al. 2010.

The Red Hill site lies along Route 120 between the villages of Hyner and North Bend in Chapman Township, Clinton County, Pennsylvania. A road cut has left a nearly one kilometer

stretch of a 30 meter high vertical exposure of the Duncannon member of the Catskill Formation (Figure 3). Nearly horizontal layers of fluvial sandstones, mudstones, siltstones, and paleosols compose the majority of the fossiliferous strata found at Red Hill. Geologic data suggests there was no marine influence at this site during the Late Devonian (Cressler 2006).

Two distinct fossiliferous layers are found at Red Hill; each layer represents a separate paleohabitat (Figure 4). An oxidized layer of mudstones, siltstones, and palaeosols represents the overbank deposit of an ancient river channel. Sediment was deposited on the overbanks of streams during avulsion events. Many of the microfossils within this layer are found within vertically narrow lenses (Figure 5). Cressler (2006) and Daeschler et al. (2009) proposed that these lenses represent vertebrate material

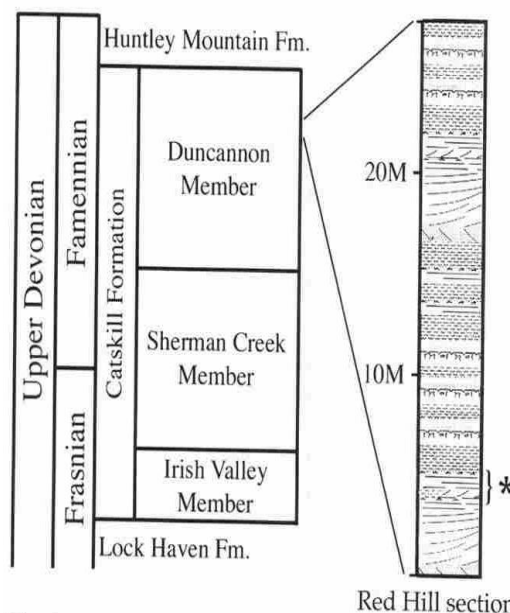
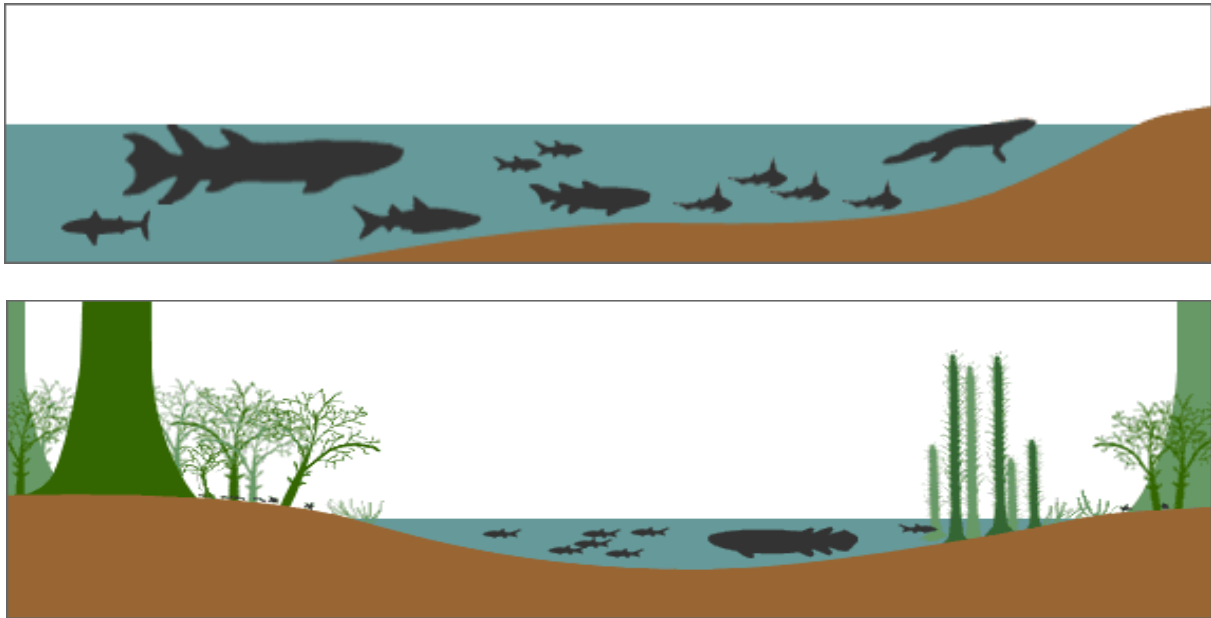


Figure 3: Geologic Setting of Red Hill. Image Credit Daeschler et al. 2009.

deposited in shallow basins on the banks of the main channels during avulsion events. When the water levels receded, associated vertebrate material remained within these basins until additional sediment from subsequent avulsion events was deposited, preserving the integrity of the lens. Many of the microfossils found within these lenses show little wear patterns, indicating that many of the remains present represent species that inhabited the immediate area around the time of deposition (Daeschler et al. 2009)

A two meter thick layer of reduced gray-green sediment at Red Hill lies below the strata representing channel margins. Daeschler et al. (2009) postulated that this layer of siltstone and

sandstone formed as yearly floods deposited sediment in oxbow lakes paralleling the flowing waterways of the Catskill Delta. These oxbow lakes were likely unconnected to the main river channel except during periods of extremely high water. This layer is characterized by a high density of plant remains interspersed with sporadic vertebrate microfossils. Noticeable wear patterns led Daeschler et al. (2009) to propose that some of these microfossils were transported into these flood plain ponds during high water events. Cressler (2006) and Cressler et al. (2010) found several specimens of fully articulated *Limnomis delaneyi*, an early actinopterygian fish, within these reduced layers. These specimens were often found together in small schools, indicating a potentially rapid drop in dissolved oxygen levels that resulted in fish kills (Cressler 2006). The presence of articulated specimens of *Limnomis* indicates that these ponds were potentially suitable habitat for a range of aquatic vertebrates.



**Figure 4: Artistic representations of the river channel margin habitat (top) and the floodplain pond habitat (bottom).
Image Credit: Dennis Murphy**

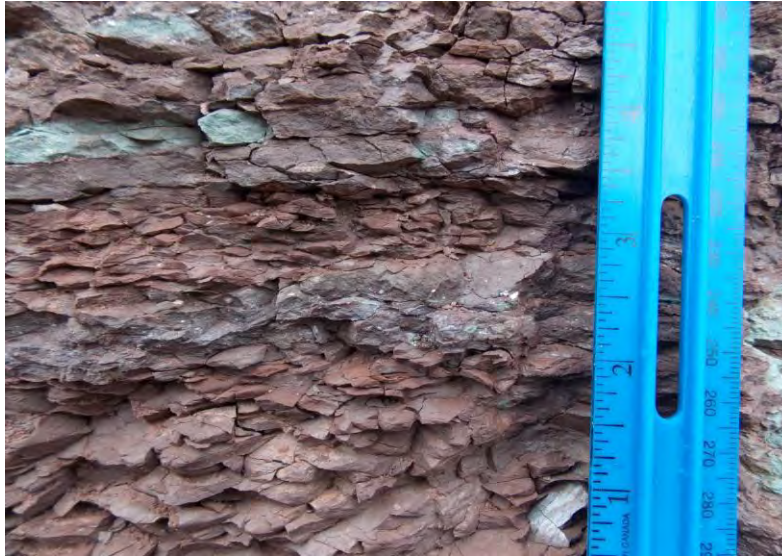


Figure 5: A cross-section of a 3cm thick microfossil lens within the river channel facies

A vast diversity of floodplain habitats have been proposed by Cressler et al. (2010) by combining sedimentological and paleobotanical data with a study of modern fine particulate fluvial systems (Figure 6). Cressler identifies two distinct stages in modern fluvial systems cycle. The first stage occurs when a main river channel breaches its banks. This leads to the creation of numerous floodplain ponds and a series of new channels that are bound by vegetation and topographic changes. Stage two occurs when a new main channel is carved upon the floodplain and water is redistributed away from many of the smaller floodplain water bodies. This causes the abandonment of many smaller channels, leaving some floodplain ponds disconnected from the main river system. These floodplain ponds were likely connected to the main river channel only during significant high-water events, creating habitat largely void of main channel influence (Cressler 2006). These ponds could have provided an environment suitable for spawning grounds and nursery habitat, and would have provided a unique ecological niche to be filled by vertebrates.



