2010

# Terrestrialization in the Late Devonian: A palaeoecological overview of the Red Hill site, Pennsylvania, USA

Walter L. Cressler III
*West Chester University of Pennsylvania*, wcressler@wcupa.edu

Edward B. Daeschler
*Academy of Natural Sciences of Philadelphia*

Rudy Slingerland
*Penn State University*

Daniel A. Peterson
*Penn State University*

## Recommended Citation

Cressler III, W.L., Daeschler, E.B., Slingerland R., and Peterson D.A. 2010. Terrestrialization in the Late Devonian: A palaeoecological overview of the Red Hill site, Pennsylvania, USA. In: Gaël Clement and Marco Vecoli [eds.], The Terrestrialization Process: Modelling Complex Interactions at the Biosphere-Geosphere Interface, pp. 111-128. The Geological Society, London 339.

# Terrestrialization in the Late Devonian: A palaeoecological overview of the Red Hill site, Pennsylvania, USA

Walter L. Cressler III[1], Edward B. Daeschler[2], Rudy Slingerland[3] and Daniel A. Peterson[3]

[1] Francis Harvey Green Library, 25 West Rosedale Avenue, West Chester University, West Chester, PA 19383, USA; wcressler@wcupa.edu

[2] Vertebrate Paleontology, Academy of Natural Sciences, 1900 Benjamin Franklin Parkway, Philadelphia, PA 19103, USA

[3] Department of Geosciences, The Pennsylvania State University, University Park, PA 16802, USA

# of words in text: 6,762
# of references: 92
# of tables: 2
# of figures: 6

Running header: Late Devonian palaeoecology at Red Hill

## Abstract

Alluvial floodplains were a critical setting during the Late Devonian for the evolution of terrestriality among plants, invertebrate and vertebrates. The Red Hill site in Pennsylvania, USA, provides a range of information about the physical and biotic setting of a floodplain ecosystem along the southern margin of the Euramerican landmass during the late Famennian age. An avulsion model for floodplain sedimentation is favoured in which a variety of inter-channel depositional settings formed a wide range of aquatic and terrestrial habitats. The Red Hill flora demonstrates ecological partitioning of the floodplain landscape at a high taxonomic level. In addition to progymnosperm forests, lycopsid wetlands, and zygopterid fern glades, the flora includes patches of early spermatophytes occupying sites disturbed by fires. The Red Hill fauna illustrates the development of a diverse penecontemporaneous community including terrestrial invertebrates and a wide range of vertebrates that were living within aquatic habitats. Among the vertebrates are several limbed tetrapodomorphs that inhabited the burgeoning shallow water habitats on the floodplain.

Although the process was already well underway by the Silurian (Edwards & Wellman 2001; Shear & Selden 2001), the Late Devonian was a time of key evolutionary innovations that made possible the further terrestrialization of life.  For example, it was during the Late Devonian that seed reproduction fully evolved in plants and the fin-to-limb transition occurred in vertebrates (Rothwell & Scheckler 1988; Clack 2002). Each of these evolutionary events occurred in association with the aquatic ecological context of their ancestral conditions, and the appearance of novel features can be seen in hindsight to have predisposed these lineages to additional physiological and morphological changes that promoted terrestrialization. As life expanded over the landscape, new ecological guilds emerged, the trophic structure of continental ecosystems became more complex (DiMichele *et al.* 2002), and the resulting transformations in the transfer of matter and energy changed the dynamics of biogeochemical cycles in the sea and atmosphere, as well as on land (Algeo *et al.* 2001). Significant aspects of the early stages of this global transition can be documented through observation and analysis of the physical and biotic conditions present on Late Devonian alluvial plains. The sedimentary sequence at the Red Hill site in Clinton County, Pennsylvania (Fig. 1), was deposited during the late Famennian age within the alluvial plain of the Catskill Delta Complex along the southern margin of the Euramerican (Larussian) landmass. The site preserves a rich sample of plants and animals that lived penecontemporaneously in floodplain habitats. Thus, Red Hill provides a comprehensive glimpse of a continental ecosystem at this important stage in the terrestrialization of life.

## Background

### *Evolutionary and ecological events on Devonian continents*

Early Devonian land-plant communities were characterized by a patchwork landscape of low-stature plants growing in monotypic clonal stands along watercourses and coastal zones (Griffing *et al.* 2000; Hotton *et al.* 2001). During the Mid-Devonian, the competition for light and spore dispersal led several plant lineages to develop secondary growth and robust architectures for enhanced height (Berry & Fairon-Demaret 2001). These included large cladoxylopsid trees (Stein *et al.* 2007), aneurophytalean shrubs, lepidosigillarioid lycopsids, and by the late Middle Devonian, archaeopteridaleans (Scheckler, 2001). Plant-community structure reached even greater levels of complexity and biomass production during the Late Devonian (Algeo & Scheckler 1998). By then, plant communities included gallery-forest trees, shrubs, herbaceous ground cover, vines, and specialized wetland plants (Scheckler 1986a, Greb *et al.* 2006). Archaeopteridalean forests became widespread from boreal to tropical latitudes (Beck 1964). All primary and secondary plant tissues, other than the angiosperm endosperm, had evolved by the end of the period (Chaloner & Sheerin 1979).

The major phylogenetic plant groups that appeared during the Late Devonian and Early Mississippian correspond broadly to distinct ecological positions in the landscape (Scheckler 1986a). While apparent niche partitioning took place among plants earlier in the Devonian, it occurred within a more limited number of groups and within a narrower range of environments (Hotton *et al.* 2001). By the Late Devonian, isoetalean lycopsids occupied permanent wetlands, zygopterid ferns were widespread in ephemeral wetlands, spermatophytes occupied disturbed sites, and archaeopteridalean progymnosperms predominated along the better-drained overbanks and levees (Scheckler 1986a, 1986c; Rothwell & Scheckler 1988; Scheckler *et al.* 1999). Once the archaeopteridaleans became extinct and the zygopterids diminished in importance at the end of the Devonian, a new pattern of ecological distribution at a high phylogenetic level had emerged (Peppers & Pfefferkorn 1970). Rhizomorphic lycopsids dominated in wetlands, ferns in disturbed environments, sphenopsids in aggradational environments such as point bars, and spermatophytes on well- to poorly-drained clastic substrates (DiMichele & Bateman 1996). Even with this phylogenetic turnover and dominance shift, the general pattern of landscape partitioning by plants at a high phylogenetic level persisted. This lasted from its origin in the Late Devonian until the drying of the global climate following the Mid-Pennsylvanian. By the

Permian, spermatophytes dominated in almost all vegetated environments, and have done so ever since (DiMichele & Bateman 1996).

The Late Devonian evolution of the seed eventually led to the adaptive radiation of spermatophytes because plants were no longer constrained to water for transfer of sperm during fertilization (Stewart & Rothwell 1993). Sexual reproduction in free-sporing plant lineages is dependent on available surficial water for its success. Numerous plant lineages evolved heterospory, in which a spore that produces female gametophytes is larger than a spore producing male gametophytes (Bateman & DiMichele 1994). Within the lignophytes, heterospory was the evolutionary precursor for the seed habit that involves the retention of megasporangia containing the female megagametophytes upon the sporophyte. Fertilization follows contact (pollination) between the wind-borne or animal-borne microspore (pre-pollen or pollen) and the retained megasporangium, after which an embryo develops within the protected environment of a seed (Rothwell & Scheckler 1988). While this decoupling of sexual reproduction from dependence on water permitted spermatophytes to radiate into dry environments, the selection pressures for retention of the megasporangium on the sporophyte took place within the periodically wet environments in which seed plant precursors evolved from their free-sporing ancestors. Factors other than success in dry environments must have been driving the unification of the gametophyte and sporophyte generations in the ancestors of spermatophytes. Therefore, during the time of their earliest diversification in the Late Devonian, seed plants were probably still minor components of plant communities that were restricted to wetlands and floodplains (DiMichele *et al.* 2006).

The earliest animals to emerge onto land were arthropods, mainly arachnids, myriapods, and some hexapods (Shear & Selden 2001). Most early terrestrial arthropods were predators and detritivores, but feeding behaviors included herbivory on spores and plant stems (Labandeira 2007). The Late Devonian provides little evidence that the array of functional feeding types among terrestrial arthropods diversified much beyond the few that originated in the Late Silurian and Early Devonian. Despite the evolutionary appearance of true roots, leaves, wood, and seeds by the Late Devonian, these plant tissues do not show evidence of extensive herbivory until the Late Mississippian-Early Pennsylvanian boundary (Labandeira 2007).

Early and Mid-Devonian vertebrates are best known from “red bed” deposits formed in marine and estuarine settings along continental margins. During the Early Devonian these strata were dominated by lineages of agnathans and acanthodians that appeared during the Silurian (Janvier 1996). Importantly, placoderms emerged in many Early Devonian faunas, and sarcopterygians also became more predominant. The dipnomorph clade first appeared and includes durophagus lungfish and predatory porolepiforms (Janvier 1996). The diversity and abundance of gnathostomes continued to increase during the Mid-Devonian with placoderm and acanthodian radiations. Early actinopterygians appeared and tetrapodomorph sarcopterygians diversified to fill a wide variety of predatory aquatic niches. By the Late Devonian, many of these groups were well established in non-marine habitats associated with vegetated floodplains.

It is during the Late Devonian that several groups of placoderms, including phyllolepids, groenlandaspidids and bothriolepids, were common in continental and marginal settings, although these groups disappeared by the end of the period. A diverse array of sarcopterygians, including porolepiforms, dipnoans, rhizodontids, and “osteolepiforms,” also were found in continental and marginal deposits. Elpistostegalian sarcopterygians first appear in the late Mid-Devonian (Givetian) and by the latter part of the Late Devonian (Famennian) the fossil record documents a variety of early, limbed forms from a range of fluvial and near-shore depositional settings across the globe (Blieck *et al.* 2007; Astin *et al.* this volume).

