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Woodland Hypothesis for Devonian Tetrapod Evolution

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ABSTRACT

The rarity of Devonian tetrapods and the absence of tetrapods during the first 14 million years of the Mississippian (Romer's Gap) have inspired hypotheses of fish-tetrapod evolutionary transition as an escape from difficult habitats such as deserts or stagnant waters. These hypotheses and Romer's Gap are tested here using depth to calcic horizon in paleosols of the northern Appalachians as a proxy for precipitation and vegetation changes during the Devonian and Mississippian. All tetrapod bones and trackways in this region, as well as fossil tree remains, were found at times of high precipitation (indicated by deep calcic paleosols), when subhumid woodlands expanded at the expense of semiarid shrublands in alluvial lowlands. No tetrapods or tree fossils were found in abundant paleosols with the shallow calcic horizons of aridland soils. The mean annual precipitation requirement of Devonian-Mississippian tetrapods and trees was at least 571 ± 72 mm. Global distribution of prototetrapods and aquatic tetrapods also shows that they lived earliest (Eifelian) in coastal lagoon or estuary margin soils of humid regions rather than in aridlands or intertidal flats. Tetrapods later spread to a variety of habitats, but continued preference for noncalcareous soils of woodlands and forests may explain Romer's Gap as a preservational artifact. A woodland hypothesis of tetrapod evolution is presented here: limbs and necks were selected for by scavenging and hunting in shallow-flooded woodlands and oxbow lakes during a unique period in Earth history, after evolution of flood-ponding trees and before effective terrestrial predator resistance.

Online enhancements: appendixes.

Introduction

Alfred Sherwood Romer (1894–1973) was a titan of vertebrate paleontology. His vision of Late Devonian tetrapod origins was a plucky fish lurching overland from a shrinking pond (Romer 1941, 1958) in semiarid, monsoonal floodplains as envisaged by Barrell (1916), using Devonian sedimentological and stratigraphic data. Such icons of the can-do spirit in the face of near-impossible odds remain celebrated in cartoons and advertising. The idea that early tetrapods had small populations in aridlands was also used to explain the paucity of evidence for the fish-tetrapod transition, especially during the first 14 million years of the Mississippian, a tetrapod-poor interval called Romer's Gap (Coates and Clack 1995). A coeval hiatus in the

terrestrial arthropod fossil record has been attributed to small populations struggling under low atmospheric oxygen levels (Ward et al. 2006) or recovering from mass extinction (Sallan and Coates 2010). Romer's theme of struggle and escape is echoed in other theories of tetrapod evolution that suggest that limbs were used to dig estivation burrows (Orton 1954), clamber over crowds of tadpoles (Warburton and Denman 1961), grasp slippery females (Martin 2004), escape coastal lagoon (Clack 2007) or lake anoxia (Thomson 1969), and avoid predation (Goin and Goin 1956; Inger 1957; Zimmer 1998, p. 102; Shubin 2008, p. 41).

These theories draw little support from recent discoveries. Early Late Devonian sarcopterygians such as *Tiktaalik* (Daeschler et al. 2006) had incipient necks and simplified fin lobes ("prototetrapods" of Long and Gordon 2004) but retained fish scales and body form. Laterally flattened tails and

other aquatic adaptations persisting in Late Devonian *Acanthostega* (Clack 1988, 2006) encouraged speculation that tetrapods with well-developed limbs used them for amplexus (reproductive coupling; Martin 2004), to escape cold water to bask in the sun and thus promote digestion and development (Carroll 2009), or for feeding in shallow vegetation-choked water (Clack 2002) rather than lurching across parched land (Zimmer 1998). Discovery of supposed near-marine tetrapods and trackways have encouraged an intertidal hypothesis for the evolutionary transition between fish and tetrapods (Blieck et al. 2007; Niedźwiedzki et al. 2010). Devonian fossil trunks of *Duisbergia* (Schweitzer and Giesen 2002), *Protocephalopteris* (Schweitzer 1999), *Wattieza* (Stein et al. 2007), and *Archaeopteris* (Cressler 2006) are evidence that trees are at least as geologically ancient as tetrapods. The monsoonal-arid paleoclimatic model of Barrell (1916) for Late Devonian red beds of Pennsylvania and New York has been long accepted (Woodrow 1985) but recently has been refined and quantified by research on paleosols (Retallack and Huang 2011). Late Devonian tetrapod bones associated with paleosols near Hyner, Pennsylvania (Retallack et al. 2009), provide evidence of excursions onto flooded plains and early tetrapod preference for woodlands rather than desert shrublands. The woodland hypothesis presented here postulates evolution of tetrapods from fish during a unique interval of earth history, after flash flooding was mitigated by evolution of woodlands but before evolution of other terrestrial predators. The woodland hypothesis invokes less struggle and escape than opportunities for excursions onto flooded plains and oxbow lakes in the shelter of newly evolved woodlands, where hunting and scavenging success in shallow water was enhanced by robust limbs and agile necks.

This study brings a new test to hypotheses of tetrapod evolution from paleoenvironmental records of Devonian-Mississippian paleosols in Pennsylvania and nearby states of Maryland and New York (app. A, available online or from the *Journal of Geology* office). Devonian paleosols provide evidence for paleoclimate, paleoatmospheric CO_2, paleovegetation, and geomorphic setting that are independent of the fossil record (Retallack and Huang 2011). Vertebrate burrows, footprints, and bones in this region are found in a variety of paleosols (Vrazo et al. 2007; Retallack et al. 2009; Storm et al. 2010; Lucas et al. 2010a, 2010b), which are not only evidence of tetrapod habitats, but of their environments of preservation (app. B, available online or from the *Journal of Geology* office). There are many

unstudied paleosols at other Devonian-Mississippian tetrapod sites around in the world (app. C, available online or from the *Journal of Geology* office), and this new paleopedological approach could profitably be applied elsewhere.