Figure 6: A modern-day example similar to the depositional model proposed by Cressler et al. (2010) from the Saskatchewan River, Canada. Image credit: Cressler et al. 2010.

Paleoclimate

Fossil evidence suggests that the red beds of the Catskill formation represent an alluvial floodplain that was located just south of the equator. Temperatures were likely warm to hot throughout most of the year. Faunal evidence, including the diversity of invertebrates found throughout the Catskill formation, indicate that a subtropical climate existed throughout the Famennian stage. Geologic data suggests that rainfall was likely highly seasonal over much of the continent. This theory is supported by the presence of evaporates, or mineral deposits that form during xeric conditions (Woodrow et al. 1973).

Cressler (2006) also concluded that significant seasonal variability existed at the Red Hill site. The abundance of charcoal throughout the reduced layer indicates that large-scale fires occurred periodically, likely during dry seasons. These remains represent some of the earliest

records of charcoal on the globe (Cressler 2001). *Archaeopteris* branches were likely deciduous, presumably as a dry season adaptation (Dimichelle et al. 1992). The presence of dense mats of *Archaeopteris* foliage suggests that these branches were shed around the same time. Plant beds suggest that storms and flooding were regular phenomena (Cressler 2006).

The presence of paleoverisols at Red Hill shows strong support for a wet and dry climate during the Late Devonian (Cressler 2006). Vertisols are a clay-based soil that shrink and swell considerably with moisture levels. They are found globally and characterize regions with distinct wet and dry seasons. Slickensides, wedge shaped aggregates, and mukgara (large cracks that form when soils shrink during dry periods) are both commonly associated with vertisol soils, and all relate to the constant swelling that occurs when the soil becomes saturated (Coulombe et al. 1996). Paleoverisols are the dominant component of the red matrix above and below the oxidized plant layers at Red Hill. The thick paleosol layer above the reduced plant layer is interspersed with vertical cracks that are characteristic of mukgara. These cracks were filled with water and sediment, producing anoxic conditions and left distinct green-gray vertical lines throughout the paleoverisols layers (Cressler 2006).

The depositional model described by Cressler (2006) indicates that flooding was a regular phenomenon at Red Hill. Cressler theorized that monsoon-like rains were a common occurrence throughout Laurentia during the Late Devonian. Plant remains found within the reduced layer support the hypothesis that flooding occurred at regular time intervals. Silt particle sizes within the reduced layers indicate that most of the plant remains were carried into these ponds under low energy avulsion events. However, multiple layers of mud-pebble conglomerate suggest that high energy flooding events also occurred. Rapid rise in water levels occurred during these

events, suggesting that short burst of significant precipitation also accompanied extended periods of steady rain (Cressler 2006).

Red Hill Flora

Terrestrial plants became increasingly complex throughout the Devonian. Bateman et al. (1998) categorized plant evolution into four successive phases. The first phase was the evolution of biochemical pathways in the earliest single celled ancestors of land plants. These cyanobacteria and early algal cells arose prior to the start of the Ordovician. The first true land plants arose during the Early to Middle Ordovician and resembled modern day bryophytes. They were low growing, lacked vascular tissues, and lacked differentiation between roots, leaves and stems (Algeo and Scheckler 1998). By the end of the Ordovician and into the Early Silurian, terrestrial plants had already begun to diverge into bryophytes, mosses, liverworts, and vascular plants, the same four major clades that exist today (Bateman et al. 1998). Bateman (1998) denotes this evolutionary period as the anatomical phase. Evidence for the first spore tetrads and the rise of alteration of generations dates to the Middle Ordovician and the Early Silurian (Kendrick and Crane 1997, Bateman et al. 1998).

Small tubes that resembled trachea are evidence that vascular tissue began developing during the Late Silurian and Early Devonian. Early vascular plants were still miniscule in stature (approximately 10 centimeters tall), and were confined to low-lying, moist areas because they relied on water for fertilization (Kendrick and Crane 1997). These plants lacked developed root systems and subsequently had very little effect on their physical environment. The earliest evidence of forked root systems, thought to belong to early lycopsids, is derived from palaeosols dated to the late Pragian Stage during the Early Devonian (Algeo and Scheckler 1998). Terrestrial plants also began to develop more advanced reproductive methods during the Early

Devonian; the tetrad spore system seen in fossils from the Ordovician slowly gave way to more highly developed, single spores (Kendrick and Crane 1997).

Arborescence (tree-like characteristics) first developed during the Middle Devonian. Mid-sized tree species representing cladoxylalean ferns, lycopsids, and the earliest progymnosperms arose in the Late Givetian (Figure 6) and proliferated throughout the remainder of the Devonian period. These forms grew into mid-sized trees and shrubs that began to dominate much of the landscape (Algeo and Scheckler 1998). Well-developed root systems also arose simultaneously, allowing plants to grow taller and inhabit dryer environments.

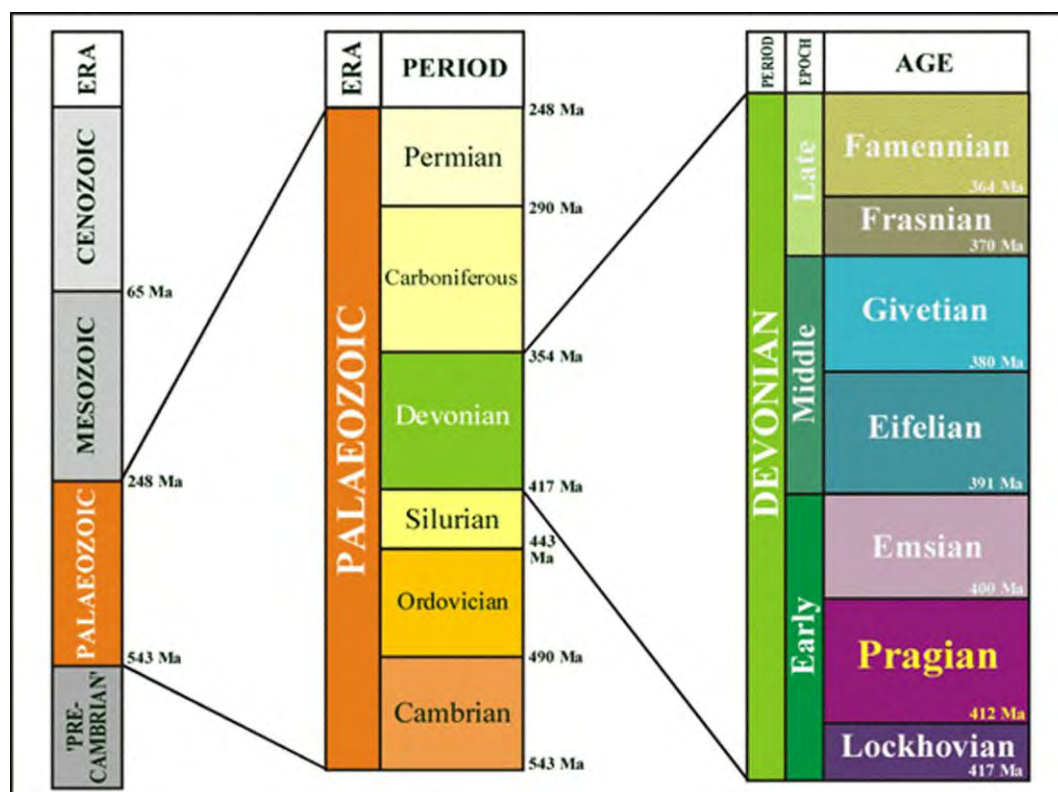


Figure 7: Timescale of the ages of the Devonian. Image Credit: University of Aberdeen.

By the Late Devonian, the first multistoried forests with ground cover, shrubs, vines and large trees covered much of the continents. Woody progymnosperm trees, the predecessors of modern day conifers, flourished during this period (Cressler 2006). Archaeopterid

progymnosperms were among the most common trees species to develop. These massive trees reached heights of over thirty meters and could possess trunk diameter up to 1.5 meters across (Cressler 2006). *Archaeopteris* were also deciduous, allowing them to conserve energy during cyclical dry periods. These species shed their lateral leaf branches annually, creating thick mats of leaf litter that helped to regulate soil moisture and pH, effectively altering soil conditions that favored the further spread of land plants (Algeo and Scheckler 1998).