Some lineages of tetrapodomorph sarcopterygians show morphological specializations in the pectoral girdles and fins that reflects experimentation in the use of the appendage for substrate locomotion. Among the rhizodontids and some “osteolepiforms” pectoral fins were used to push off from the substrate (Davis *et al.* 2004). Within the basal elpistostegalian lineage, pectoral fins developed a limb-like endoskeletal configuration and other specializations that may have allowed these animals to move through very shallow waters via substrate contact (Daeschler *et al.* 2006). It is within the elpistostegalian lineage that this configuration of fins with wrist, elbow, and shoulder joints lead to the development of limbs with digits, and thus, to the origin of tetrapods.

The Late Devonian witnesses early tetrapods that still were linked closely to aquatic ecosystems (Clack & Coates 1995; Clack 2002). As the record of the fin-to-limb transition has improved, we have gained a better understanding of the sequence of anatomical changes with the goal of reconstructing the acquisition of features that eventually allowed terrestriality. Fully terrestrial vertebrates do not appear in the fossil record until the Visean (352 – 333 Mya). The period between the origin of limbs (in the Late Devonian) and fully terrestrial habits (in the Visean) has been called Romer’s Gap, and more data is slowly emerging that will elucidate details of this critical interval in tetrapod history (*eg.*, Clack & Finney 2005).

According to recent models, the large increase in plant biomass and corresponding increase in depth of rooting and soil formation on Late Devonian floodplains led to a significant alteration of biogeochemical cycles in which enhanced weathering on the continents and the influx of plant detritus into fluvial systems increased nutrient availability in aquatic environments, and were possibly a causal factor for periodic marine anoxia (Algeo & Scheckler 1998). Black shale deposition in the epicontinental seaways record the anoxic episodes possibly resulting from these eutrophic conditions (Algeo *et al.* 2001). The Late Devonian black shale horizons are global in extent, and are associated with major marine extinctions, particularly of stromatoporoid-tabulate reef communities (McGhee 1996). Decline of $CO_2$ levels in the atmosphere and subsequent climate cooling have also been attributed to this weathering and burial of organic carbon, resulting in a brief glacial episode at the end of the Devonian (Caputo, 1985; Algeo *et al.* 2001).

Models of fluctuating atmospheric $O_2$ levels for the Devonian and Carboniferous have been used recently to invoke causal mechanisms for terrestrial diversification patterns (Ward *et al.* 2006; Labandeira 2007). After their first major diversification in the Late Silurian-Early Devonian, low oxygen levels during the Mid- to Late Devonian are postulated as a cause for the suppression of further diversification of terrestrial arthropods until the late Mississippian (Labandeira 2007). The suppression of evolutionary diversification by low oxygen levels also has been invoked as an explanation for Romer's Gap, the 15 million-year interval between the Late Devonian and late Mississippian with few known tetrapod fossils (Ward *et al.* 2006). In contrast, Clack (2007) points to the diverse Visean East Kirkton tetrapod fauna that demonstrates significant evolutionary advancements occurred during the Romer's Gap interval that simply has not been preserved or recovered from the fossil record. Because atmospheric oxygen levels are higher than contemporaneous aquatic oxygen levels, Clack (2007) postulates that anoxic conditions caused by decaying plant matter in freshwater ecosystems were a driving force in the evolution of air-breathing in tetrapodomorph fishes and their limbed descendents. These varying causal models represent ongoing efforts to relate evolutionary and ecological events to global biogeochemical changes in the Earth system.

### *Tectonics and depocenters in the Late Devonian*

The evidence for Late Devonian evolutionary and ecological terrestrial events is derived from sedimentary basins at the convergent and extensional margins of Late Devonian land masses (Friend *et al.* 2000). The Late Devonian land surface consisted of Euramerica (Laurussia) and Gondwana and the smaller continents of Siberia, Kazakhstan, North China, South China, as well as numerous microcontinents and islands (Scotese & McKerrow 1990). These landmasses generally were converging as part of the assembly of the supercontinent Pangaea during the mid-Palaeozoic. By the Late Devonian, major sedimentary basins were well-developed between components of Laurussia and Gondwana as the Iapetus Ocean closed between them. Many classic Late Devonian fossil sites in the Appalachian Basin of North America, East Greenland, Arctic Norway, the United Kingdom, Ireland, Belgium, Germany, the Baltics, and Russia are located in sediments resulting from Caledonide tectonic activity or post-orogenic collapse (Friend *et al.* 2000). By the Late Devonian, the onset of subduction along the northwestern edge of Euramerica resulted in the Antler and Ellesmerian Orogenies and on the western edge of Gondwana resulted in the Bolivarian Orogeny (Scotese & McKerrow 1990). This activity resulted in sedimentary deposits with fossils of Late Devonian terrestrial organisms in western North America, Arctic Canada, Venezuela, and Colombia. Smaller scale tectonic activity occurred on the eastern end of Gondwana and among the nearby microcontinents which created basins in Australia, Central Asia, North China, and South China (McMillan *et al.* 1988).

## Depositional Setting at Red Hill

### *Catskill Formation*

The Red Hill site is a road cut exposure of the Duncannon Member of the Catskill Formation (Woodrow *et al.* 1995). During deposition, sedimentation in Pennsylvania was dominated by a westward prograding shoreline complex with three deltaic depocenters (Dennison & Dewitt 1972; Rahmanian 1979; Smith & Rose 1985; Williams & Slingerland 1986), one of which occupied the center of the state (Fig. 2). These were fed by rivers that arose in the Acadian Highlands to the east, and flowed westward across a proximal alluvial plain (Sevon 1985; but see Bridge & Nickelsen 1986 for an alternative view) onto a vast low gradient coastal plain where sediments were deposited within an upper deltaic or lower alluvial plain setting. The alluvial plain rivers across the border in New York State are documented to have been low sinuosity, perennial, laterally-migrating single channels (Bridge & Gordon 1985). Bankfull discharges calculated at four cross sections, thought to be within about 10 km of the shoreline, ranged from 40 to 115 $m^3$-$sec^{-1}$. Although similar small rivers are recognized in eastern Pennsylvania (Sevon 1985), by the time the coastal plain had prograded through central Pennsylvania, the rivers were fewer in number and larger in dimension (Rahmanian 1979; Williams 1985). The low palaeolatitude (less than 20°) resulted in a tropical climate with alternating wet and dry seasons along the southern edge of the Euramerican landmass (Woodrow & Sevon 1985).

### *Depositional Model*

Traditional views of sedimentation in upper alluvial and coastal plain settings envision a single-thread meandering river continually feeding fine-grained sediment to a slowly aggrading floodplain as the alluvial ridge accumulates coarser-grained sediment. However, recent studies of modern fine-grained fluvial systems that are experiencing avulsions show that these systems cycle through two stages with a typical period on the order of 1000 years (Smith *et al.* 1989; Soong & Zhao 1994; Slingerland & Smith 2004). Stage I begins when a channel changes course by permanently breaching its levee. Here, a sediment wedge is constructed, headed at, or near, the avulsion site and prograding down-current as additional sediment is transported and deposited at the margins. Intense alluviation of the floodplain is fueled by the large drop in energy as the system evolves from a single channelized flow into rapidly evolving distributary channels of the alluvial wedge. These channels, in turn, debouche into waters ponded on the floodplain, the result of pre-existing channel levees and the high friction of floodplain vegetation (Fig. 3). Deposition proceeds by basinward extension of coalescing splays and lacustrine deltas fed by anabranching networks of distributary channels. The splays and deltas build into the transient lakes created by flooding due to the avulsion. In the process of progradation, new channels form by crevassing and bifurcation at channel mouths, and others lengthen by basinward extension. Both serve to deliver new sediment to the flooded basin so that further progradation can continue. Deposits of this stage are commonly: 1) coarser-grained crevasse splays assuming a variety of lobate, elliptical, or elongate shapes and usually containing multiple and variously sized distributary channels that route water and sediment to and beyond the splay margins (Smith 1986; O'Brien & Wells 1986; Bristow 1999b); and 2) finer-grained lake and distal splay deposits in which rapid burial has preserved organic debris from oxidation.

Stage II of the avulsion cycle is marked by distributary channels that begin to flow sub-parallel to the parent channel, once again following the regional slope. Small channels on the floodplain are 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 peat and soil formation to resume on the floodplain. The new trunk channel incises into its earlier avulsion deposits, creating a new meander belt that has a width about twice the meander amplitude. Incision occurs because all of the water is now collected into one channel of steeper slope than exists in Stage I. This meander belt width is relatively narrow, and only a small fraction of the floodplain deposits are reworked into meander belt deposits; the bulk of the floodplain deposits consists of Stage I avulsion fill (Fig. 4).

In the Red Hill outcrop, Stage I deposits are characterized by packages of red hackly weathering mudstones, faintly laminated siltstones with gently inclined bedding, and very fine sandstones exhibiting cross-bedding, cut-and-fill structures, and flat-based, convex-upwards bars that pinch-out laterally over tens of meters (ribbon sandstones of Fig. 4). The bars are flat-laminated and thinly bedded, with bedding surfaces often littered with plant debris. These sandstones are interpreted as deposits of proximal splays and splay-channel complexes while the siltstones and mudstones accumulated in ponds and more distal portions of the splay. The Stage I deposits at Red Hill contain the fossil-bearing facies with a variety of articulated, closely associated and isolated skeletal remains. Stage II sedimentation is represented by floodplain palaeosols identified by increased clay content, extensive slickenside surfaces, abundant caliche nodules up to 1 cm in diameter, and root traces. Whether peats of paleosols form during this stage depends upon whether the water table in the avulsion deposits remains high or is lowered as waters are collected into the more efficient single-thread channel of the newly forming meander belt. At the western end of the outcrop channel belt deposits are found. There are four avulsion cycles within the sequence exposed at the east end of the Red Hill outcrop. The earliest of these cycles (Fig. 5) shows the most extensive Stage I deposits (around 3 m thick) and is the primary fossiliferous zone at Red Hill, the source of the material on which this palaeoecological analysis is based. The thickness of the Stage I deposits in this cycle may reflect greater proximity to the parent channel at the time of that particular avulsion event. Successive Stage I packages are thinner (less than 2 m thick).