Material and Methods

Geological sections in Pennsylvania and adjoining Maryland and New York (figs. 1, 2) were measured using level and tape. Depth to calcic horizon, color, and other critical features of the paleosols were measured with a cloth tape and Munsell color chart (figs. 3, 4). Paleosol development was estimated on a five-stage scale of Retallack (2001). Geological sections were chosen because of good exposure and being used for prior work on paleosols (Retallack 1985; Driese and Mora 1993; Driese et al. 1993b, 2000; Fastovsky et al. 1993). The Catskill composite section of Rickard (1975) was reoccupied at as many exposures as available to create a new paleoenvironmental record for correlation with New York marine sequences. Ages of paleosols were based on spore (Traverse 2003), ammonoid (Kirchgasser 1985), and conodont zones (Over 1997; Over et al. 2003) and in the Mauch Chunk Formation by paleomagnetic reversal stratigraphy (Opdyke and DiVenere 2004). In other cases, local stratigraphic correlations were used (Sevon and Woodrow 1985; Bjerstedt and Kammer 1988; Edmunds 1997; Schultz 1999). Previous definition of pedotypes based on 185 paleosols at Hancock, Newport, Selinsgrove, and Hyner (Retallack 1985; Retallack et al. 2009) is here extended to observation of 973 additional paleosols from 77 additional localities (figs. 1, 2; Retallack and Huang 2011). The fossil tetrapod bone locality studied in Pennsylvania is 1 mile west of Hyner (N41.346183° W77.6800°) in Clinton County (Retallack et al. 2009). Pennsylvania tetrapod footprint and burrow localities of Vrazo et al. (2007), Storm et al. (2010), and Lucas et al. (2010a, 2010b) were also examined for paleosols (see apps. A, C for details): (1) Hazelton (Asbian, ca. 332 Ma: N40.989833° W76.025167°): (2) Hometown (Serpukhovian, ca. 319 Ma: N40.81456° W75.97809°); (3) Indian Run Reservoir (Brigantian, ca. 328 Ma: N40.657842° W76.23061,°); (4) Jim Thorpe (Asbian, ca. 332 Ma: N40.867667° W75.734833°); (5) Lavelle (Brigantian, ca. 328 Ma, and Pendleian, ca. 325 Ma levels: N40.7251° W76.36586°); (6) Nescopeck (Ivorian, ca. 347 Ma: N41.007600° W76.166433°); (7) Pottsville (Brigantian, ca. 329 Ma, at Mount Carbon: N40.67418° W75.86689° and Tumbling Run: N40.657833° W76.2265°); (6) Saint Johns (Ivorian, ca. 347 Ma: N41.058° W76.86667°); (8) Tamaqua
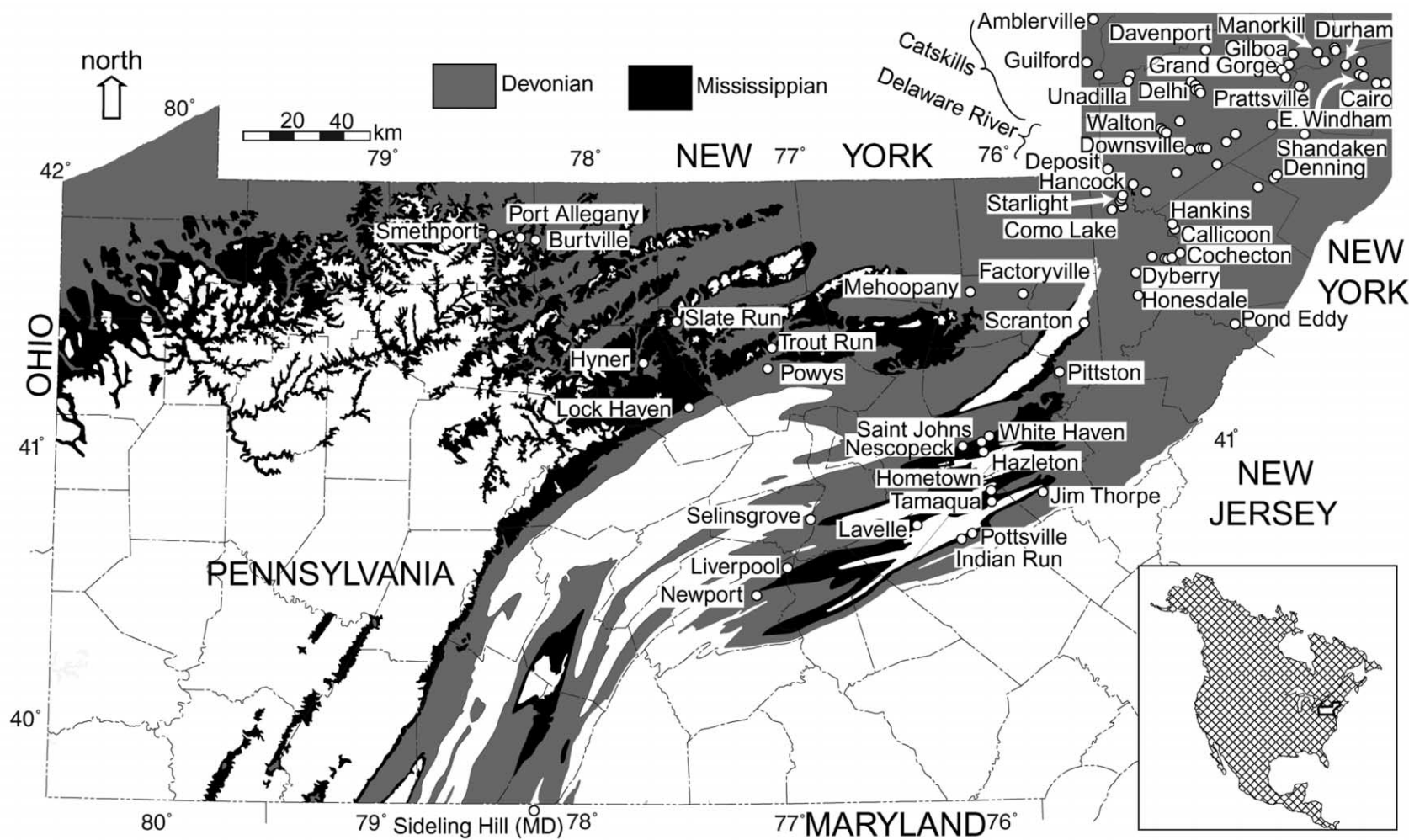
Figure 1. Geological map and paleosol localities in Pennsylvania and nearby Maryland and New York (for detail of New York, see fig. 2).
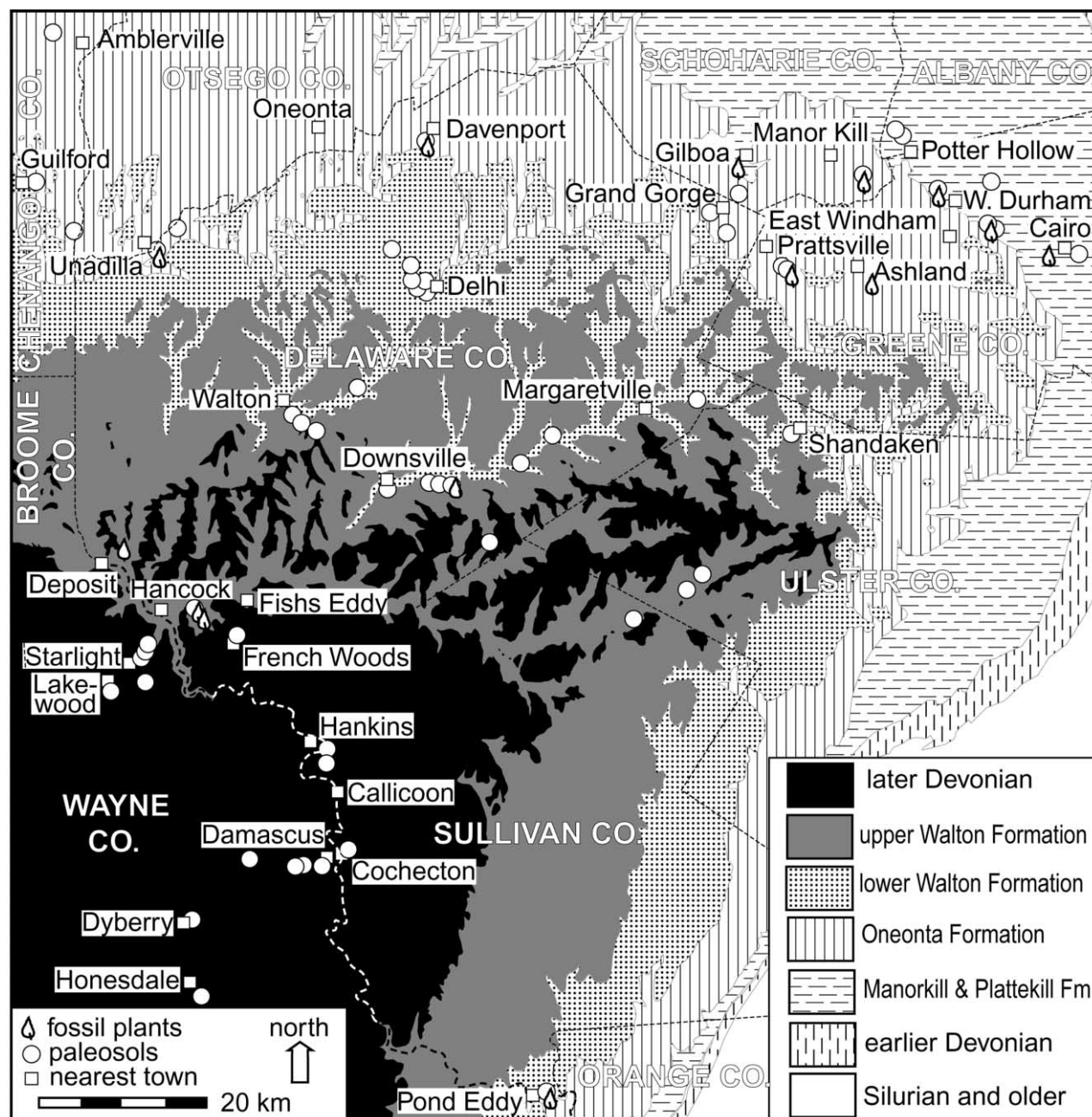
Figure 2. Geological map of localities in the Catskill Mountains and Delaware Valley of New York and northeastern Pennsylvania.