Heterospory (production of various sized spores) developed during the Devonian. Over time, morphological adaptations led to the development of the first true seeds. These early seeds consisted of a single spore that developed into a megagametophyte with a protective covering; this covering aided in the process of fertilization by a microgametophyte. This new reproductive method prevented desiccation of gametes and allowed for dispersal into previously uninhabitable environments. The development of seed-bearing plants, deep penetrating roots, and tall, woody trunks allowed for rapid increases in plant diversity throughout the Late Devonian and the Carboniferous (Algeo and Scheckler 1998).

Cressler (2006) conducted a paleoecological overview of the flora at Red Hill to understand habitat partitioning by plant taxa in Late Devonian forests. Cressler's study focused on a meter thick layer of reduced sandstone and siltstones that represented ponded environments upon the floodplain. He excavated a dozen small quarries along a 64 meter transect that spanned from the shoreline toward the middle of the floodplain pond. In each quarry, Cressler created flat bedding surfaces that ranged in size from 0.13 to 0.51 square meters. He then removed layers of rock ranging from three to eight centimeters. After the removal of each subsequent rock layer, Cressler laid down a grid, and identified all plant remains at randomly selected coordinates (Cressler 2006).

Cressler (2006) determined that plant material was most often deposited into these floodplain ponds under low energy conditions. Occasional evidence, such as the presence of pebbles and associated layer of vertebrate remains, support the theory that high-energy flooding events occasionally deposited organic material into these floodplain ponds. Cressler found that *Archaeopteris* remains were the most commonly identified plant fossil found during his project. Numerous branches with leaves, including one with identifiable sporangia, were found throughout the matrix. *Rhacophyton* ferns constituted 38% of the identifiable plant remains, lycosid stem fragments consisted of 4.5% of remains, and remains of early gymnosperms and barinophytes composed the remaining plant specimen identified (Cressler 2006).

Numerous charcoal fragments were littered throughout the matrix. Analysis showed that the majority of the charcoal fragments were from *Rhacophyton* species; no evidence of *Archaeopteris* charcoal remain has yet been found. Cressler (2001) concluded that these remnants were evidence of the earliest know wildfires. *Rhacophyton* were shallowly rooted ferns. Cressler concluded that these species would have been most susceptible to desiccation during cyclical dry seasons that characterized the Catskill Delta during the Late Devonian. These fires were ignited by the first storms at the beginning of the wet season, and charcoal fragments were washed into water bodies during the yearly flooding events (Cressler 2001).

The terrestrialization, growth, and diversification of plants gave rise to perhaps the greatest oxygenation event in Earth's history (Dahl et al. 2010). Berner (2006) estimates oxygen concentration peaked at approximately 25% atmospheric concentration during the Early Devonian, a level well above the present atmospheric levels (PAL) of 21%. Over the next thirty million years, oxygen rates plummeted to a mere 12% of the earth's atmosphere. Levels slowly rose over the next 100 million years; however, atmospheric oxygen levels did not reach PAL

until the Middle Mississippian (Berner 2006). Ward et al. (2006) theorized that this drop in oxygen resulted in the Frasnian-Famennian extinction event, and briefly depressed vertebrate species diversification. The cause of this large decrease in oxygen remains uncertain, but evidence suggests that oxygen levels dropped in marine environments across the globe. Goodfellow et al. (1988) suggest that the rapid decline in oxygen levels and the rise in marine anoxic conditions are characteristic of a large-scale meteor impact.

Even though oxygen levels declined during the Late Devonian, Dahl et al. (2010) suggests that initial increases in oxygen levels facilitated the growth of species and led to the rise of the high energy predators that appearing in the Middle and Late Devonian. In addition to significantly increasing oxygen levels, Dahl et al. (2010) postulated that the rise of terrestrial plants also intensified the hydrological cycle by accelerating ground water evaporation into the atmosphere. Increased precipitation levels facilitated greater levels of erosion and the swift transport of nutrients into aquatic ecosystems, facilitating the development of a larger trophic base. This larger trophic base in turn facilitated larger populations of aquatic animals, which would have intensified rates of speciation (Dahl et al. 2010). Clack (2012) suggests that this decline in atmospheric oxygen could have favored the rise of early tetrapods. Clack (2012) explores the possibility that decreased oxygen levels in aquatic environments would have favored the development of air gulping. The great oxygenation resulting from the rise of terrestrial plants fostered increased species diversity and allowed for species to grow to a larger size, but Clack (2012) suggests that the period of low oxygen also could have favored traits that led to the first tetrapod lineages.

The impacts of terrestrial plants on Late Devonian climate and global ecosystems cannot be understated. Plants transformed barren rock into nutrient rich soils in their quest global

dominance (Algeo and Schekler 1998). Newly formed soils were easily eroded during large avulsion events toward the end of the Devonian. Rivers sprawled over the continents, leading to a dramatic increase in freshwater habitat availability. Fossil and geologic evidence suggests shallow streams meandered through thick vegetation-choked ponds, and large rivers with deep channels cut across landmasses. Numerous animal species adapted to these new habitats, fostering the emergence of the first tetrapods (Cressler 2006).

Rise of Vertebrates

Fishes were the first vertebrates to appear in the fossil record. A rapid increase in fish species diversity occurred during the Devonian Period. The history of vertebrates can be traced to *Pikaia gracilens*, an early cephalochordate found in shale formations of British Columbia dating to the Middle Cambrian. This species possessed a notochord, a dorsal nerve cord, and fin rays similar to modern lancelets (Long 1995). The earliest fish, known as agnathans, do not appear in the fossil record until the Early Ordovician. These early fish lacked jaws and teeth. However, the development of paired limbs, dentine-like tissue, the sensory line system, complex eye muscle patterns, and semicircular canals within the inner ear all first arose in early agnathans. These early fish species flourished until the Early Devonian (Long 1995).

The first gnathostomes, or jawed fishes, likely arose during the Late Ordovician, but significant osteichthyan material does not appear until the Late Silurian (Yu et al. 2010). Gnathostomes possessed developed jaws, jointed gill arches, and retained the complex lateral line systems and inner ear structures of earlier agnathans (Janvier 1996). Chondrichthyans (cartilaginous fishes) were among the earliest jawed vertebrates to appear. Fossilized placoid scales have been dated to the Early Silurian, but these early cartilaginous species likely lacked teeth and functional jaws (Long 1995). The first true chondrichthyan fossils date to the Early

Devonian, when teeth began to appear in the fossil record. By the end of the Devonian, more than 30 species of chondrichthyans were found world-wide (Long 1995).

The earliest sharks appear to be closely related to the placoderms, another family of fish that flourished throughout the Devonian. Placoderms first appear in strata dating to the Silurian Period. These early jawed fishes possessed bony plates that formed a protective covering on their head and trunk. Fossil evidence suggests placoderms and chondrichthyans arose from a common ancestor: both groups possess external claspers for mating, eyestalks, similar pelvic fin structure and anatomically similar braincases (Long 1995). Placoderm diversity increased rapidly throughout most of the Devonian, with members exploiting a range of habitats. Large predatory species, such as *Dunkleosteus*, likely attained lengths of over 6 meters. Many of these species filled the top predatory niches prior to the rise of sarcopterygian (lobe-finned) fishes (Long 1995).

The origin of the earliest osteichthyans (bony fishes) dates back to the Late Silurian. Osteichthyans developed an internal bony skeleton, highly evolved gill arches, and patterns of overlapping scales (Long 1995). Swim bladders also developed within this group, allowing fish to regulate buoyancy, thus saving substantial amounts of energy and allowing pectoral fins to evolve for breaking and maneuverability, rather than providing lift. Swim bladders were eventually modified in lungfish and some sarcopterygians to function as a primitive gas exchange organ, setting the stage for the rise of the first air breathing organisms (Long 1995).

Osteichthyans diversified into three main groups during the Early Devonian: the sarcopterygians, dipnoans, and actinopterygians. Remains of actinopterygians, or ray-finned fish, dating to 410 million years ago represent the earliest evidence of bony fish species. This group possessed a single dorsal fin, long and slender bodies, and extended jaws with numerous small

teeth, characteristics distinguishing them from other osteichthyans (Long 1995). This group continued to diversify throughout the Devonian and by the Carboniferous they were dominant fish fauna. In terms of diversity, actinopterygians are still the largest taxonomic grouping of fish species today (Long 1995).