*Taphonomic considerations*

The source of fossil remains at Red Hill is a vertically narrow (3 m) but laterally broad (approximately 200 m exposed) sequence of fossiliferous strata. There is considerable lateral variation within this fossiliferous zone reflecting the heterogeneity produced by the variety of depositional facies in the avulsion model. 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, hence, 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 and diagenetic conditions (perhaps more acidic) 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.

### *Distribution of habitats at Red Hill*

The floodplain habitats at Red Hill provided a range of conditions for the cohabitation of plants and animals. 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.

### *Age of the deposit*

Palynological analysis has placed Red Hill within the poorly calibrated VH palynozone (Traverse, 2003), but it is less ambiguously attributed to the VCo palynozone (*sensu* Streel et al. 1987), within the Famennian Stage, Late Devonian Period. This zone is defined by the first occurrence of the palynomorph index species *Grandispora cornuta* Higgs and *Rugispora flexuosa* (Juschko) Streel, among others (Richardson & McGregor 1986; Streel & Scheckler 1990). A revision of Late Famennian zonation in Belgium will possibly place Red Hill firmly within the VH Spore Zone (Maziane *et al.* 1999) and, thus, within the *trachytera* to middle *expansa* Conodont Zones of the upper Famennian Substage (Streel & Loboziak 1996).

## Red Hill Flora and Fauna

### *Floral diversity*

The floral characteristics of the site are typical of a Late Devonian plant assemblage, a subtropical *Archaeopteris* forest (Table 1). Four *Archaeopteris* leaf morphospecies are dominated by *A. macilenta* and *A. hibernica* (Fig. 6a). 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* (Fig. 6c). The early diversification of arborescent lycopsids are represented by numerous decorticated stems, some identifiable as *Lepidodendropsis*. Also, well-preserved remains of cormose isoetalean bases and stems been described as *Otzinachsonia beerboweri* (Cressler & Pfefferkorn 2005). Spermatophytes are present as both *Moresnetia*-like cupules (Fig. 6b) and *Aglosperma* sp (Cressler 2006). The palynological age of the strata make it coeval with the ages of other sites with earliest recorded spermatophytes in Belgium and West Virginia (Fairon-Demaret & 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 have not been discovered so far at Red Hill, are the sphenopsids and cladoxylaleans.

### *Faunal diversity*

Table 2 presents a list of Red Hill fauna recognized to date. The arthropod fauna is likely only a very limited subset of the invertebrate community that was in the floodplain ecosystem. A trigonotarbid arachnid (Fig. 6f) and a archidesmid myriapod (Fig. 6e) each have been described from the standing water taphofacies, but greater diversity is evidenced by enigmatic body impressions, burrow traces, and walking traces (Fig. 6d). 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*, one of the most common taxa from the site (Daeschler *et al.* 2003). Fin spines and pectoral girdle elements of the acanthodian *Gyracanthus* (cf. *G. sherwoodi*), are also quite common. Among the bony fish fauna (osteichthyans), the small palaeoniscid actinopterygian, *Limnomis delaneyi* (Fig. 6h), and the large tristichopterid sarcopterygian, *Hyneria lindae*, are the dominant components. Early tetrapod remains are very rare and are represented by isolated skeletal elements, although recent analysis suggests that at least three penecontemporaneous taxa are present (Daeschler *et al*. 2009).

## Palaeoecological Setting at Red Hill

### *Vegetation*

A previous palaeoecological analysis of the Red Hill plant community 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 (Cressler 2006). Taphonomic and fossil-distribution evidence was derived from the systematic sampling of the floodplain pond deposit containing plant fossils that had undergone little or no transport. The evidence provided in that prior 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-Palaeozoic plant communities (DiMichele & Bateman 1996). The pattern of plant distribution at Red Hill was similar to that seen in other Late Devonian palaeoecological studies (Scheckler 1986a, 1986c; Rothwell & 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 they apparently flourished following fires that cleared the *Rhacophyton* groundcover. This is indicated by a succession of *Rhacophyton*-to-charcoal-to-spermatophyte remains within the small-scale stratigraphic profile (Cressler 2006).

The interpretation of distinct habitat-partitioning among the plants relies upon taphonomic and fossil distribution evidence, and, is thus indirect. Other studies further suggest a patchwork mosaic of monotypic stands of vegetation in the Late Devonian. For example, the dense accumulation of shed deciduous branches (Scheckler 1978; DiMichele *et al.* 1992) on the floor of *Archaeopteris* forests could have prevented or restricted understory growth. Paleosol and root-trace distribution has been used to suggest that deeply-rooted *Archaeopteris* and shallowly-rooted plants of other species were growing in different parts of the landscape (Retallack 1997).

### *Fire dynamics*

The occurrence of abundant charcoal at Red Hill is evidence of the importance of wildfires in the ecology of this early forest ecosystem (Cressler 2001, 2006). Previous work based on light microscope and SEM analysis of preserved xylem in the charcoal samples only showed evidence of *Rhacophyton* being burned in this landscape (Cressler 2001). An earlier ecological interpretation suggesting that the shallowly-rooted *Rhacophyton* became desiccated during the dry season and became vulnerable to burning, whereas the deeply-rooted *Archaeopteris* was relatively unaffected by fire is perhaps unfounded. The abundance of small fragments of *Rhacophyton*-derived charcoal in the floodplain pond sediments reflects taphonomic sorting bias in the earlier sampling (Cressler 2001, 2006). Since these previous publications, a 2 cm piece of charcoal has been found in a sandstone lens at Red Hill that most likely came from *Archaeopteris* (*Callixylon*) wood. Furthermore, reflectance analysis on Red Hill charcoal (mean $R_o$ = 4.4%; mode = 4.75%) indicates that the fires were predominantly 575° C, and within the temperature range of modern forest crown fires (Hawkins, 2006), and a similar phenomenon may have existed among *Archaeopteris* forests.

Nevertheless, the pattern of centimeter-scale succession in the sampled plant horizon at Red Hill shows the appearance of spermatophytes following the burning of *Rhacophyton* in presumed ground fires on a local scale. Perhaps spermatophytes were able to establish themselves quickly in burned patches due to their unified sporophyte and gametophyte generations. Obstructions imposed on their air-borne pollination mechanism by surrounding dense vegetation also would have been reduced. In any case, fire became an important factor in the dynamics of Late Devonian plant communities, contributing to the frequently changing spatio-temporal distribution of plants in the patchwork mosaic of this landscape.

### *Role of organic debris*

The increase in size and distribution of land plants in the Late Devonian increased the amount of organic matter available for burning, as well as for both nutrient availability and burial in depositional systems (Algeo *et al.* 2001). Evidence for high organic detrital influx into the fluvial regime is readily apparent at Red Hill. Floodplain pond deposits contain a high density of organic matter consisting of well-preserved foliage and stems of plants, fragmented debris, and charcoal. Many of the bedding surfaces within the reduced siltstone facies are dark in colour (Munsell N 4/*) due to organic content.

Along with organic debris, mineral nutrients entered the aquatic ecosystem at an increased rate due to increased soil weathering by plants (Algeo & Scheckler 1998). Evidence for nutrient-laden waters in the Catskill Delta system, and the micro-organisms that were supported, can be found at other localities where dense concentrations of filter feeding bivalves (cf. *Archanodon* sp.) are preserved in living position (unpublished data).

The increase in stature and rooting depth of riparian vegetation not only stabilized floodplains and affected the dynamics of channel and floodplain pond formation, but the influx of large plant debris into the aquatic ecosystem had structural implications for underwater habitats as well. Smaller organisms had more complex areas in which to hide, and larger organisms had more complex substrates over and through which to move. While the influx of organic matter enriched these environments and supported diverse aquatic ecosystems, it also created enhanced conditions for anoxia (Algeo & Scheckler 1998).

### *Trophic structure of the Red Hill ecosystem*

The following is a hypothetical model of trophic relationships based on evidence from sedimentology, taphonomy, and the interpretation of functional morphology. This model is necessarily simple in order to avoid over-interpretation.

By the Late Devonian there was an increase in primary productivity on land that became a source of a large volume of organic debris that was metabolized by micro-organisms in freshwater ecosystems. Aquatic invertebrates probably were taking advantage of this resource, but the evidence at Red Hill is limited to the activity of trace makers. There is no evidence of herbivory on living plant tissues but detritivores are in evidence, including the myriapods *Orsadesmus rubecollis* (Fig. 6e) and a putative myriopod trackway (Fig. 6d). Predatory terrestrial invertebrates included the trigonotarbid *Gigantocharinus szatmaryi* (Fig. 6f), as well as reported remains of scorpions which have not yet been described.

Among vertebrates, the groenlandspidids *Groenlandaspis pennsylvanicus* and *Turrisaspis elektor* were small to moderately-sized placoderms with ventrally oriented mouths suggesting that these animals were detritus feeders at the water-sediment interface. Their head-and-body shape also suggests a hydrodynamic design for staying close to the substrate. The same feeding mode also may apply to the phyllolepid placoderm, *Phyllolepis rosimontina*, which is less common at the site. The large gyracanthid acanthodian, *Gyracanthus* (cf. *G. sherwoodi*), was probably an open-water filter feeder, subsisting on primary producers and small primary consumers within the water column. The small chondrichthyan, *Ageleodus pectinatus*, is known only from isolated teeth found primarily in the microfossil taphofacies. The teeth show no sign of wear facets (Downs & Daeschler 2001) and the autecology of this form is poorly known although the teeth reflect a function to process soft-bodied prey. The presence of a single dorsal fin spine of *Ctenacanthus* sp. suggests an aberrant occurrence of this chondrichthyan that is known primarily from marine deposits including the Cleveland Shale, a distal equivalent of the Catskill Formation.