(Serpukhovian, ca. 320 Ma: N40.78493° W75.96236°), (9) White Haven (Asbian, ca. 332 Ma: N40.05167° W75.77588°). Paleoclimatically sensitive measures of paleosols at these localities are listed in table 1, and data from published sources on unusually complete fossil tetrapods are given in table 2.

Information on Devonian-Mississippian fish and tetrapod habitats elsewhere in the world (app. C) is from cited publications, but personal field observations were made at several localities: Beartooth Butte (Wyoming N44.952952° W109.609892°), Zachełmie (Poland N50.96860° E20.69185°), Mount Crean (Antarctica S77.85° E159.6023°), Thurso (Scotland N58.600763° W3.533871°), Red Hill (Nevada N40.055039° W116.357226°), Howitt Spur

Figure 3. Geological sections of Devonian paleosols in New York and Pennsylvania. Degree of development of the individual paleosols is after Retallack (2001). Also shown are measurements (cm) of depth to calcic horizon (*filled circles*), as a proxy for mean annual precipitation, and thickness of paleosols (*open circles*), as a proxy for mean annual range of precipitation (Retallack 2005*a*).

Figure 4. Geological sections of Devonian-Pennsylvanian paleosols in New York, Pennsylvania, and Maryland. Degree of development 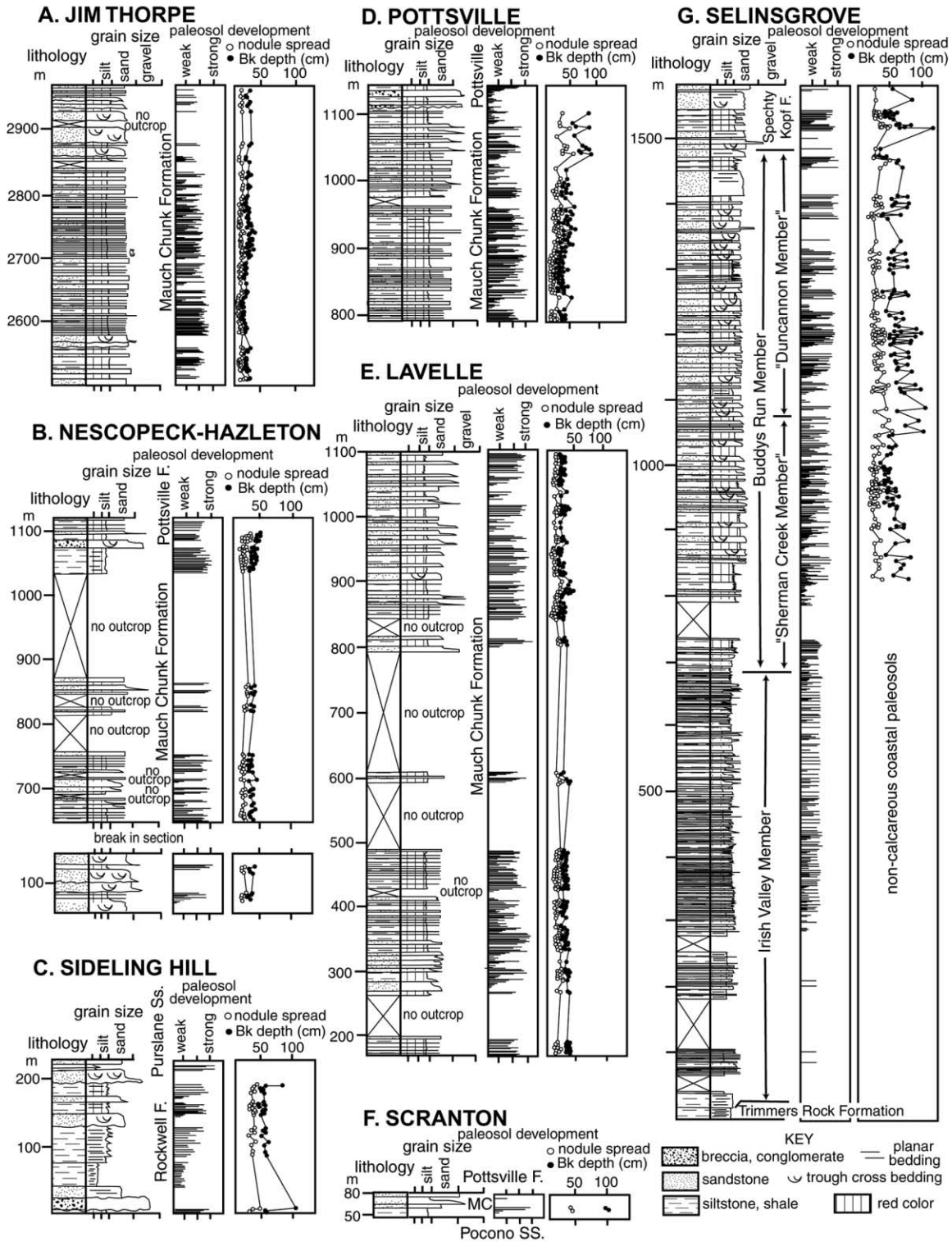of the individual paleosols is after Retallack (2001). Also shown are measurements (cm) of depth to calcic horizon (*filled circles*), as a proxy for mean annual precipitation, and thickness of paleosols (*open circles*), as a proxy for mean annual range of precipitation (Retallack 2005*a*).