Dipnoans, (lungfish) arose during the Early Devonian. The earliest lungfish had thick rhombic scales, a heterocercal caudal fin, and two dorsal fins and resembled other early sarcopterygians. Porolepiform and Osteolepiform sarcopterygians appear in the fossil record around the same time as dipnoans; however, their phylogeny is unclear. Sarcopterygians are distinguished by their unique hinged braincase, that divides into two sections by an intracranial joint. Sarcopterygians have well-developed labyrinthodont fangs accompanied by a series of smaller teeth and robust shoulder girdles. Ossified pectoral fins first developed in early sarcopterygians while primitive limb bones developed in the fins of osteolepid and rhizodontin sarcopterygians. From sarcopterygians fish evolved the first specie of tetrapods in the Late Devonian (Long 1995).

Materials and Methods

Data were collected at the Red Hill roadcut exposure located along Route 120 (41.34450 N, -77.689487 W) near North Bend, Pennsylvania. Fossils were collected from two distinct strata representing Fammenian Age habitats: an oxidized stratum representing the sediments from the main river channel margins and a reduced stratum representing sediment from highly vegetated floodplain ponds. Four quarries were excavated at the Red Hill site with two quarries in each stratum (Figure 8). Quarries one and two were located within the reduced strata. Quarry one measured 0.0737 cubic meters, and Quarry 2 measured 0.652 cubic meters. Quarries 3 (0.339 m³, Figure 9) and 4 (0.750 m³) were each located in the oxidized layer.

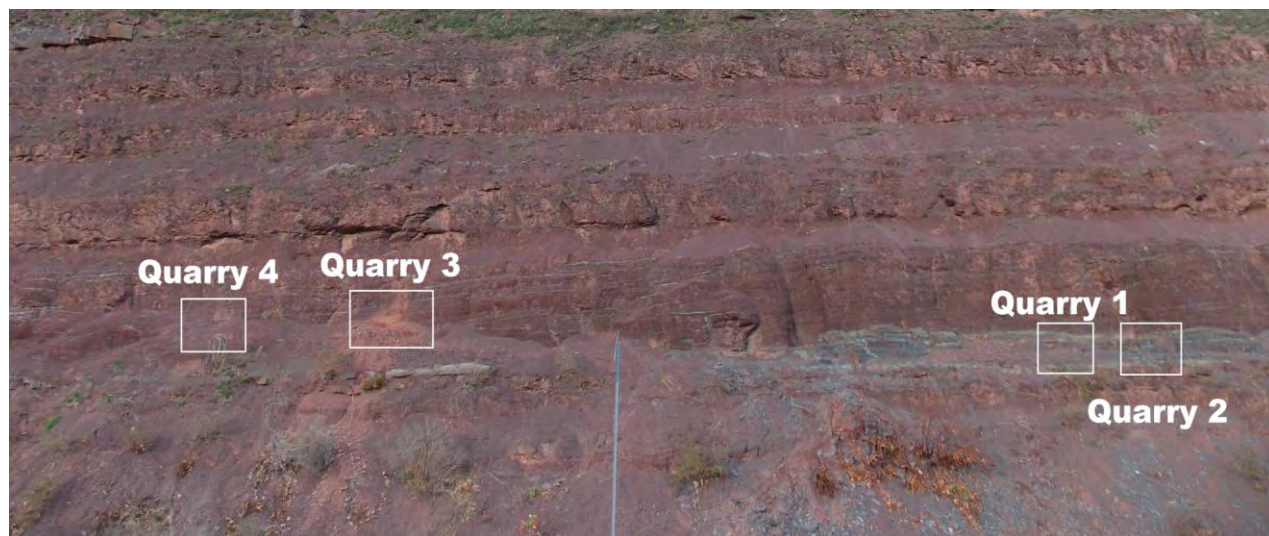


Figure 8: Location of quarry sites at Red Hill. Image credit: David Broussard



Figure 9: Excavation of Quarry 3. Image credit: Cory Trego

Potential quarry sites were selected based on thickness of overburden and ease of access. Quarry sites were analyzed to determine locations where larger sections of rock could be removed somewhat efficiently. Once quarry sites were selected, large sections of stone were removed using sledge hammers, pry bars, chisels, and rock hammers. Larger sections of rock were struck to reveal naturally occurring weak spots in the matrix. Chisels and rock hammers were used to split the rock along these seams. After each split, the newly exposed surface was thoroughly searched for vertebrate remains. All rock fragments were then broken into smaller pieces and again searched for microfossils. Vertebrate fossils found during excavation were identified to the most specific taxonomic level possible. These data were entered into a field

notebook under the appropriate quarry number after the discovery of each specimen. Walter Cressler and Ted Daeschler assisted with specimen identification. Data were later organized into an excel spreadsheet after returning from the field site. A chi-square analysis of a contingency table was used to compare if there were statistically significant differences between columns to determine if differences in the number of fossil specimen collected were statistically significantly different between each stratum.

Description of Taxa

The most commonly found fossils were teeth and scales of *Hynertia lindae* (Figures 10, 11, and 12). *H. lindae*, a large tristochopterid sarcopterygian fish, was first described by Thomson (1968) after the collection of skull and jaw fragments near the town of North Bend, Pennsylvania, prior to the excavation of the Red Hill roadcut. Thomson's first specimen measured an estimated 250 centimeters long (Thomson 1968). Additional fossils collected since Thomson's original discovery place the maximum length of *H. lindae* around three meters, making it the largest fish species found at Red Hill and likely the apex predator (Cressler 2010). Teeth of *H. lindae* are characterized by infolding of orthodontine, giving them a distinct labyrinthodont pattern (Bishop 2013). *H. lindae* scales range from rounded to an elongated shape, but are characterized by concentric ring patterns and a distinct boss in the center of the scale. The skull plate of *H. lindae* has thick dermal plates arranged in a pattern characteristic of other sarcopterygians, and the scales lack the cosmine coating of more primitive sarcopterygians (Thomson 1968). The shoulder girdle of *H. lindae* consists of a cleithrum and a clavicle, and resembles that of Devonian Tristichopterid *Eusthenopteron* (Thomson 1968).

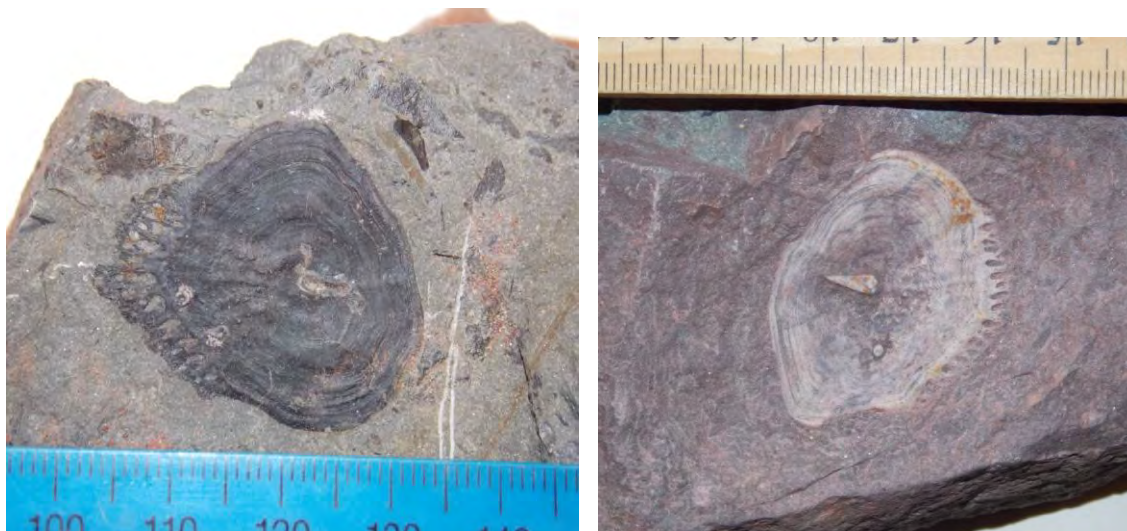


Figure 10: Scales from *Hyneria lindae*. The scale on the left was collected in the reduced strata representing floodplain ponding habitat, while the scale on the right was collected from the oxidized layers representing river channel margins. Image credit: David Broussard.



Figure 11: A typical labrynthodont tooth of *Hyneria lindae*. Image credit: David Broussard.



Figure 12: Artist's rendition of *Hyneria*. Photo credit: Flick Ford.