The palaeoniscid actinopterygian *Limnomis delaneyi* (Fig. 6h) was small (4 to 6 cm total length) and best preserved in the floodplain pond taphofacies where large numbers of articulated individuals have been collected. Some beds within the channel margin and microfossil taphofacies also contain a large amount of disarticulated material from *L. delaneyi*, or similar palaeoniscid(s). These primitive actinopterygians had sharp teeth and presumably ate small invertebrates and perhaps a variety of organic debris, providing an important link between the invertebrate and vertebrate components of the ecosystem.

Dipnoan (lungfish) toothplates (Fig. 6g) are rare at Red Hill and have been found primarily in the potentially-transported or reworked material of the microfossil taphofacies. Significant dipnoan skull material or scales have not been recognized. The tooth plates were presumably for a durophagous diet. Several articulated specimens of a distinctive rhizodontid sarcopterygian (Fig. 6i), presently undescribed, have been recovered only from the plant-rich siltstone of the floodplain pond taphofacies. These large (50 cm long) rhizodontids are the only articulated sarcopterygians known in this depositional setting. Its occurrence in pond sediments and the presence of large dentary, coronoid, and palatal fangs imply that this rhizodont was a predator that specialized in ponded backwater settings on the floodplain. The remaining sarcopterygian fauna are also medium to large-sized predators. At least one taxon of megalichthyid is present, although there is cosmine-covered skull material and scales that represent a range of body sizes, with estimated total lengths from 30 cm to 100 cm. The tristichopterid *Hyneria lindae* was the largest of the sarcopterygians, reaching a length of up to 3 m, and was the top predator in the ecosystem. This taxon may have fed upon all other fish and early tetrapod species. Although taphonomic bias due to preservational and collecting factors may influence the sample, the scales and teeth of *H. lindae* are among the most commonly encountered fossils at Red Hill.

The early tetrapods were also predatory animals, eating fish and perhaps invertebrates. As with other coeval tetrapods, particularly those known from relatively complete remains such as *Acanthostega gunnari* and *Ichthyostega* sp., these animals probably relied on aquatic ecosystems, and had a limited capacity for effective terrestrial locomotion. Red Hill is the only Late Devonian site that has produced at least three penecontemporaneous early tetrapod taxa (Daeschler *et al.* 2009). *Densignathus rowei* was the most robust taxon with a wide lower jaw including large coronoid fangs as found in more primitive tetrapodomorphs and some early tetrapods such as *Ventastega curonica* (Daeschler 2000: Ahlberg *et al.* 1994, 2008). The shoulder girdle of *Hynerpeton bassetti* (Fig. 6j) indicates a smaller taxon with a pectoral girdle similar to *Acanthostega gunnari* (Daeschler *et al.* 1994, 2009). Several small skull elements of a whatcheerid-like early tetrapod recently have been recognized. These indicate a more derived, steep-sided skull shape that may reflect modifications to the mechanics of respiration and prey capture (Daeschler *et al.* 2009). The diversity of early tetrapods at Red Hill, though known from only fragmentary material, indicates ecological specialization even at this early stage in tetrapod evolution. It seems likely such diversity is a reflection of the diverse ecological opportunities that were present on the floodplains where a range of habitats were formed by shifting geomorphic regimes and lowland vegetation.

The Red Hill faunal assemblage is uniquely diverse in the Catskill Formation and includes several taxa that are not known from other sites in the formation. Also of interest is the notable absence of the antiarch placoderm *Bothriolepis* and the porolepiform sarcopterygian *Holoptychius* at Red Hill. *Bothriolepis* and *Holoptychius* remains are very common in most other Catskill Formation sites, and are common components of Late Devonian freshwater and marginal deposits around the world. The absence of these forms at Red Hill may speak to the palaeoenvironmental setting rather than a significant biostratigraphic difference. As far as can be judged from palynomorph biostratigraphy, the Red Hill assemblage is the same age as many *Bothriolepis* and *Holoptychius* bearing sites in the Catskill Formation and so we must conclude that the Red Hill ecosystem was not suitable for these taxa. The fact that Red Hill produces a unique fauna and that some taxa that are common at most other Catskill Formation sites are absent at Red Hill suggests that the paleoenvironmental setting at Red Hill is rare among Catskill Formation sites.

## Discussion

### *Palaeobiogeographic distribution of the Red Hill flora and fauna*

*Archaeopteris* forests were distributed nearly globally and its fossil remains are known from nearly every sedimentary basin with Late Devonian terrestrial deposits. This includes many North American localities in the Appalachian Basin (Scheckler 1986c; Cressler 2006), as well as Alberta (Scheckler 1978) and Arctic Canada (Andrews *et al.* 1965); South American localities in Venezuela (Berry & Edwards 1996); Eurasian localities in Great Britain and Ireland (Chaloner *et al.* 1977), Belgium (Kenrick & Fairon-Demaret 1991), Svalbard (Nathorst 1900, 1902), Eastern Europe and Russia (Snigirevskaya, 1988, 1995a), Siberia (Petrosyan 1968), and China (Cai 1981, 1989; Cai *et al.* 1987); African localities in Morocco (Gaultier *et al.* 1996; Meyer-Berthaud *et al.* 1997) and South Africa (Anderson *et al.* 1995); Australian localities (White 1986); and possibly Antarctica (Retallack 1997).

*Archaeopteris*, and to some extent *Rhacophyton*, are worldwide floral biomarkers for the Late Devonian. When considered with other floral elements, the plant assemblage at Red Hill most closely resembles coeval assemblages elsewhere in the Appalachian Basin, especially Elkins, West Virginia (Scheckler 1986b). They share many elements, including a variety of *Archaeopteris* species, *Rhacophyton*, *Gillespiea*, *Barinophyton sibericum*, arborescent lycopsids, and spermatophytes. The Elkins locality is more diverse, preserving both sphenopsids and a cladoxylalean. Elkins is interpreted as a deltaic shoreline deposit (Scheckler 1986b) in contrast to the alluvial plain interpretation for Red Hill. Perhaps a more important factor in their similarity is their geographic and temporal proximity. The localities of the Evieux Formation in Belgium are also of coeval palynozones, and have the most similar plant assemblages to their North American counterparts (Kenrick & Fairon-Demaret 1991). Dispersal between these sites would have occurred over a single landmass during the Late Devonian. Such general and qualitative biogeographic assessments need to be followed by quantitative analyses of floral assemblage similarity to test further hypotheses of biogeographic origin and dispersal.

Wilson *et al.* (2005) recognized Late Devonian biogeographic continuity in archipolypodan millipedes from the Euramerican landmass, including *Orsadesmus rubecollus* from Red Hill. The Appalachian vertebrate fauna has biogeographic affinities to Famennian sites from both the Euramerican and Gondwanan landmasses. These similarities are particularly striking with groenlandaspidid and phyllolepid placoderms, gyracanthid acanthodians, the chondrichthyan *Ageleodus pectinatus,* and the large tristichopterid sarcopterygian, *Hyneria lindae,* which is closely related to *Eusthenodon* spp., a taxon with a global distribution in the Famennian. This cosmopolitan Famennian fish fauna is in contrast to Frasnian faunas in which the Euramerican and Gondwanan landmasses do not share significant elements. This pattern of Frasnian endemism and Famennian cosmopolitanism is presumably a reflection of tectonic processes bringing Euramerican and Gondwanan landmasses into close enough contact to allow dispersal of organisms that were unable to cross marine barriers.

### *The use of ecological models to explain the origins of tetrapods*

This palaeoecological profile of the Red Hill site provides a view of the status of terrestrialization towards the end of the Late Devonian. The range of depositional settings at the site and the penecontemporaneous nature of the deposits provide a diversity of fossil evidence for the interpretation of a relatively *in-situ* ecosystem. As seen here and in other Late Devonian deposits, plants had established complex communities by this time, and invertebrates had a well-established terrestrial foothold. Even though many morphological characteristics important for terrestrial life had evolved among tetrapodomorphs, all vertebrates were still essentially aquatic. The conditions at Red Hill can more confidently be said to reflect selective pressures among tetrapodomorphs for life in shallow, obstructed, and fluctuating waters rather than for full terrestriality. Multiple lines of evidence, as provided herein, can help in the construction of palaeoecological models of the physical and biotic interactions in which early tetrapods evolved, diversified, and eventually became fully terrestrial.

By the Late Devonian, the extensively vegetated alluvial floodplains provided enhanced landscape stabilization by means of deeper rooting depth, habitat amelioration through shading, nutrient enrichment of adjacent waters, and increased complexity of shallow water habitats through plant debris accumulation. The avulsion cycles created floodplain geomorphologic regimes that provided a dynamically shifting range of habitats, accompanied by an annual wet-and-dry seasonality that altered access to shallow water habitats and resources in the shorter term. This range of habitats includes shallow channel and wetland interfluve settings that supported productive ecosystems. Access to shallow water habitats could have provided a refuge for the earliest tetrapods to escape predation from larger, and perhaps faster swimming sarcopterygians. The resources in these habitats may have been out of reach of most large-bodied sarcopterygian predators, except for those that could navigate with appendages capable of support and locomotion across the shallow water substrates. Other morphological changes along the tetrapodomorph lineage, such as loss of scale cover and median fins, and development of a neck, may also have been related to locomotion and successful prey capture in these habitats (Daeschler *et al.* 2006).

The hypotheses outlined above need to be tested further. As the study of tetrapod terrestriality proceeds, it will be necessary to develop palaeoecological models based on multiple lines of evidence including sedimentology, taphonomy, functional morphology, developmental biology, biogeochemistry, and other disciplines that can be synthesized to provide a holistic picture of these ancient non-analog ecosystems.

## References Cited

Ahlberg, P. E., Luksevics, E. & Lebedev, O. 1994. The first tetrapod finds from the Devonian (Upper Famennian) of Latvia. *Philosophical Transactions of the Royal Society of London B*, **343**, 303-328.

Ahlberg, P. E., Clack, J. A., Luksevics, E., Blom, H. & Zupins, I. 2008. *Ventastega curonica* and the origin of tetrapod morphology. *Nature*, **453**, 1199-1204.