Table 1.   Estimated Size and Paleoprecipitation of Devonian-Mississippian Tetrapods

Locality	Fossil taxon	Fossil type	Fossil length (mm)	Estimated tetrapod BL (m)	Pedotype	Bk depth (cm)	Burial (km)	MAP (mm)
Hazelton	*Palaeosauropus primaevus*	Glenoid-acetabulum	200	.7	Conyngham	43	10.1	584 ± 147
Hometown	*Palaeosauropus primaevus*	Glenoid-acetabulum	200	.7	Nescopeck	84	9.3	837 ± 147
Hyner	*Densignathus rowei*	Jaw	182	1.0	Hyner	82	5.5	813 ± 147
Hyner	*Hynerpeton bassetti*	Scapulocoracoid	49	.7	Hyner	82	5.5	813 ± 147
Hyner	*Hynerpeton bassetti*	Jaw	103	.6	Hyner	82	5.5	813 ± 147
Lavelle	Unnamed	Burrow	600	.6	Lavelle	52	8.6	652 ± 147
Lavelle	*Palaeosauropus primaevus*	Glenoid-acetabulum	200	.7	Lavelle	39	8.7	548 ± 147
Lavelle	*Palaeosauropus primaevus*	Glenoid-acetabulum	200	.7	Lavelle	52	8.7	652 ± 147
Nescopeck	*Hylopus* sp.	Glenoid-acetabulum	90	.3	Dunmore	98	9.8	893 ± 147
Nescopeck	*Hylopus* sp.	Pes	25	.2	Dunmore	98	9.8	893 ± 147
Pottsville	*Palaeosauropus primaevus*	Glenoid-acetabulum	200	.7	Nescopeck	42	9.6	722 ± 147
Pottsville	*Palaeosauropus primaevus*	Pes	88	.9	Nescopeck	42	9.6	722 ± 147
Tamaqua	*Palaeosauropus sp.*	Glenoid-acetabulum	190	.6	Nescopeck	61	9.3	837 ± 147
Tamaqua	*Palaeosauropus sp.*	Pes	44	.4	Nescopeck	61	9.3	837 ± 147

Note.   BL = body length; Bk depth is depth in paleosol to carbonate nodules or mottles; MAP = mean annual precipitation.

(Australia S37.16872° E146.59834°), Canowindra (Australia S33.59902° E148.56639°), Bunduburrah (Australia S33.53215° E147.71958°), and Lehi (Utah N40.383275° W111.961269°).

Appalachian Paleosols

Paleosols from the Catskill, Mauch Chunk, and equivalent formations in Pennsylvania and adjacent Maryland and New York (bars in paleosol development columns of figs. 3, 4) are useful indications of former soils (pedotypes), stratigraphic correlation (pedostratigraphy), and changes in paleoclimate and vegetation (paleoenvironments). Deep diagenetic alteration in Pennsylvania ranging to lower greenschist facies metamorphism in New York (Sarwar and Friedman 1995; Mora et al. 1998) compromises some isotopic and other geochemical interpretations (Retallack et al. 2009), but this study emphasizes robust physical features, such as calcic horizons of cream to white nodules in red clayey matrix beneath the truncated upper part of the paleosols (fig. 5).

A pedotype is simply a kind of paleosol, recognized in the field from a type profile and used as a basis for further interpretation (Retallack 1994).

Pedotypes are named for localities, such as the Hyner pedotype, but are not confined to that locality. Pedotypes are recognized from pedologically significant aspects of profiles, such as drab versus red color (a proxy of former waterlogging; Retallack 2001), clarity of original sedimentary bedding (a proxy of degree of development in alluvial soils; Driese and Mora 1993), and distribution of calcareous nodules (a proxy of paleoclimate; Retallack 2005a). Using this procedure, the thousands of paleosols in the northern Appalachian Devonian and Mississippian can be reduced to a manageable number of pedotypes. Pedotypes are a field classification of preservable features of paleosols independent of the taxonomy of modern soils, and their terminology, analysis, and interpretation are developed elsewhere (Retallack 1985; Retallack et al. 2009a; Retallack and Huang 2011).

This article focuses on a prominent field criterion distinguishing the most abundant calcareous, nodular, red pedotypes: paleosols with deep horizons of carbonate nodules (Hyner pedotype), as distinct from those with shallow calcic horizons (Bucktail pedotype; figs. 3, 4, 5A, 5B), which reflect subhumid and semiarid climates, respectively (Retallack 2005a). Deep calcic paleosols are also more

Table 2. Sizes of Unusually Complete Devonian-Carboniferous Tetrapod Fossils

Taxon	Acetabular-glenoid length (mm)	Pes length (mm)	Jaw length (mm)	Scapulo-coracoid length (mm)	Body length (m)	Source
Acanthostega gunnari	192	42	141	38	.72	Ahlberg et al. 2005
Eldeceeon rolfei	130	62	85	25	.41	Smithson 1994
Ichthyostega stensioei	340	71	190	82	1.1	Ahlberg et al. 2005
Pederpes finneyae	260	86	178	52	.96	Clack and Finney 2005
Dendrerpeton acadianum	125	32	75	43	.45	Holmes et al. 1998
Temnocorpichnus isaacleai	83	19	38	Not known	.21	Lucas et al. 2010*a*
Linear regression variables	*x*	*x*	*x*	*x*	*y*	This study
m	.0035	.0108	.0056	.0122	*y*	This study
b	−.019	.082	−.017	.140	*y*	This study
r²	.97	.64	.98	.74	*y*	This study
Standard error (*y* in *m*)	.07	.24	.05	.18	*y*	This study

clayey, slickensided, and deeply weathered than shallow calcic paleosols (Retallack et al. 2009; Retallack and Huang 2011). These other characteristics, as well as caliche conglomerates in overlying sandstones, mark those rare deep calcic paleosols that were eroded before they were covered. Five such cases (at Downsville, Hancock, Nescopeck, Lavelle) were not included in the 1158 measured paleosols (fig. 6). Where outcrops were extensive (at Starlight, Hankins, Newport, and Hyner), six uneroded paleosols were found a few tens of meters along the strike from where they had been eroded completely by paleochannels. Also measured was the thickness of paleosol with nodules (*open symbols* in figs. 3, 4), which is a proxy in modern soils for degree of seasonalilty, or difference between mean monthly precipitation of the wettest and driest months (Retallack 2005*a*). Thickness of paleosol with nodules showed more subdued trends than depth to nodules (figs. 3, 4) and was not useful for pedostratigraphy. The nodules, whether deep or shallow, are all micritic, low-magnesium calcite, with displacive and replacive calciasepic porphyroskelic microfabric, typical for soils and paleosols, and not benches with crystic cements like groundwater calcretes (Retallack et al. 2009).