Plates belonging to two different species of placoderms were the second most abundant vertebrate fossils found during this study (Figures 13 and 14). Placoderms were jawed, armored fishes that arose during the Silurian and proliferated throughout the much of the Devonian until their extinction 360 million years ago (Long 1995). They are characterized by fused or jointed bony plates that surround the anterior end of the body (Long 1995). Three different species of placoderms have been found described from Red Hill, but *Groenlandaspis pennsylvanica* and *Turrisaspis elektor* are most the common (Cressler et al. 2010). Plates of *T. elektor* were the most abundant placoderm remains found in this study. These two species were the first groenlandaspids found in the United States (Daeschler et al. 2003). Other members of this family have been found in Australia, Turkey, and Greenland, suggesting they were found globally during the Late Devonian (Daeschler et al. 2003). Cressler et al. (2010) noted that members of this family have ventrally oriented mouths and a body design that suggests they fed on detritus along the substrate of streams, making them ideally suited for life in both the main river channel and floodplain ponds.

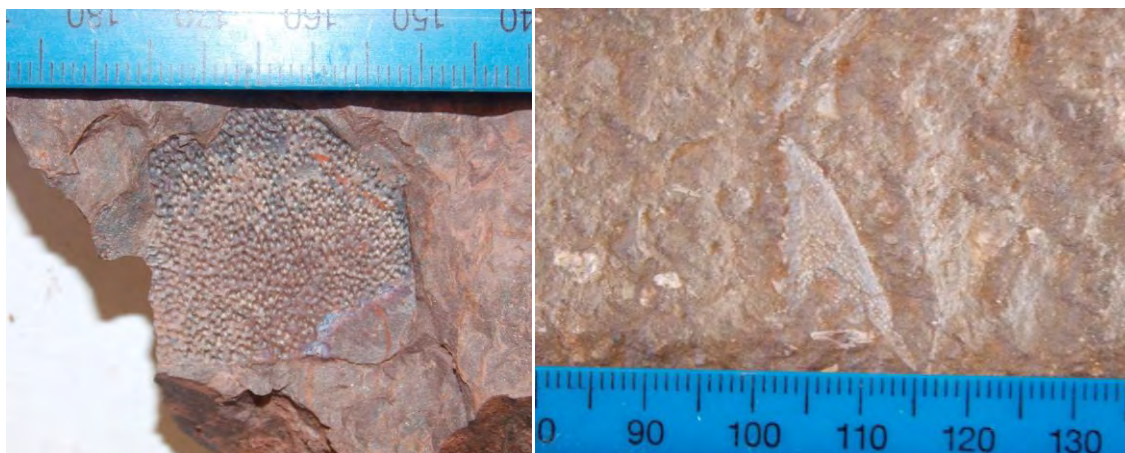


Figure 13: Plates from the placoderm *Turrissapis elector* found within the oxidized channel margin facies. Image credit: David Broussard.

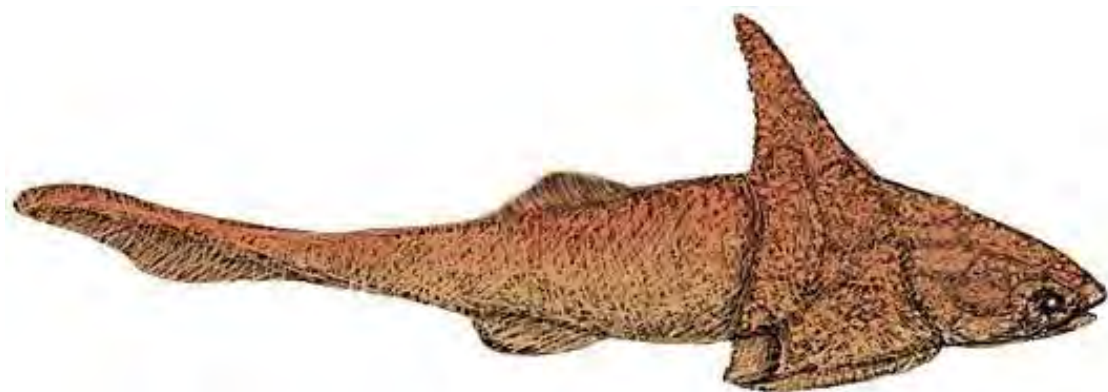


Figure 14: Artistic representation of *Turrissapis elector*. Image credit Dennis Murphy

Scales of an unidentified species of a megalichthyid sarcopterygian fish were identified in both facies at Red Hill (Figures 15 and 16). These scales were distinguished by a rhombic shape and have a thick cosmine coating, giving them a polished appearance. This genus was first described in 1834 by Agassiz from specimen found in the United Kingdom (Miall 1885). Skull fragments and scales suggest average body size ranged from 30-100cm (Cressler 2010).

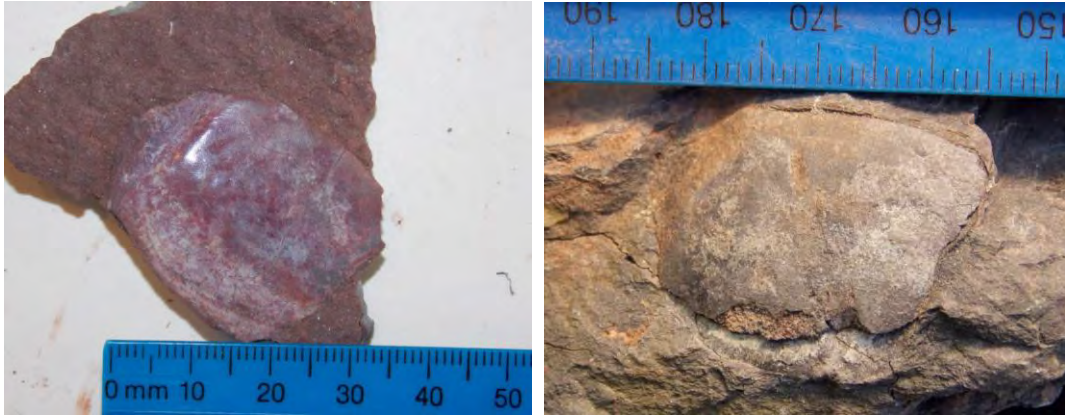


Figure 15: Cosmid scales of an unidentified species of a megalichthyid sarcopterygian fish. Image credit: David Broussard

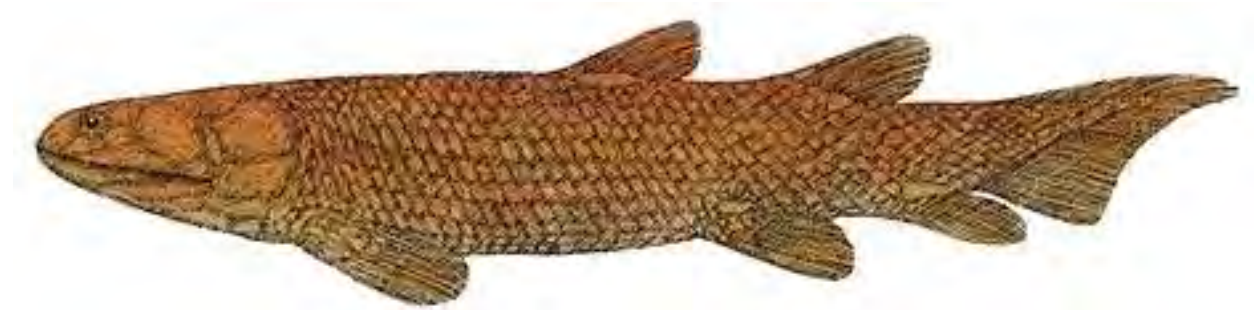


Figure 16: Artistic representation of the Red Hill megalichthyid. Image credit Dennis Murphy

Several pectoral spines of an unidentified acanthodian species belonging to the genus *Gyracanthus* were found in both reduced and oxidized strata at Red Hill (Figure 17).

Acanthodians were a group of fishes whose common name is “spiny sharks” due to a number of bony spines located along their dorsal and pectoral fins (Long 1995, Figure 18). *Gyracanthus* are members of the Climatiform type of acanthodians. These were the largest acanthodians and were characterized by significant bony protrusions around their shoulder girdles. Gyracanthids first appeared in the Middle Devonian, and could potentially grow up to a meter in length. By the Late Devonian and into the Carboniferous, these species spread throughout the Northern Hemisphere. The only fully described member of this genus is *Gyracanthides murrayi*, which was first described from southeastern Australia (Long 1995). This unique group of fishes first arose during the Silurian, but proliferated throughout the Devonian. Even though numerous

species of acanthodians have been described, very little is known about their anatomical structure because they most likely lacked an ossified skeleton (Long 1995). Spines were originally thought to deter predators, but current hypotheses explain the presence of bony spines as a means to provide balance and buoyancy control (Long 1983).