Algeo, T. J. & Scheckler, S. E. 1998. Terrestrial-marine teleconnections in the Devonian: Links between the evolution of land plants, weathering processes, and marine anoxic events. *Philosophical Transactions of the Royal Society of London, B*, **353**, 113-130.

Algeo, T. J., Scheckler, S. E. & Maynard, J. B. 2001. Effects of Middle to Late Devonian spread of vascular land plants on weathering regimes, marine biotas, and global climate. *In:* Gensel, P. G. & Edwards, D. (eds) *Plants invade the land: Evolutionary and environmental perspectives*. Columbia University Press, New York, 213-236.

Anderson, H. M., Hiller, N. & Gess, R. W. 1995. *Archaeopteris* (Progymnospermopsida) from the Devonian of southern Africa. *Botanical Journal of the Linnean Society*, **117**, 305-320.

Andrews, H. N., Phillips, T. L. & Radforth, N. W. 1965. Paleobotanical studies in Arctic Canada. I. *Archaeopteris* from Ellesmere Island. *Canadian Journal of Botany*, **43**, 545-556.

Astin, T. R., Marshall, J. E. A., Blom, H. & Berry, C. R. this volume. The sedimentary environment of the Late Devonian East Greenland tetrapods. *In*: Vecoli, M. & Clement, G. (eds) *The Terrestrialization Process: Modelling Complex Interactions at the Biosphere-Geosphere Interface*. The Geological Society, London.

Banks, H. P. 1980. Floral assemblages in the Siluro-Devonian. *In*: Dilcher, D. L. & Taylor, T. N. (eds) *Biostratigraphy of Fossil Plants*. Dowden, Hutchinson, & Ross, Pennsylvania, 24 p.

Bateman, R. M. & DiMichele, W. A. 1994. Heterospory: the most iterative key innovation in the evolutionary history of the plant kingdom. Biological Reviews, **69**, 345-417.

Beck, C. B. 1964. Predominance of *Archaeopteris* in Upper Devonian flora of western Catskills and adjacent Pennsylvania. *Botanical Gazette*, **125**, 126-128.

Berry, C. M. & Edwards, D. 1996. The herbaceous lycophyte *Haskinsia* Grierson and Banks from the Devonian of western Venezuela, with observations on leaf morphology and fertile specimens. *Botanical Society of the Linnean Society*, **122**, 103-122.

Berry, C. M. & Fairon-Demaret, M. 2001. The Middle Devonian flora revisited. *In:* Gensel, P.G. & Edwards, D. (eds) *Plants invade the land: evolutionary and environmental perspectives*. Columbia University Press, New York, 120-139.

Blieck, A., Clement, G., Blom, H., LeLievre, H., Luksevics, E., Streel, M., Thorez, J. & Young, G. C. 2007. The biostratigraphical and palaeogeographical framework of the earliest diversification of tetrapods (Late Devonian). *In*: Becker, R. T. & Kirchgasser, W. T. (eds) *Devonian Events and Correlations*. Geological Society, London, Special Publications, **278**, 219-235.

Bridge, J. S. & Gordon, E. A. 1985. Quantitative interpretation of ancient river systems in the Oneonta Formation, Catskill Magnafacies. *In*: Woodrow, D. L. & Sevon, W. D. (eds) *The Catskill Delta*. Geological Society of America, Boulder, CO, Special Papers, **201**, 163-181.

Bridge, J. S. & Nickelsen, B. H. 1986. Reanalysis of the Twilight Park Conglomerate, Upper Devonian Catskill Magnafacies, New York State. *Northeastern Geology*, **7**, 181-191.

Bristow, C. S. 1999. Crevasse splays from the rapidly aggrading sand-bed braided Niobrara River, Nebraska: effect of base-level rise. *Sedimentology,* **46**, 1029-47

Cai C. 1981. On the occurrence of *Archaeopteris* in China. *Acta Palaeontologica Sinica*, **20**, 75-80.

Cai C. 1989. Two *Callixylon* species from the Upper Devonian of Junggar Basin, Xinjiang. *Acta Palaeontologica Sinica*, **28**, 571-578.

Cai C., Wen Y. & Chen P. 1987. *Archaeopteris* florula from Upper Devonian of Xinhui County, central Guangdong and its stratigraphical significance (In Chinese with English summary). *Acta Palaeontologica Sinica*, **26**, 55-64.

Caputo, M. V. 1985. Late Devonian glaciation in South America. Palaeogeography, Palaeoclimatology, Palaeoecology, **51**, 291-317.

Chaloner, W., Hill, A. J. & Lacey, W. S. 1977. First Devonian platyspermic seed and its implications for gymnosperm evolution. *Nature*, **265**, 233-235.

Chaloner, W. & Sheerin, A. 1979. Devonian macrofloras. *In*: House, M. R., Scrutton, C. T. & Bassett, M. G. (eds) *The Devonian system: a Palaeontological Association International*

*Symposium*. The Palaeontological Association, London, UK, Special Papers in Palaeontology, 145-161.

Clack, J. A. 2002. *Gaining ground: the origin and evolution of tetrapods*. Indiana University Press, Bloomington, Indiana, 369 pp.

Clack, J. A. 2007. Devonian climate change, breathing, and the origin of the tetrapod stem group. *Integrative and Comparative Biology,* **47**, 510-523.

Clack, J. A. & Finney, S. M. 2005. *Pederpes finneyae*, an articulated tetrapod from the Tournasian of Western Scotland. *Journal of Systematic Palaeontology*, **2**, 311-346.

Clack, J. A. & Coates, M. I. *Acanthostega gunnari*, a primitive, aquatic tetrapod? *Bulletin du Museum National d'Histoire Naturelle*, **4**, 359-372.

Cressler, W. L. III. 2001. Evidence of the earliest known wildfires. *Palaios* **16**: 171-174.

Cressler, W. L. III. 2006. Plant palaeoecology of the Late Devonian Red Hill locality, north-central Pennsylvania, an *Archaeopteris*-dominated wetand plant community and early tetrapod site. *In*: Greb, S. F. & DiMichele, W. A. (eds) *Wetlands Through Time*. Geological Society of America, Boulder, CO, Special Papers, **399**, 79-102

Cressler, W. L. & Pfefferkorn, H. W. 2005. A Late Devonian isoetalean lycopsid, *Otzinachsonia* *beerboweri*, gen. et sp. nov., from north-central Pennsylvania, U.S.A. *American Journal of Botany*, **92**, 1131-1140.

Daeschler, E. B. 2000. Early tetrapod jaws from the Late Devonian of Pennsylvania, USA. *Journal of Palaeontology,* **74**, 301-308.

Daeschler, E. B., Shubin, N. H., Thomson, K. S. & Amaral, W. W. 1994. A Devonian tetrapod from North America. *Science*, **265**, 639-642.

Daeschler, E. B., Frumes, A. C. & Mullison, C. F. 2003. Groenlandaspidid placoderm fishes from the Late Devonian of North America. *Records of the Australian Museum*, **55**, 45-60.

Daeschler, E. B., Shubin, N. H. & Jenkins, F.A., Jr. 2006. A Devonian tetrapod-like fish and the evolution of the tetrapod body plan. *Nature*, **440**, 757-763.

Daeschler, E. B., Clack, J. A. & Shubin, N. H. 2009. Late Devonian tetrapod remains from Red Hill, Pennsylvania, USA: How much diversity? *Acta Zoologica,* **90** (Suppl. 1), 306-317.

Davis, M. C., Shubin, N. H. & Daeschler, E. B. 2004. A new specimen of *Sauripterus taylori* (Sarcopterygii, Osteichthyes) from the Famennian Catskill Formation of North America. *Journal of Vertebrate Paleontology*, **24**, 26-40.

Dennison, J. M. & DeWitt, W., Jr. 1972. Redbed zone produced by sea level drop at beginning of

Devonian Cohocton Age delimits Fulton and Augusta Lobes of Catskill delta complex. *In*: Dennison, J. M. *et al.* (eds) *Stratigraphy, Sedimentology, and Structure of Silurian and Devonian Rocks Along the Allegheny Front in Bedford County, PA, Allegheny County, MD, and Grant County, WV*. Pennsylvania Topographic and Geologic Survey, Harrisburg, PA, Guidebook for the 37th Annual Field Conference of Pennsylvania Geologists, 114 p.

DiMichele, W. A. & Bateman, R. M. 1996. Plant paleoecology and evolutionary inference: two examples from the Paleozoic. *Review of Palaeobotany and Palynology*, **90**, 223-247.

DiMichele, W.A. & Hook, R.W., rapporteurs; Beerbower, R., Boy, J. A., Gastaldo, R. A., Hotton III, N., Phillips, T. L., Scheckler, S. E., Shear W. A. & Sues, H.-D., contributors. 1992. Paleozoic terrestrial ecosystems. *In*: Behrensmeyer, A. K., Damuth, J. D., DiMichele, W. A., Potts, R., Sues, H.-D. & Wing, S. L. (eds) *Terrestrial ecosystems through time*. University of Chicago Press, Chicago, IL, 205-325.

DiMichele, W. A., Phillips, T. L. & Pfefferkorn, H. W. 2006. Paleoecology of Late Paleozoic pteridosperms from tropical Euramerica. *Journal of the Torrey Botanical Society*, **133**, 83-118.

Downs, J. P. & Daeschler, E. B. 2001. Variation within a large sample of *Ageleodus pectinatus* teeth (Chondrichthyes) from the Late Devonian of Pennsylvania, USA. *Journal of Vertebrate Paleontology*, **21**, 811-814.

Edwards, D. & Wellman, C. 2001. Embryophytes on land: the Ordovician to Lochkovian (Lower

Devonian) record. *In*: Gensel, P. G. & Edwards, D. (eds) *Plants invade the land: evolutionary and environmental perspectives*. Columbia University Press, New York, 3-28.

Fairon-Demaret, M. & Scheckler, S. E. 1987. Typification and redescription of *Moresnetia zalesskyi* Stockmans, 1948, an early seed plant from the Upper Famennian of Belgium. *Bulletin de L'Institut Royal les Sciences Naturalles de Belgique, Sciences del la Terre*, **57**, 183-199.