Appalachian Pedostratigraphy

Depth to calcic horizons in paleosols shows a lognormal distribution (Retallack 2009*a*, 2009*b*; Retallack et al. 2009). Rare deep calcic paleosols are scattered among a background of numerous shallow calcic paleosols. Northern Appalachian paleosols show a striking pattern of frequent perturbation in the Late Devonian (fig. 3) but fewer strong perturbations in the Mississippian (fig. 4). The irregularity through time of paleoclimatically related strong

perturbations can be used as a tool for pedostratigraphic refinement of correlation of local measured sections.

Pedostratigraphy is akin to magnetostratigraphy, but with the paleoclimatic signal of deep and shallow calcic paleosols rather than normal and reversed paleomagnetism. Both magnetostratigraphy and pedostratigraphy have a binary (on/off) marker, make correlations assuming constant sedimentation rate (thus relative thickness as a proxy for relative duration), and also need supporting data from biostratigraphy and lithostratigraphy. Nevertheless, correlation of unique sequential patterns of deep calcic paleosols can be used to improve correlations within stratigraphic frameworks established by other means. The lithostratigraphic framework of figure 6, for example, is directly based on formations and their correlations established by Rickard (1975), Sevon and Woodrow (1985), Bjerstedt and Kammer (1988), Edmunds (1997), and Schultz (1999). The Catskill composite section (fig. 3*E*) has been correlated at several levels with marine rocks in eastern New York (Rickard 1975; Sevon and Woodrow 1985). A distinctive clayey bed (deep calcic paleosol) within the paleosol sequence of the middle Manorkill Formation in road cuts near East Windham has been mapped laterally to the west by Johnson and Friedman (1969) to the famous Gilboa fossil forests (Mintz et al. 