Figure 17: Pectoral spines from an unnamed species of *Gyracanthus*. Image credit: David Broussard.

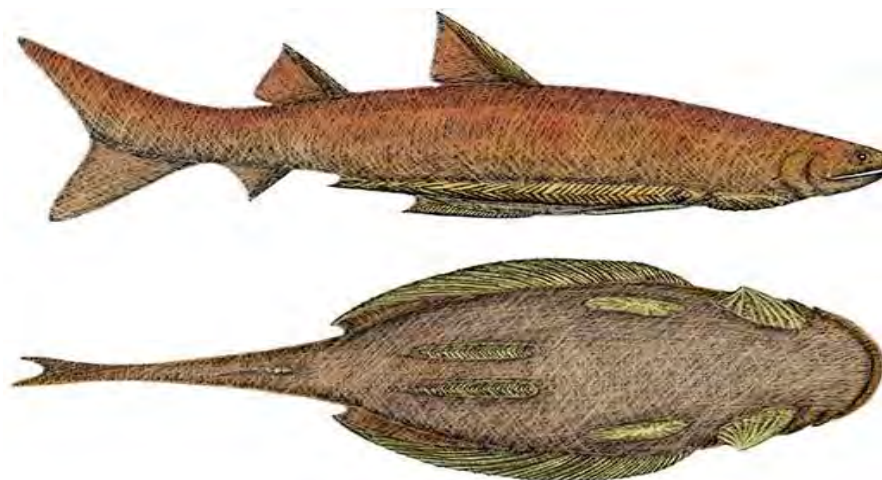


Figure 18: Artistic Representation of *Gyracanthus murrayi*. Image credit Dennis Murphy

Several specimen of *Limnomis delaneyi* were found at Red Hill within the reduced plant layer (Cressler et al. 2010, Daeschler 2000, Figure 19). *L. delaneyi* are among the earliest actinopterygian, or ray-finned fishes. Fossil evidence from the Baltic region suggests ray-finned fishes diverged from sarcopterygians at the end of the Silurian. The earliest North American actinopterygian does not appear in the fossil record until twenty million years after the

appearance of the first members of this class (Daeschler 2000). This species was described by Daeschler (2000) from numerous body casts found in the plant-rich reduced zone. Anoxic conditions, as evidenced by the green-gray color of the facies, were present when many of these specimens were preserved, suggesting that they likely inhabited these shallow pond environments at the time of death. Several small schools were found within the reduced floodplain pond facies, suggesting a significant and rapid drop in levels of dissolved oxygen. From data on body size and tooth morphology, Daeschler (2000) concluded that these small fish were likely invertivores that occupied a new niche arising as a result of developing freshwater ecosystems.



Figure 19: Shown left is a body fossil impression of *Limnomis* found in the reduced plant layer. At right is an artistic representation of *Limnomis delaneyi*. Image credit Dennis Murphy.

Numerous small teeth belonging to an early species of freshwater shark, *Ageleodus pectinatus*, are interspersed throughout the oxidized facies at Red Hill (Figure 20). Chondrichthyans first arose approximately 420 million years ago, as evidenced by scale patterns found in Early Silurian-aged strata (Long 1995). *A. pectinatus* was originally described in 1867 from remains found in Carboniferous marine deposits in England. Downs and Daeschler (2001) studied these teeth under an electron microscope and found that they showed very few wear patterns, a characteristic similar to the teeth of modern sharks that replace their teeth every few

weeks. Earlier sharks from the Paleozoic exhibited much slower teeth replacement, meaning that this species may have made an evolutionary advancement to replace broken and worn teeth more quickly. During their study at Red Hill, Downs and Daeschler (2001) found that teeth ranged in size from 0.8 mm to 8.7 mm and had 3 to 33 cusps; average size was 2.5 mm long with 5-10 cusps. The presence of this shark species at Red Hill reinforces the theory that chondrichthyans began to exploit freshwater habitats by the end of the Devonian (Downs and Daeschler 2001; Long 1995).



Figure 20: Various size teeth from *Ageleodus pectinatus*, a Late Devonian freshwater shark. Scale bar 1mm. Photo credit Ted Daeschler.

Results

A total of 293 vertebrate microfossils were recorded during the study. These fossils included teeth and scales of *H. lindae*, dermal bony plates of *Groenlandaspis* placoderms, scales of megalichthyid sarcopterygian fish, *Gyracanthus* sp. spines, teeth of *A. pectinatus*, and body impressions of *L. delaneyi*. A total of 17 *H. lindae* scales, 3 *H. lindae* teeth, 12 placoderm plates, 5 megalichthyid scales, 2 *Gyracanthus* spines, and 2 *Limnomis* partials were found in the reduced strata. A total of 128 *H. lindae* scales, 33 *H. lindae* teeth, 72 placoderm plates, 37 megalichthyid scales, 11 *Gyracanthus* spines, and 10 *A. pectinatus* teeth were collected from the oxidized strata (See Table 2).

A Chi Square analysis on a contingency table was used to determine if the differences between the numbers of vertebrate remains found in each layer were statistically significant (Tables 3 and 4). The Chi square test revealed that the results were statistically significant at the 0.05 confidence level ($\chi^2=15.2$; $p=0.019$). I concluded that the differences in species diversity determined from vertebrate fossils found at each site were not due to random chance.

Discussion

Significantly more vertebrate fossils were found within the strata representing the main channel margins than in the strata representing flood plain ponds. Differences in species diversity between these paleohabitats could be explained by the proximity of each site to main river channels, habitat variability, and varying taphonomic conditions. Biodiversity is directly correlated to changes in habitat variability resulting from hydrological connectivity to flood plain water bodies (Sullivan and Watzin 2009). Today, every lotic, or river system, differs in its morphology and hydrology. Floodplains develop through both lateral and vertical erosion of landscapes causing floodplain water bodies to form in a multitude of ways. Oxbow lakes form from abandoned channels caused by lateral migration of the main river channel. Marshes and floodplain ponds form when water scours sediment adjacent to the main river channel, creating areas at or just below the water table (Amoros and Bornette 2002). The structure of floodplain water bodies at Red Hill varies considerably. Cressler (2006) found that floodplain environments ranged from well-drained shallow areas with significant plant growth to established wetlands, indicating that a wide range of habitats were available for aquatic vertebrates.

In modern systems, species diversity and habitat fidelity strongly correspond to the structure and proximity of floodplain water bodies to the main river channel (Amoros and Bornette 2002). The conduciveness of aquatic habitat to support vertebrates varies based on size,

depth, shape, connectivity to main river channels, and the distance to main river bodies (Amoros and Bornette 2002). Sullivan and Watzin (2009) found that river systems with floodplain water bodies have significantly higher levels of fish species diversity. The presence of these water bodies increased the area of habitat available for aquatic species, supporting the premise that large areas can generally support more species. For instance, oxbow lakes along the Champlain Valley in Vermont provide temperature regimes, depths, flow rates, structure, and shading area that differed from main river channels, allowing for additional niches. (Sullivan and Watzin 2009).

Today, habitable areas within floodplain systems oscillate seasonally. Higher precipitation levels in the spring and fall increase the size of floodplain water bodies, and large-scale avulsion events can reconnect floodplain bodies with the main river channels. Even seasonal floodplain bodies have significant impacts on species diversity because they provide spawning habitat and additional refuge for smaller fish species during critical times of the year (Sullivan and Watzin 2009).

Differences in biotic diversity between main river channels and associated floodplain ponding environments is often associated with variation in temperature, turbidity, nutrient content, and substrate composition in modern aquatic ecosystems (Amoros and Bornette 2002). Temperature is influenced by the origin of the water, including groundwater and inflowing streams, shading, and surface area of the floodplain body. Today, temperatures can vary by as 17 C across the same floodplain system (Amoros and Bornette 2002). Higher temperatures lead to lower concentrations of oxygen, increasing stress on fish species living in warmer water (Dahl and Hammerlund 2011). This could render floodplain ponds inhospitable to larger sacopterygian fish species during the warm and dry periods of the Late Devonian. Temperature and dissolved

oxygen fluctuation may explain why fewer sarcopterygian microfossils were found within the floodplain facies. These pond environments may have served as seasonal spawning areas or could have offered suitable habitat for smaller species year round, but larger fish species were not well adapted to thrive in these environments.