Friend, P. F., Williams, B. P. J., Ford, M. & Williams, E. A. 2000. Kinematics and dynamics of Old Red Sandstone basins. *In*: Friend, P. F. & Williams, B. P. J. (eds) *New perspectives on the Old Red Sandstone*. Geological Society, London, Special Publications, **180**, 29-60.

Galtier, J., Paris, F. & Aouad-Debbaj, Z. E. 1996. La présence de *Callixylon* dans le Dévonien supérieur du Maroc et sa signification paléogéographique. *Compte Rendu de l'Académies des Sciences Paris* (Série IIa), **322**, 893-900.

Griffing, D. H., Bridge, J. S. & Hotton, C. L. 2000. Coastal-fluvial palaeoenvironments and plant palaeoecology of the Lower Devonian (Emsian), Gaspé Bay, Québec, Canada. *In*: Friend, P. F. & Williams, B. P. J. (eds) *New Perspectives on the Old Red Sandstone*. Geological Society, London, Special Publications, **180**, 61-84.

Hawkins, S. J. 2006. Fossil charcoal in Devonian-Mississippian shales: Implications for the expansion of land plants, paleo-atmospheric oxygen levels and organic-rich black shale accumulation. Unpublished M.S. Thesis, University of Kentucky, Lexington, KY, 151 p.

Hotton, C. L., Hueber, F. M., Griffing, D. H. & Bridge, J. S. 2001. Early terrestrial plant environments: an example from the Emsian of Gaspé, Canada. *In*: Gensel, P. G. & Edwards, D. (eds) *Plants Invade the Land: Evolutionary and environmental perspectives*. Columbia University Press, New York, 179-212.

Janvier, P. 1996. *Early Vertebrates*. Oxford Science Publications, Clarendon Press, Oxford, Oxford Monographs on Geology and Geophysics, **33**, 393 p.

Kenrick, P. & Fairon-Demaret, M. 1991. *Archaeopteris roemeriana* (Göppert) sensu Stockmans, 1948 from the Upper Famennian of Belgium: anatomy and leaf polymorphism. *Bulletin de l'Institute Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, **61**, 179-195.

Labandeira, C. 2007. The origin of herbivory on land: initial patterns of plant tissue consumption by arthropods. *Insect Science*, **14**, 259-275.

Maziane, N., Higgs, K. T. & Streel, M. 1999. Revision of the Late Famennian zonation scheme in eastern Belgium. *Journal of Micropalaeontology*, **18**, 117-125.

McGhee, G. R. 1996. The Late Devonian mass extinction: the Frasnian/Famennian crisis. New York, Columbia University Press, Critical Moments in Paleobiology and Earth History Series, 303 p.

McMillan, N. M. J., Embry, A. F. & Glass, D. J. (eds). 1988. *Devonian of the World, Proceedings of the Second International Symposium on the Devonian System*. Canadian Society of Petroleum Geologists, Calgary, Alberta, Canada, Memoirs, **14**.

Meyer-Berthaud, B., Wendt, J. & Galtier, J. 1997. First record of a large *Callixylon* trunk from the Late Devonian of Gondwana. *Geology Magazine*, **134**, 847-853.

Nathorst, A. G. 1900. Die oberdevonische Flora (die "Ursaflora) der Bären Insel. *Bulletin of the Geological Institute of Upsala*, No. 8, **Vol. IV**, Part 2, 1-5.

Nathorst, A. G. 1902. Zur oberdevonische Flora der Bären-Insel. *Kongliga Svenska Vetenskaps-Akademiens Handlingar*, **36**, 1-60.

O'Brien P. E. & Well, A. T. 1986. A small alluvial crevasse splay. *Journal of Sedimentary Petrology*, **56**, 876-79.

Peppers, R. A. & Pfefferkorn, H. W. 1970. A comparison of the floras of the Colchester (No. 2) Coal and the Francis Creek Shale. *In*: Smith, W. H. *et al.* (eds) *Depositional environments in parts of the Carbondale Formation - Western and Northern Illinois*. Illinois State Geological Survey, Springfield, IL, Illinois State Geological Survey Field Guidebook Series, 61-74.

Petrosyan, N. M. 1968. Stratigraphic importance of the Devonian flora of the USSR. *In*: Oswald, D. H. (ed) *International Symposium on the Devonian System, 1*. Alberta Society of Petroleum Geology, Calgary, Alberta, Canada, 579-586.

Rahmanian, V. D. 1979. *Stratigraphy and sedimentology of the Upper Devonian Catskill and uppermost Trimmers Rock Formations in central Pennsylvania*. PhD thesis, The Pennsylvania State University.

Retallack, G. J. 1997. Early forest soils and their role in Devonian global change. *Science*, **276**, 583-585.

Richardson, J. B. & McGregor, D. C. 1986. Silurian and Devonian spore zones of the Old Red Sandstone continent and adjacent regions. *Geological Survey of Canada, Bulletin*, **364**, 1-79.

Rothwell, G. W. & Scheckler, S. E. 1988. Biology of ancestral gymnosperms. *In*: Beck, C. B. (ed) *Origins and evolution of gymnosperms*. Columbia University Press, New York, 85-134.

Rothwell, G. W., Scheckler, S. E. & Gillespie, W. H. 1989. *Elkinsia* gen nov., a Late Devonian gymnosperm with cupulate ovules. *Botanical Gazette*, 150, 170-189.

Scheckler, S. E. 1978. Ontogeny of progymnosperms. II. Shoots of Upper Devonian Archaeopteridales. *Canadian Journal of Botany*, **56**, 3136-3170.

Scheckler, S. E. 1986a. Floras of the Devonian-Mississippian transition. In: Gastaldo, R. A. & Broadhead, T. W. (eds) *Land plants: notes for a short course*. University of Tennessee, Knoxville, TN, Studies in geology, **15**, 81-96.

Scheckler, S. E. 1986b. Old Red Continent facies in the Late Devonian and Early Carboniferous of Appalachian North America. *Annales de la Société Géologique de Belgique*, **109**, 223-236.

Scheckler, S. E. 1986c. Geology, floristics and paleoecology of Late Devonian coal swamps from Appalachian Laurentia (U.S.A.). *Annales de la Société Géologique de Belgique*, **109**, 209-222.

Scheckler, S. E. 2001. Afforestation – the first forests. *In*: Briggs, D. E. G. & Crowther, P. (eds) *Palaeobiology II*. Blackwell Science, Oxford, 67-71.

Scheckler, S. E., Cressler, W. L., Connery, T., Klavins, S. & Postnikoff, D. 1999. Devonian shrub and tree dominated landscapes. *XVI International Botanical Congress, Abstracts*, **16**, 13.

Scotese, C. R. & McKerrow, W. S. 1990. Revised world maps and introduction. *In*: McKerrow, W. S. & Scotese, C. R. (eds) *Palaeozoic palaeogeography and biogeography*. The Geological Society, London, Memoirs, 1-21.

Sevon, W. D. 1985. Nonmarine facies of the Middle and Late Devonian Catskill coastal alluvial plain. *In*: Woodrow, D.L. & Sevon, W.D. (eds) *The Catskill Delta*. Geological Society of America, Boulder, CO, Special Papers, **201**, 79-90.

Shear, W. A. & Selden, P. A. 2001. Rustling in the undergrowth: animals in early terrestrial ecosystems. *In*: Gensel, P. G. & Edwards, D. (eds) *Plants invade the land: evolutionary and environmental perspectives*. Columbia University Press, New York, 29-51.

Snigirevskaya, N. S. 1988. The Late Devonian - The time of the appearance of forests as a natural phenomenon. *In*: *Contributed papers: the formation and evolution of the continental biotas, L.*: 31st Session of the All-Union Palaeontological Society, 115-124, (in Russian).

Snigirevskaya, N. S. 1995. Archaeopterids and their role in the land plant cover evolution. *Botanicheskii Zhournal*, **80**, 70-75, (in Russian with English summary).

Slingerland, R. & N. D. Smith. 2004. River avulsions and their deposits. *Annual Review of Earth and Planetary Sciences*, **32**, 257-285.

Smith, D. G. 1986. Anastomosing river deposits, sedimentation rates and basin subsidence, Magdalena River, northwestern Colombia, South America. *Sedimentary Geology*, **46**, 177-96.

Smith A. T. & Rose, A. W. 1985. Relation of red-bed copper- uranium occurrences to the regional sedimentology of the Catskill Formation in Pennsylvania. *In*: Woodrow, D. L. & Sevon, W. D. (eds) *The Catskill Delta*. Geological Society of America, Boulder, CO, Special Papers, **201**, 183-197.

Smith, N. D., Cross, T. A., *et al.* 1989. Anatomy of an avulsion. *Sedimentology*, **36**, 1-23.

Soong T. W. M. & Zhao Y. 1994. The flood and sediment characteristics of the Lower Yellow River in China. *Water International*, **19**, 129-37

Stein, W. E., Mannolini, F., Hernick, L. V., Landing, E. & Berry, C.M. 2007. Giant cladoxylopsid trees resolve the enigma of the Earth's earliest forest stumps at Gilboa. *Nature*, **446**, 904-907.

Stewart, W. N. & Rothwell, G. W. 1993. *Paleobotany and the evolution of plants*. Cambridge University Press, Cambridge, UK, 521 p.

Streel, M. & Scheckler, S. E. 1990. Miospore lateral distribution in upper Famennian alluvial lagoonal to tidal facies from eastern United States and Belgium. *Review of Palaeobotany and Palynology*, **64**, 315-324.

Streel, M. & Loboziak, S. 1996. 18B: Middle and Upper Devonian miospores. In: Jansonius, J. & McGregor, D. C. (eds) *Palynology: Principles and Applications*. Vol. 2: Applications. Ch. 18: Paleozoic spores and pollen. American Association Stratigraphic Palynologists Foundation, College Station, Texas, 579-587.