2010) and black shales at the base of the upper Tully Limestone, and the biological overturn that House (2002) calls the Pumilio event. Another deep calcic paleosol at the very top of the Manorkill Formation at East Windham correlates laterally with the basal Geneseo Shale overlying the Tully Member, which House (2002) calls the Geneseo event. The Givetian fauna of the Tully Limestone includes ammonoids of the *Pharciceras amplexum* zone (Kirchgasser
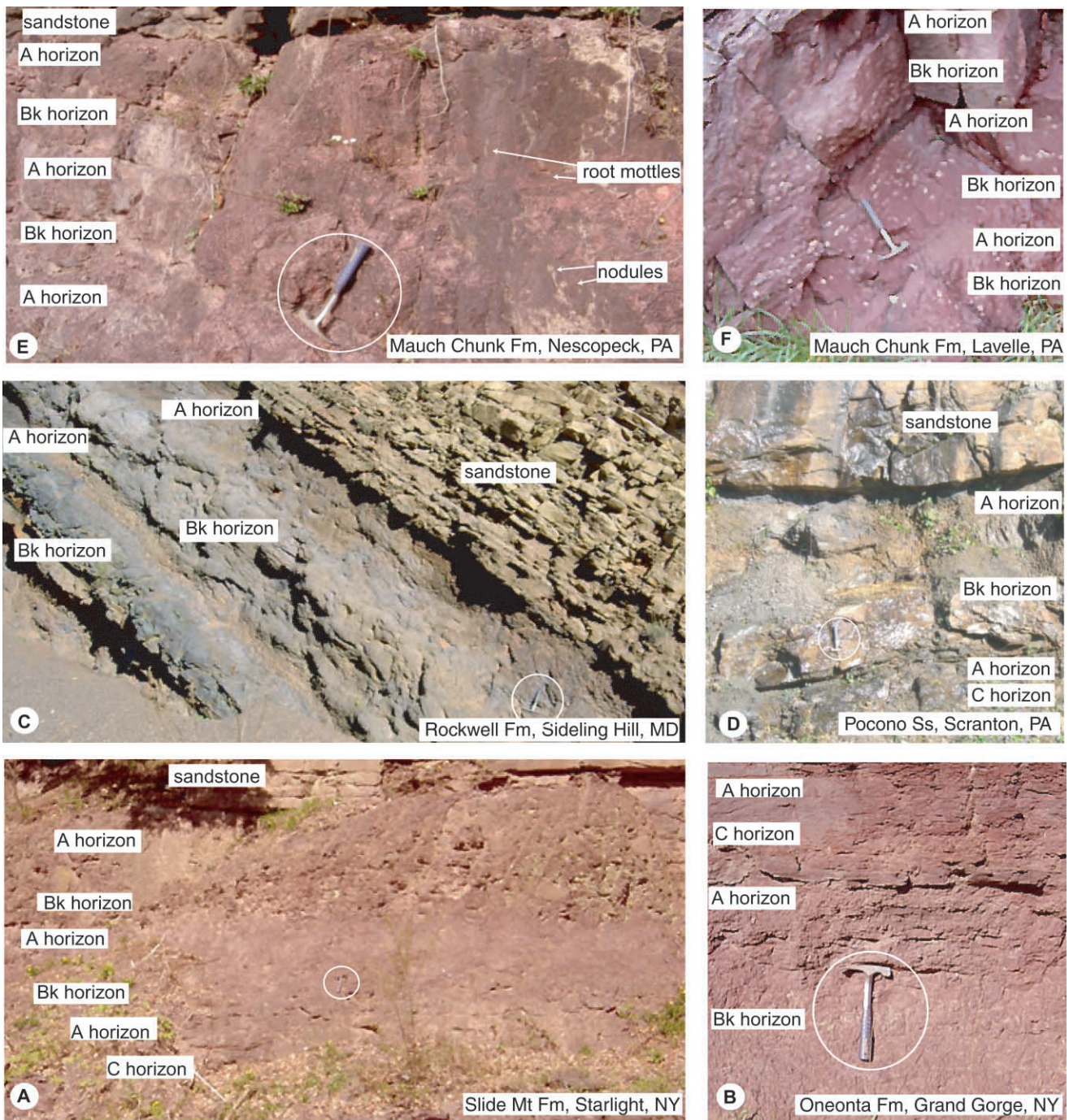
Figure 5. Outcrop photographs of Devonian and Mississippian paleosols. *A*, Deep calcic (Hyner pedotype) and shallow calcic (Bucktail pedotype) paleosols in the Slide Mountain Formation (latest Frasnian), on an old railroad grade near Starlight, PA; *B*, shallow calcic (Bucktail pedotype) and weakly developed (Renovo pedotype) paleosols in the Oneonta Formation (Frasnian) southwest of Grand Gorge, NY; *C*, deep calcic and vertic (Dunmore pedotype) paleosols in the Rockwell Formation (Mississippian) at Sideling Hill, MD; *D*, deep calcic and vertic (Dunmore pedotype) paleosols in the Pocono Sandstone (Mississippian), at Dunmore exit from I-84N near Scranton, PA; *E*, shallow calcic (Nescopeck pedotype) paleosols in the Mauch Chunk Formation (Mississippian) on I-70W near Nescopeck, PA; *F*, shallow calcic (Lavelle pedotype) paleosols in the Mauch Chunk Formation (Mississippian) south of Lavelle, PA. Hammer for scale (*circled*) has 25-cm-long handle.
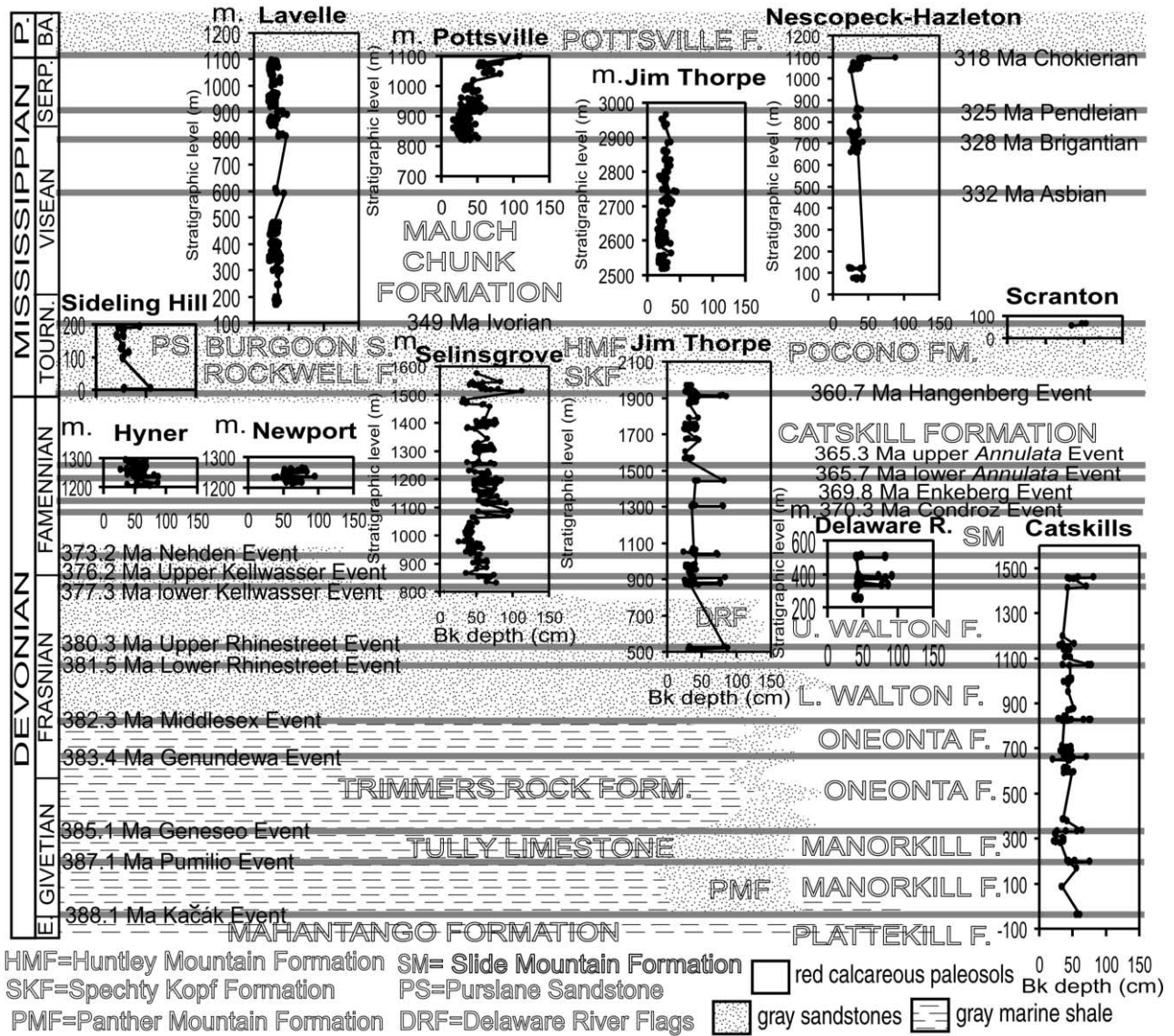
Figure 6. Late Devonian–Mississippian pedostratigraphy of Pennsylvania, Maryland, and New York. Depth to calcic horizon in individual sections is plotted to various scales reflecting local sediment accumulation rates adjusted to show temporal correlation of deep calcic spikes. Parts of the sections without data are fluvial paleochannels and noncalcareous paleosols.