Turbidity, a measure of the amount of solids suspended in water, is highly influenced by the water's source. Groundwater contains few suspended solids, while connectivity to main river ways often increases turbidity. Murky water reduces plant growth and phytoplankton, further reducing oxygen available for fish species. High nutrient content also leads to more turbid water. Nutrient content generally increases with connectivity to flowing water bodies. High amounts of nutrients can be deposited in floodplain water bodies during avulsion events (Tockner et al. 1999). Nutrient content at the Red Hill site would have been quite high due to the expected frequency of large floods and the vast amount of decaying organic matter deposited in these waterways (Cressler 2006). Dissolved oxygen levels would have been reduced in turbid conditions, further rendering these environments unsuitable for larger fish species.

Substrate size and composition are important factors in determining plant growth, creating invertebrate habitat, and providing proper protection in spawning grounds. Connectivity to the main river channel and the distance from the main channel has the greatest impact on substrate size. Deposition conditions also affect the size of substrate particulate: water bodies within a low-energy depositional setting will have substrate composed of fine particulate organic matter. Higher energy deposition rates lead to larger substrate size: the higher the energy level, the larger the substrate size (Amoros and Bornette, 2002). The floodplain pond faces at Red Hill resulted from a low energy depositional setting (Cressler 2006). Occasional high energy avulsion events deposited larger mudstones and pebbles within the pond, as evidence by discrete layers of

noticeably larger substrate (Cressler 2006). During the majority of their existence, the beds of these ponds were likely covered in fine organic matter, limiting substrate available for spawning of larger fish species as well as limiting invertebrate growth (Amoros and Bornette 2002).

Sullivan and Watzin (2009) found that habitat partitioning among fish of different feeding strategies was common in the Champlain Valley today. Generalist feeders appeared to be opportunistic, and were found in both floodplain water bodies and in the main river channel. Larger predatory fish, such as brown trout (*Salmo trutta*), northern pike (*Esox lucius*), and smallmouth bass (*Micropterus dolomieu*) were only found in the main river channels. These fish species require higher oxygen levels due to their body size. At Red Hill, *Gyracanthus*, *H. lindae*, and placoderm remains were found in both strata. Significant wear patterns on microfossils from larger fish species indicate that avulsion events may have transported either living or deceased specimen into these ponds. *L. delaneyi* were found only within the reduced facies, but they have been found within the channel margin facies during prior excavation efforts (Daeschler 2000). Both Daeschler (2000) and Cressler et al. (2010) found numerous fully articulated *L. delaneyi* imprints in the standing water facies. Some of these fish were found in small schools, suggesting that they lived together in these floodplain bodies at the time of death. The presence of *Gyracanthus*, placoderms, and *L. delaneyi* in both floodplain and river channel margin environments suggests that these fish may have been generalist feeders that fed on detritus, algae, or early arthropods (Long 1995). Generalist feeders may also change their habitat selection to avoid predation (Aadland 1993). Standing water along the floodplain was full of dense vegetation (Cressler 2006), and would have offered exceptional protection against predatory species.

Numerous *H. lindae* scales were also interspersed throughout both facies. Many *H. lindae* scales found within the reduced layer showed significant wear patterns, suggesting that they had been carried into these floodplain ponds posthumously by a large avulsion event. The large size of *H. lindae* and the unidentified species of megalichthyid likely would have made life in these aquatic ponds difficult for these species. The distinct green-gray coloring of these facies suggests that oxygen levels would have remained low, because iron within the sediment was not oxidized to the characteristic red color found in other strata (McBride 1974). Larger predatory fish require significantly more oxygen to survive than their smaller counterparts, even though they have slower metabolic rates and require less oxygen per unit of mass (Dahl and Hammerlund 2011). Predator distribution is also affected by forage availability. Most extant large-bodied fish prefer moderate to deep pools due to the abundance of oxygen and prey sources. The main river channels would have been a more suitable environment for larger sarcopterygians, explaining the greater density of large predatory fish remains in layers representing the river channel margins (Sullivan and Watzin 2009).

The Red Hill site is of particular interest to evolutionary biologists due to the presence of early tetrapod remains. The swampy floodplain habitats that formed during the Late Devonian were likely integral in the evolution of early tetrapods (Westenburg 1999). Remains from three different species of tetrapods have been found at Red Hill (Daeschler et al. 2009). The first tetrapod material found were remains of *Hynierpeton bassetti*, a species described by Daeschler et al. (1994). A partial left cleithrum, scapulocoracoid, portion of the lower right jaw, the left humerus and several skull fragments were collected from a single microfossils lens within the channel margin facies. These remains represented the first tetrapod specimen found in North America, outside of Greenland (Daeschler et al 2009). A second species, *Designathus rowei*, was

described by Daeschler (2000) from posterior portions of the right and left low jaw, anterior portions of the left lower jaw, left femur and right jugal collected from various microfossil lenses within the channel margin facies. A third species of tetrapod has been identified from several skull fragments. These fragments most closely resemble a species of *Whatcheeriidae* tetrapod that was found in a Carboniferous stratum in Scotland. Due to the limited material from this tetrapod, this species has yet to be described (Daeschler et al. 2009).

Daeschler et al. (2009) concluded that the habitat variety offered by the floodplain ponds, channels, and wetlands helped foster to diversification among early tetrapod species. The earliest tetrapods were sarcopterygian fish that developed robust limb bones as well as other skeletal traits allowing a more diverse terrestrial lifestyle. Early evolutionary biologist concluded that drying conditions favored the contemporaneous rise of lungs and limbs (Long 1995). More recent evidence suggests that these events in fact arose millions of years apart, and had very little relation to one another (Clack 2012). Air breathing first evolved in osteichthyes during the Late Silurian as an adaptation to anoxic water conditions found in inland water bodies (Graham 1997), yet the first limbed tetrapods did not arise until the Middle Devonian, and the ability to fully support weight on land not occur until the Late Devonian, at the earliest (Graham 1997). Osteolepid and Rhizodontid sarcopterygian fishes possessed precursors of limb bones seen in modern terrestrial vertebrates. However, the environmental conditions that favored the elongation and thickening of limb bones in sarcopterygians to become the limbs of the earliest amphibian species are still unclear. The emergence of swamps and shallow flood plain water bodies, coupled with fluctuating water levels could explain why these adaptations were favored (Clack 2012). The layer representing shallow and heavily vegetated floodplain water bodies

found at Red Hill is an exceptional example of the development of these early transitional ecosystems.

Several key transitions occurred in the gradual transformation of fish skeletons into tetrapod skeletons. Clack (2012) compares *Eusthenopteron fordii*, a Middle Devonian sarcopterygian fish, to *Acanthostega*, a Late Devonian tetrapod from Greenland, to illustrate the major morphological changes that occurred during the transition from lobe-finned fish to tetrapods. Several significant structural changes occurred in the skull, shoulders, and limbs of early lobe-finned fish that allowed them to thrive in shallow water environments. First, more advanced tetrapod species lost the extrascapulars and the supracleithrals, bones connecting the shoulder girdle to the back of the skull plate. This, coupled with several less prominent changes in the structure of the skull, forced muscular, rather than skeletal, support for the head. This allowed for the development of the first true neck, allowing tetrapods to move their head laterally and vertically. In *Acanthostega*, gill arches developed into tongue supports, making this organism able to grasp prey in terrestrial environments. This adaptation provided greater jaw strength, and was highly advantageous for feeding on arthropods and other prey in terrestrial environment (Clack 2012). The posterior end of tetrapod skulls became shorter and more dorsoventrally flattened over time, while they developed a longer snout and larger eyes located closer to the top of the head (Clack 2012).

The shoulder girdle and limb bones underwent the greatest transformation in the transition of fish to tetrapods. The design of the shoulder region in fish provided a smooth transition from the skull to the body for optimal hydrodynamics, and provided support for gills and jaw muscle attachment. The shoulder girdle of sarcopterygian fishes consisted of the supracleithral bones, the cleithrum, the clavicle, and the midline interclavicles. In tetrapods,

these bones transitioned to become the two scapulas with supporting coracoids and the clavicles (Clack 2012).