Traverse, A. 2003. Dating the earliest tetrapods: A Catskill palynological problem in Pennsylvania. *Courier Forschungs - Institut Senckenberg*, **241**, 19-29.

Ward, P., Labandeira, C., Laurin, M. & Berner, R. A. 2006. Confirmation of Romer's Gap as a low oxygen interval constraining the timing of initial arthropod and vertebrate terrestrialization. *Proceedings of the National Academy of Sciences,* **103**, 16818-16822.

White, M. E. 1986. *The greening of Gondwana, Frenchs Forest, New South Wales*. Reed Books Pty. Ltd., 84.

Williams, E. G. 1985. Catskill sedimentation in central Pennsylvania. *In*: *Central Pennsylvania Geology Revisted*. The Pennsylvania State University, University Park, PA, Guidebook for the 50th Annual Field Conference of Pennsylvania Geologists, 20-32.

Williams, E. G. & Slingerland, R. 1986. Catskill sedimentation in central Pennsylvania. *In*: Sevon, W. D. (ed) *Selected Geology of Bedford and Huntingdon Counties*. Pennsylvania Bureau of Topographic and Geologic Survey, Harrisburg, PA, Guidebook for the 51st Annual Field Conference of Pennsylvania Geologists, 73-79.

Wilson, H. M., Daeschler, E. B. & Desbiens, S. 2005. New flat-backed archiplypodan millipedes from the Upper Devonian of North America. *Journal of Paleontology*, **79**, 738-744.

Woodrow, D. L. & Sevon, W. D., (eds). 1985. *The Catskill Delta*. Geological Society of America, Boulder, CO, Special Papers, **201**, 246 p.

Woodrow, D. E., Robinson, R. A. J., Prave, A. R., Traverse, A., Daeschler, E. B., Rowe, N. D. & Delaney, N. A.. 1995. Stratigraphic, sedimentological and temporal framework of Red Hill

(Upper Devonian Catskill Formation) near Hyner, Clinton County, Pennsylvania: Site of the oldest amphibian known from North America. *In*: J. Way (ed): *Field Trip Guide, 60th Annual Field Conference of Pennsylvania Geologists*, Lock Haven University, Lock Haven, PA, 16 pp.

## Figure Captions

Fig. 1. Location of the Red Hill site, Clinton County, Pennsylvania, USA.

Fig. 2. General depositional setting of the Appalachian basin during deposition of the strata at Red Hill. The illustration represents the position of the shoreline during the Frasnian Stage. By the Fammenian, when the strata at Red Hill were deposited, the shoreline had prograded further west, and the locality lay in the upper alluvial to lower coastal plain.

Fig. 3. Depositional environments during Stage I of the avulsion model envisioned for Red Hill sedimentation. Watercolor from Cumberland Marshes of the Saskatchewan River, SK, Canada. Evolutionary innovations described in the text are thought to have arisen in a similar terrestrial setting.

Fig. 4. Schematic cross-section of alluvial deposits showing stratigraphic relationships of Stage I and Stage II. Fossiliferous strata discussed in text originate from Stage I deposits.

Fig. 5. Graphic log of the earliest and thickest Stage I deposits at Red Hill showing location of fossiliferous zone with respect to these avulsion deposits.  See text for details.

Fig. 6. Examples of floral and faunal elements from the fossiliferous zone. (**a**), *Archaeopteris* sp.; (**b**), spermatophyte cupule; (**c**), *Rhacophyton ceratangium*; (**d**), unidentified arthropod trackway; (**e**), *Orsadesmus rubecollus*; (**f**), *Gigantocharinus szatmaryi*; (**g**), unidentified dipnoan toothplate; (**h**), *Limnomis delaneyi*; (**i**), unidentified rhizodontid sarcopterygian; (**j**), shoulder girdle of *Hynerpeton bassetti*. Black scale bars = 2cm. White scale bars = 5mm.