1985; Work et al. 2007), and conodonts of the *Polygnathus varcus* zone (Sparling 1999). Conodont biostratigraphy of New York (Over 1997; Over et al. 2003) also dates the following Frasnian levels: (1) Genundewa Limestone in the middle *Mesotaxis falsiovalis* zone and Genundewa event of House (2002), (2) basal Middlesex Shale in the *Palmatolepis transitans* zone and Middlesex event of House (2002), (3) basal Rhinestreet Shale (Moreland Shale Member) in the upper *Palmatolepis punctata* zone and the Rhinestreet event of House (2002). These

different levels of black shales and biotic events (House 2002) were correlated by Rickard (1975) and Sevon and Woodrow (1985) with (1) middle Oneonta Formation, (2) basal Lower Walton Formation, and (3) basal Upper Walton Formation, respectively. Each of these levels has deep calcic paleosols in unusually clayey red beds within the Catskill composite section, in contrast with more common gray sandstones and shallow calcic paleosols (fig. 3E). Times of unusually high rain precipitation inferred from paleosols correspond to black shale and faunal

overturn events regarded by Brett et al. (2009) as times of high sea level, elevated temperature, and oceanic anoxia.

These correlations based on biostratigraphy and lithostratigraphy (Rickard 1975; Sevon and Woodrow 1985) can be refined and tested by graphical pedostratigraphy (figs. 6, 7). Direct correlation of stratigraphic levels of these four marine levels (Geneseo-Rhinestreet) in central New York near Penn Yan (section from Bergin 1964), with stratigraphic levels of deep calcic paleosols in the Catskills composite section, is shown in figure 7A. This procedure allows identification of additional events such as the Kačák and upper and lower Kellwasser events of House (2002). These latter are the doublet of closely spaced deep calcic paleosols that can be used to match sequences from the Slide Mountain and Walton formations of the Catskill Mountains and Delaware River in New York with the nearby Catskill Formation of Jim Thorpe and Selinsgrove, Pennsylvania. This stratigraphic pattern in the correlated sections reflects transient paleoclimatic perturbations at long, then short, then long intervals of time. These correlations rely on comparable semiarid to subhumid paleoclimates for all the sections, as indicated by the dominance of calcareous paleosols in them (figs. 3, 4). These correlations also assume a constant local rate of sedimentation but not the same sedimentation rate from location to location (note different meter scales in fig. 6). Mississippian sections can be correlated in a comparable fashion (fig. 6), although magnetostratigraphy is available for the Mauch Chunk Formation at Jim Thorpe (Opdyke and DiVenere 2004). Milankovitch-scale paleoclimatic cyclostratigraphy can also be used to date these paleosol sections (Retallack et al. 2009), but is beyond the temporal resolution needed for this study.

Deep calcic spikes may not only be useful for regional paleoclimatic correlation (figs. 6, 7A), but internationally (fig. 7B). The distinctive irregular stratigraphic spacing of local paleoclimatic spikes corresponds to that of black shales in marine sequences in Europe and North America, which have been named as global change events (House 2002) and dated within radiometrically calibrated time scales (Gradstein et al. 2004; Kauffman 2006). The stratigraphic spacing of deep calcic spikes in Pennsylvania and New York are highly correlated with the radiometric ages of global change events: $R^2 >$ 0.96 and F-test probabilities from regression ANOVA are <0.001 for Catskills, Jim Thorpe, and Selinsgrove sections (fig. 7). Similar results to these correlations of stratigraphic position and geological time have been gained by direct graphic correlation
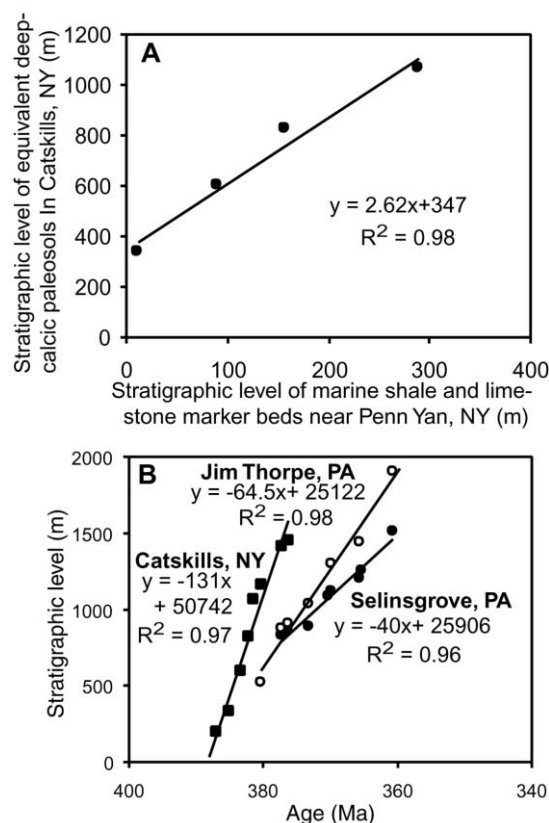

Figure 7. Correlation of North American deep calcic (>50 cm) paleosols with global biotic crises (House 2002; named in fig. 3) at Selinsgrove, Jim Thorpe, and Catskills sections. High correlation coefficients confirm local near-linear sediment accumulation rates. Declining slopes and thicknesses to right reflect lower sediment accumulation rates westward from Acadian mountain sources.

of meter levels of German black shales and Appalachian deep calcic paleosols (Retallack et al. 2009). These high correlations for all observed deep calcic paleosol horizons confirm the underlying assumptions of regional semiarid-subhumid paleoclimates of pedocal paleosols and constant sediment accumulation rates. Different biomes and disconformities would have resulted in poor correlations and offset linear fits in comparable graphic correlation of fossils (Shaw 1964).

The German and North American midwestern black shales are evidence of spikes of oceanic anoxia corresponding to biotic turnover and carbon cycle crises apparent from carbon isotopic studies (Racki et al. 2008; Brett et al. 2009), including such mass extinctions as the Frasnian-Famenian boundary (Joachimski et al. 2002; Chen and Tucker 2003). Causes proposed for black shales and paleoclimatic-

geochemical spikes are widely debated and include bolide impact, methane clathrate mobilization, thermogenic methane from intrusion of coals, or biotic eutrophication (Algeo et al. 1995; House 2002; Buggisch and Joachimski 2006). Regardless of their causes, Devonian-Mississippian transient black shale events can now be correlated with spikes in paleosol calcic depth attributed to unusually humid paleoclimate: as much as 839 ± 147 mm mean annual precipitation for decompacted deep calcic Hyner paleosols versus as little as 434 ± 147 mm for decompacted shallow calcic Bucktail paleosols at Hyner, estimated using transfer functions from modern soils (Retallack et al. 2009). Furthermore, correlation with these internationally dated events confirms that sedimentation rates declined westward from source areas in the northern Appalachian Devonian and Mississippian (different slopes in fig. 7).

Appalachian Paleoenvironments

Some of the Appalachian paleosols are noncalcareous and formed in disturbed, swampy, or marginal marine habitats (Retallack 1985), but most have subsurface nodules of micrite (fig. 5), with the isotopic composition and petrographic texture of pedogenic carbonate (Driese and Mora 1993; Driese et al. 2000; Retallack et al. 2009). In modern soils, greater depth to carbonate nodules is directly related to higher mean annual precipitation and soil respiration (Retallack 2005a). Most paleosols of the northern Appalachian Devonian and Mississippian have shallow calcic horizons and thus indicate aridlands, as envisaged by Barrell (1916), though there are many deep calcic paleosols of subhumid paleoclimates. Depths to calcic horizon can be used as a proxy for mean annual precipitation (Retallack 2005a) after correction for burial compaction (Sheldon and Retallack 2001), and they thus imply short-lived episodes of unusually humid paleoclimate every few million years during the Late Devonian but at 10–20 million-year intervals during the Mississippian. Both measured depths and estimates of paleoprecipitation after decompaction are shown on primary and secondary X-axes, respectively, of figure 8.

Another field measure taken was thickness of soil with carbonate nodules (*open symbols* in figs. 3, 4), which is the vertical distance between the highest and lowest nodule within a profile. This measure in modern soils is directly proportional to precipitation differences between the wettest and driest months (Retallack 2005a). None of the De-

vonian and Mississippian paleosols of the northern Appalachians had nodules spread as widely (1 m) as in monsoonal soils and paleosols of Pakistan (Retallack 1991), contrary to monsoonal interpretations of paleoclimate by Barrell (1916). Paleogeographic restorations of Pennsylvania now place it at a paleolatitude of 32°S on a southward-projecting promontory of the Old Red Continent (Joachimski et al. 2002), where monsoonal circulation would not be expected.