During the transition from lobe-fins to tetrapods, the pelvic girdle underwent several significant transformations. The pelvic girdle in sarcopterygians was small and unconnected to the vertebral column and served to support the posterior fins. In tetrapods, the pelvic girdle became thickened and developed a large blade for attaching muscles of supporting limbs. Shubin et al. (2014) described the pelvic girdle in five specimens of *Tiktaalik roseae*, a Late Devonian tetrapodomorph from Nunavut, Canada. The pelvic girdle of *T. roseae* appears to bridge the gap between the transitions that occurred during the evolution of tetrapodomorphs, like *E. fordii*, into early tetrapods, like *Acanthostega*. The pelvic girdle of *T. roseae* is more robust than most other tetrapodomorph species, and yet lacked the connection to the sacral rib, a trait seen in more advance tetrapods. The relative size compared to total body length matches more closely with tetrapods like *Acanthostega* and *Ichthyostega*, and the iliac blade extends to the vertebral column, a trait not seen in any fish species. However, the left and right sides of *T. roseae*'s pelvic girdle remained unfused, a characteristic typically seen in more primitive tetrapodomorphs, like *E. fordii* (Shubin et al. 2014).

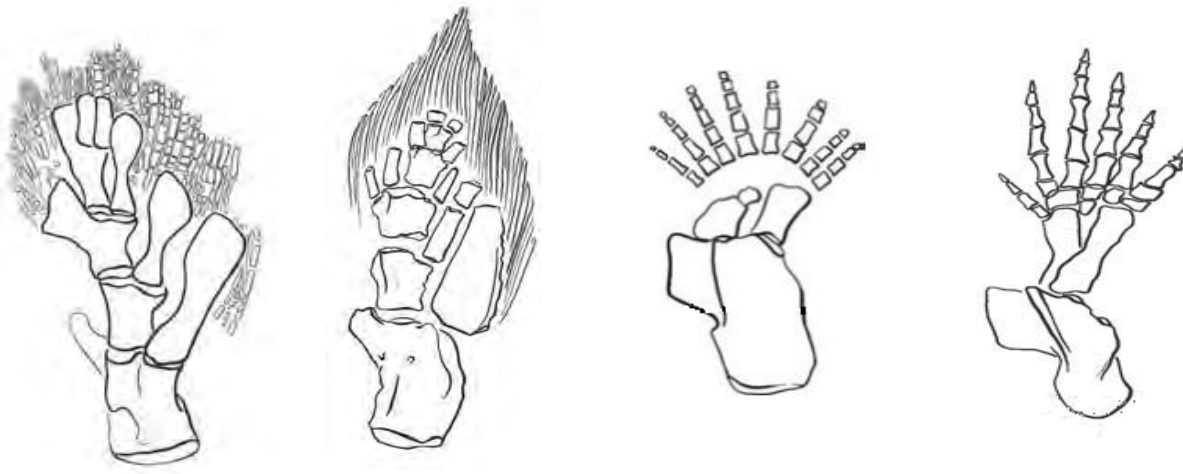


Figure 21: Evolution of pectoral fins. From left to right: pectoral limb of *Eusthenopteron*, a Devonian sarcopterygian fish; pectoral fin of *Tiktaalik*, a Late Devonian tetrapodomorph; pectoral fin of *Acanthostega*, a Late Devonian tetrapod, and pectoral fin of *Tulerpeton*, a close relative of *Acanthostega*. Note the thickening of the humerus, radius, and ulna, and the appearance of digits.

Fin supports in sarcopterygians developed into clearly defined appendages in tetrapods.

The first axial radial that attached fin supports to the pelvic girdle developed into the humerus in anterior limbs, and the femur in posterior limbs. The radius and ulna and tibia and fibula are connected by complex joints in tetrapods, allowing for much greater limb movement (Clack 2012, Figure 21). Shubin et al. (2006) noted that these changes were taking place in sarcopterygians far before the rise of the first limbed tetrapods.

The pectoral fins of *T. roseae* possessed joint structures in the phalanges and wrists, allowing for extension and contraction of the limbs (Shubin et al. 2006). Position of the pelvic girdle, scapula, and fins suggests that *T. roseae* could support itself in an upright posture using the fins as a base of support. Developmental changes within the axial system, such as the development of more robust ribs and increased overlap of the vertebra, also support the idea that skeletal changes were occurring within *T. roseae* that allowed for greater support of body weight. However, even with these skeletal adaptations, *T. roseae* still most likely lived in an aquatic habitat (Shubin et al. 2006).

Ahlberg and Milner (1995) noted that the flattened body plans and crocodilian-like skulls of *Panderichthys*, a Frasnian age osteolepiform fish, suggests that these body forms began to arise before major transitions occurred within the limbs of sarcopterygians fishes. They conclude that this flattened body style may have allowed them to fill a shallow water predatory niche. Dorsally located eyes allowed these species to see prey on the surface of the water. Coates and Clack (1991) note that early tetrapod limbs with digits evolved for use in aquatic environments, rather than a response to terrestrialization forced by the shrinking of freshwater habitats (Ahlberg and Milner 1995). The floodplain ponds at Red Hill likely provided optimum shallow water habitat for the evolution of early transitional species. The development the dorsally-ventrally flattened body plan seen in early tetrapods was likely influenced by the emergence of the floodplain ponding habitat that first arose during the Late Devonian. The development of a true neck, paddle-like fins allowing a wide range of movements, and a flattened body plan and would have been highly adaptive within shallow swampy regions along Late Devonian waterways.

Conclusions

The significant difference in vertebrate microfossil numbers between the reduced and oxidized strata indicates that these two paleoenvironments had differing physical and chemical parameters. However, taphonomic conditions could also explain some of the variation in microfossil density between these two habitats. Additional variation in diversity could be explained by transportation of vertebrate material from upstream during large avulsion events. While the depositional model put forth by Daeschler et al. (2009) could lead to the preservation of remains from most of the species present in the area at the time of deposition, many of the microfossils from the reduced strata show wear patterns that could have resulted from posthumous transport. Some of the vertebrate remains in each stratum could have been

transported from other locations that offered a significantly different environment than that of Red Hill. To account for this variation, wear patterns on fossils must be examined to determine the percentage of material that was carried over longer distances. The excavation of additional quarries is necessary to better understand species diversity within each paleohabitat and to develop a complete picture of habitat partitioning during the Late Devonian. Determining species distribution is a small piece of a larger puzzle that is necessary to constructing a comprehensive picture of the habitats in the Late Devonian. Coupled with information about paleobotany, sedimentology, and comparative vertebrate anatomy, this information will help to shed light on the ecological conditions that existed during the Late Devonian, and may provide information on the selective pressures that led to the rise of the first tetrapods.

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Appendix I.

Table 2. Summary of results comparing microfossil type and number found in each quarry.

Fossil Type	Quarry Number						Total
	<u>Reduced Zones</u>			<u>Oxidized Zones</u>			
	1	2	Total Reduced	3	4	Total Oxidized	
<i>H. lindae</i> scales	16	1	17	89	22	111	128
Placoderm plates	10	2	12	53	7	60	72
<i>H. lindae</i> teeth	2	1	3	23	7	30	33
Megaliichthyid scales	5	0	5	28	4	32	37
<i>Gyracanthus</i> spines	2	0	2	8	1	9	11
<i>A. pectinatus</i>	0	0	0	8	2	10	10
<i>L. delaneyi</i>	2	0	2	0	0	0	2
Total	37	4	41	209	43	252	293

Table 3. Contingency Table: Data

	Total Reduced	Total Oxidized
Fossil Type		
<i>H. lindae</i> scales	17	111
Placoderm plates	12	60
<i>H. lindae</i> teeth	3	30
Megalichthyid scales	5	32
<i>Gyracanthus</i> spines	2	9
<i>A. pectinatus</i>	0	10
<i>L. delaneyi</i>	2	0
Total	41	252

Table 4. Contingency Table: Expected Frequencies

	Total Reduced	Total Oxidized
Fossil Type		
<i>H. lindae</i> scales	17.9	110
Placoderm plates	10.1	61.9
<i>H. lindae</i> teeth	4.62	28.4
Megalicthyid scales	5.18	31.8
<i>Gyracanthus</i> spines	1.54	9.46
<i>A. pectinatus</i>	1.4	8.6
<i>L. delaneyi</i>	0.28	1.72
$\chi^2=15.2$	Degrees of Freedom=6	$P=0.019$