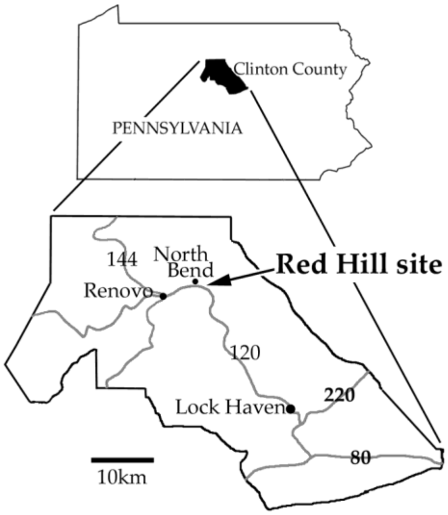

Figure 1

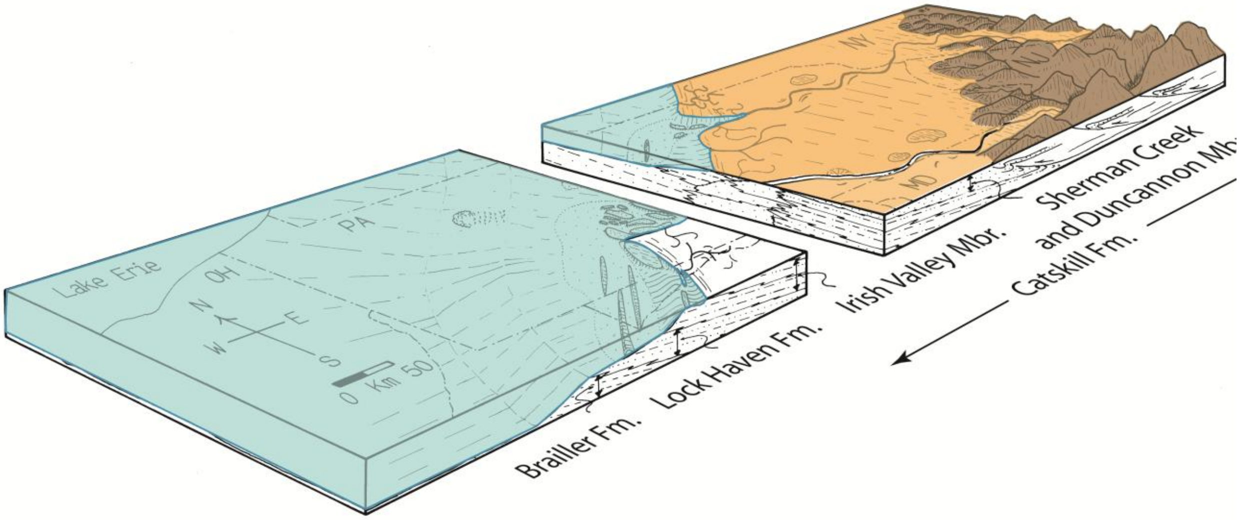

Figure 2

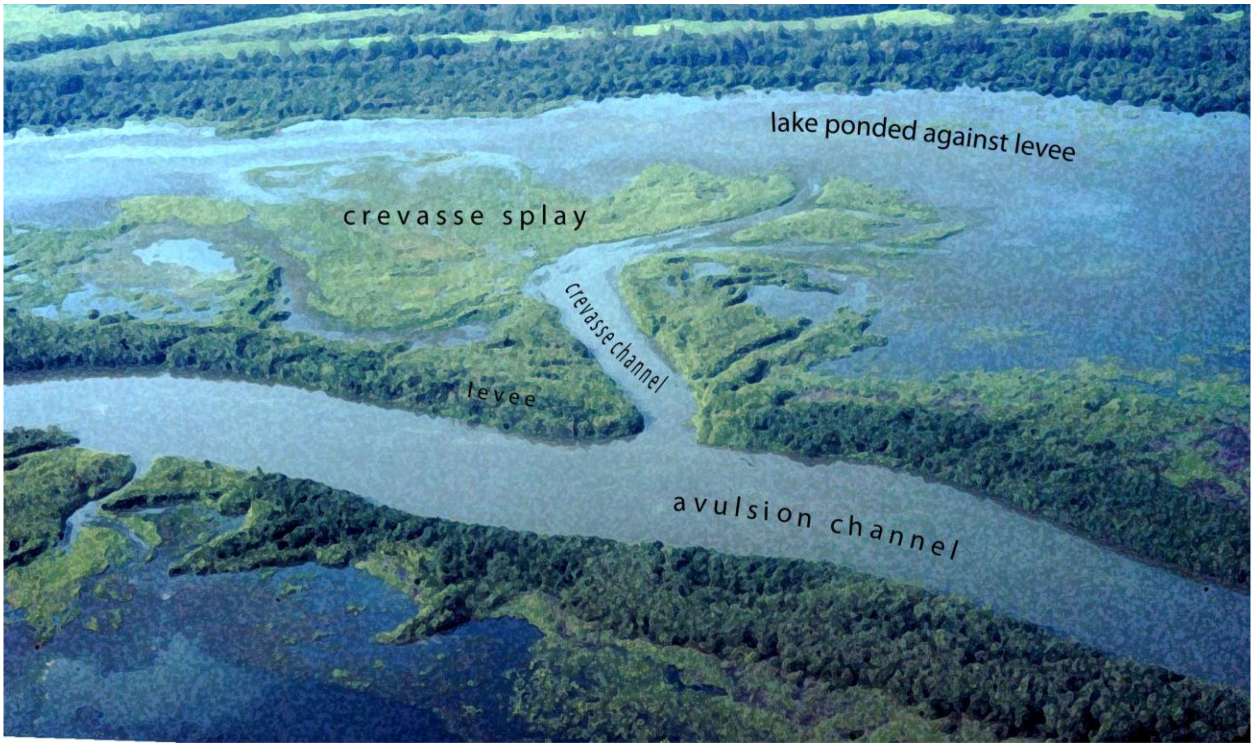

Figure 3

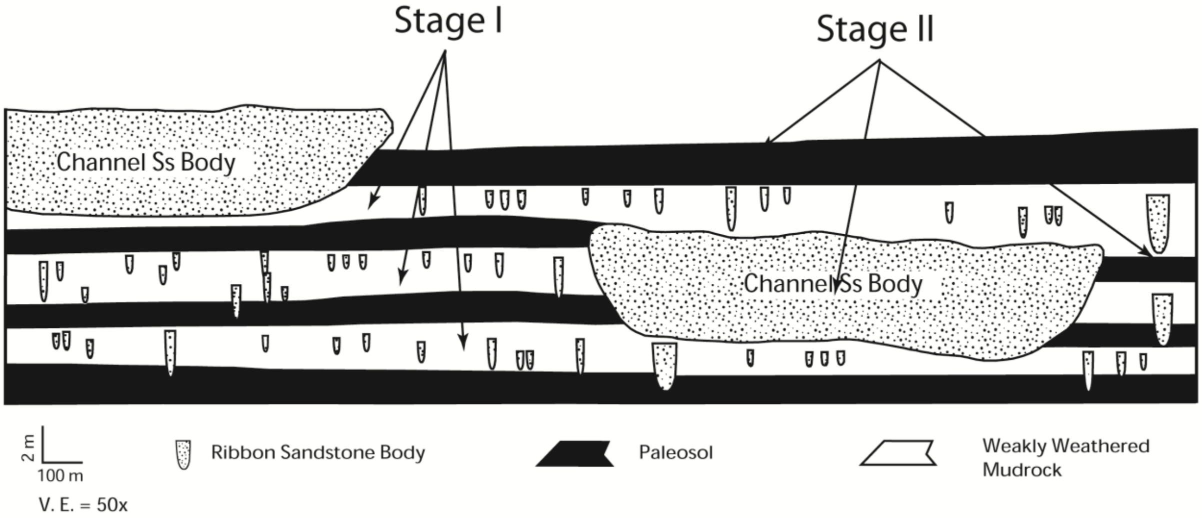

Figure 4

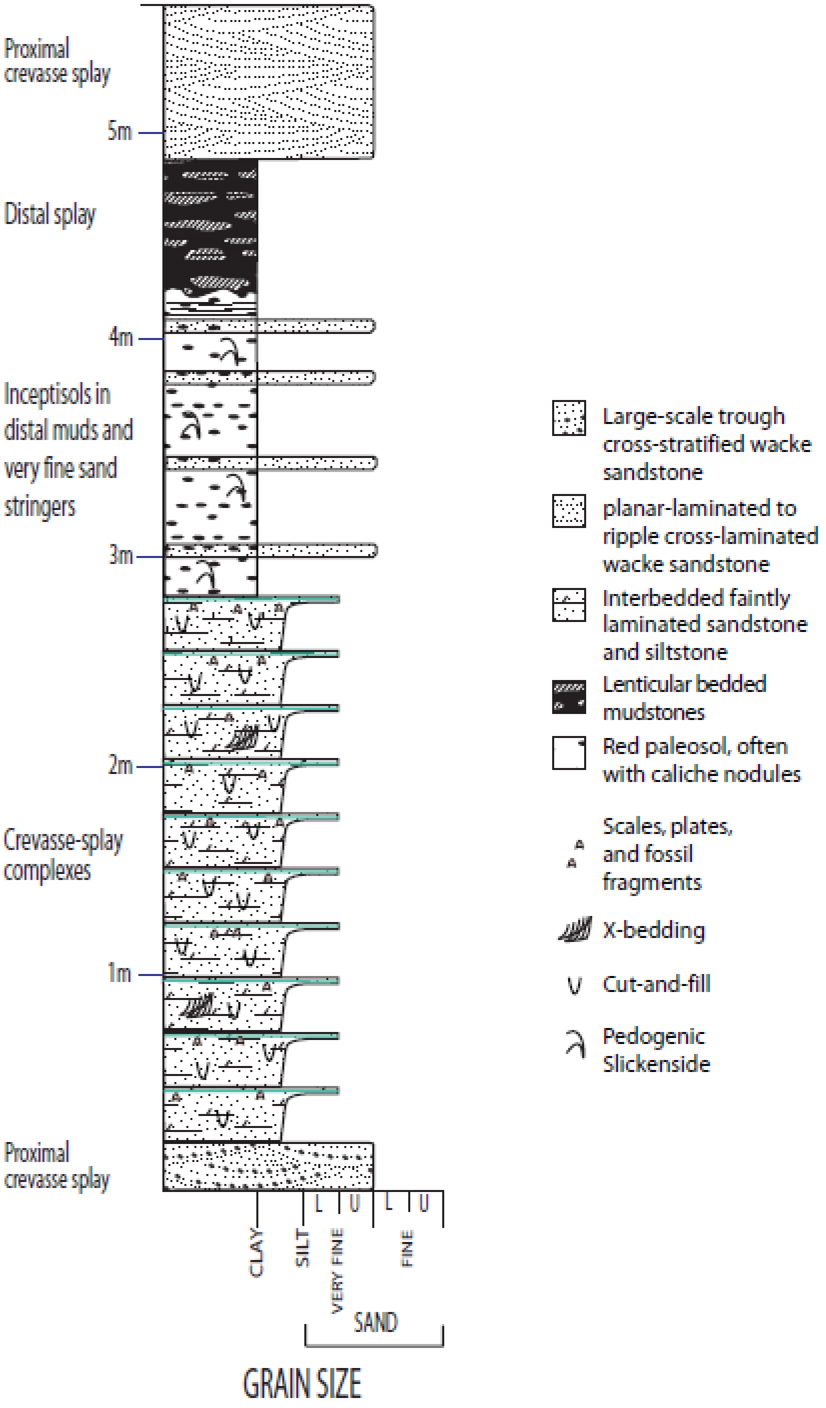
Proximal crevasse splay
5m
Distal splay
4m
Inceptisols in distal muds and very fine sand stringers
3m
2m
Crevasse-splay complexes
1m
Proximal crevasse splay
L
U
L
U
CLAY
SILT
VERY FINE
FINE
SAND
GRAIN SIZE
Large-scale trough cross-stratified wacke sandstone
planar-laminated to ripple cross-laminated wacke sandstone
Interbedded faintly laminated sandstone and siltstone
Lenticular bedded mudstones
Red paleosol, often with caliche nodules
Scales, plates, and fossil fragments
X-bedding
Cut-and-fill
Pedogenic Slickenside

Figure 5

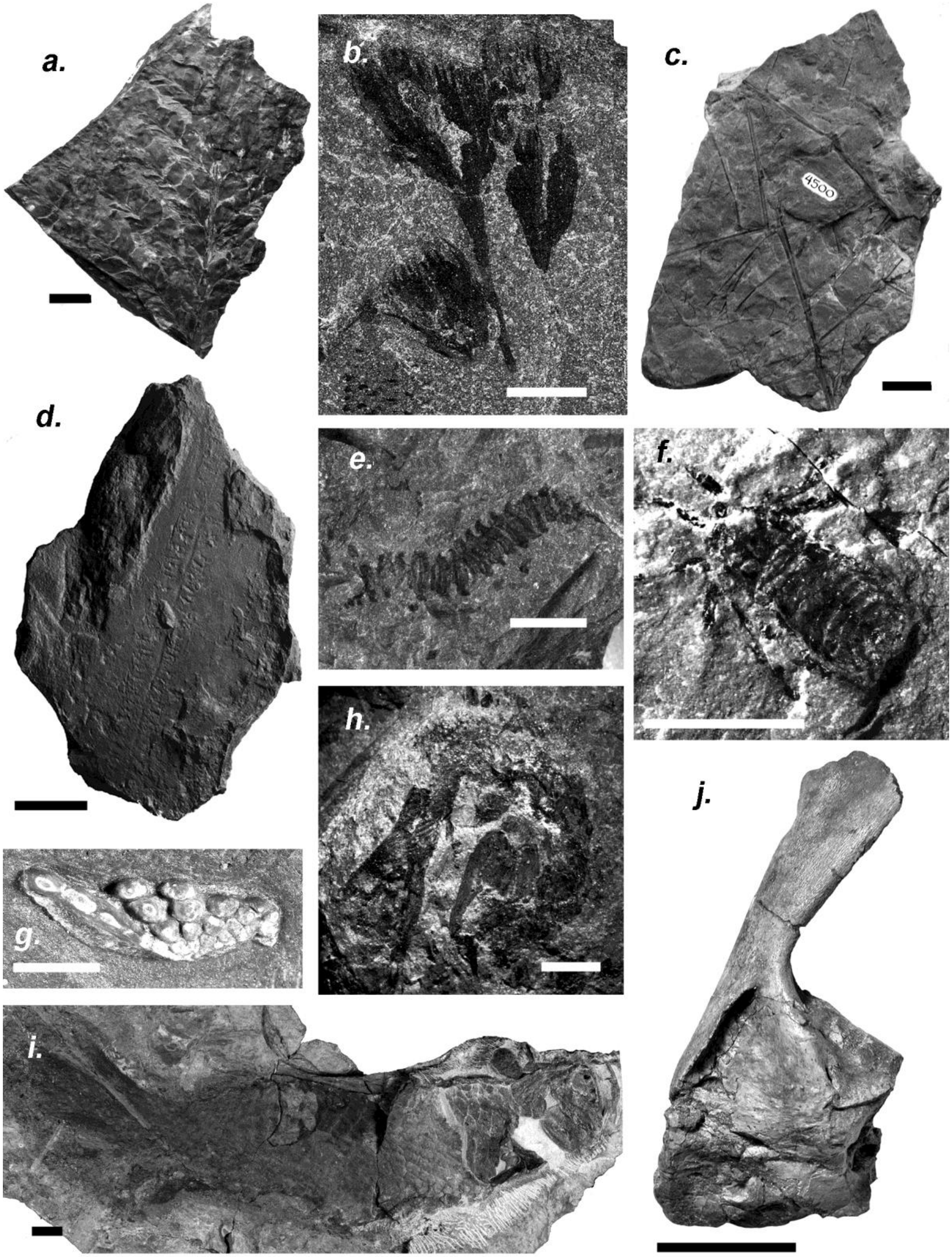

Figure 6