Pedogenic carbonate isotopic compositions for some of the Late Devonian subhumid spikes have been analyzed for atmospheric CO_2 change and indicate transient rise from a base level of 700–1275 ppmv for shallow calcic paleosols to 3685–4261 ppmv for deep calcic paleosols (Mora et al. 1996; Cox et al. 2001; Retallack et al. 2009; Retallack and Huang 2011). Spikes of carbon dioxide and precipitation on land may also have been times of transient low oxygen levels in the atmosphere, as implied by mass-balance modeling (Ward et al. 2006). The mass-balance modeling is at a coarser scale (10 m.yr.) than this study, but it shows lowest oxygen levels (13%) during the Givetian and Frasnian interval cluttered with frequent paleoclimatic perturbations rather than early Mississippian Romer's Gap, when oxygen levels were calculated to be about 17%. There is no support for such long-term low levels of O_2 from fossil charcoal distributions (Scott and Glaspool 2006), so that the 10-m.yr. binned estimates of Ward et al. (2006) are averaging transient O_2 minima with background higher O_2 levels. The modeled record of low oxygen is a better explanation for mass extinction at the Frasnian-Famennian boundary (Buggisch and Joachimski 2006) than the early Mississippian dearth of fossils known as Romer's Gap (contra Coates and Clack 1995).

Deep calcic and noncalcareous paleosols of the Middle Devonian (Givetian) in New York also have large stumps and root traces and the general profile form of woodland soils (Retallack 1985, 1997a; Driese et al. 2000). These are not the geologically oldest known trees. Cladoxyl trees (*Protocephalopteris*) date back to the upper Emsian to lower Eifelian of Spitsbergen (Schweitzer 1999) and other cladoxyl trees (*Duisbergia*) to the mid-Eifelian (AD Mac spore zone) of Germany (Schweitzer and Giesen 2002). Comparable cladoxyl trees (*?Duisbergia*, *Wattieza*) did not arrive in New York until the mid-Givetian in the Manorkill and Panther Mountain formations (Stein et al. 2007; Mintz et al. 2010; Retallack and Huang 2011). Progymnosperm trees (*Svalbardia*) also appeared earlier in Spitsbergen
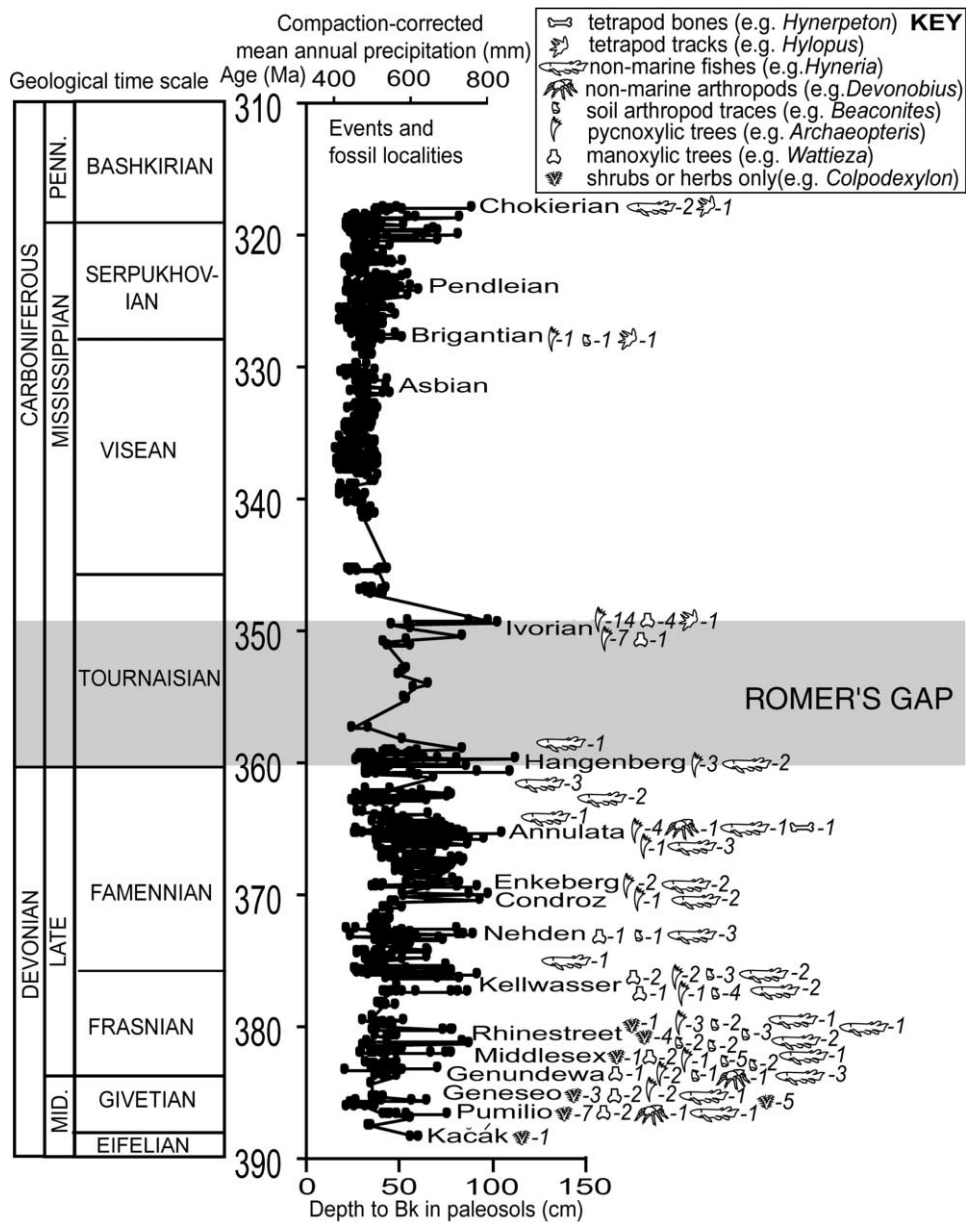
Figure 8. Composite time series of the paleoprecipitation proxy of depth to carbonate horizon in paleosols and fossil localities during the Late Devonian and Mississippian of northern Appalachia. Tetrapod bones and trackways are only found at transient episodes of humid forested paleoclimate in a long-term regime of semiarid shrubland paleoclimate. Numbers following symbol are numbers of localities (see apps. A–C, available online or from the *Journal of Geology* office).

(mid-Givetian; Schweitzer 1999) than the earliest progymnosperm trees (later Givetian; ?*Svalbardia*) in the Manorkill Formation of New York (Banks et al. 1985; Meyer-Berthaud et al. 1999; Mintz et al. 2010; Retallack and Huang 2011). The advent of trees and black shales were considered connected by Algeo et al. (1995) and Algeo and Scheckler

(1998), who proposed that deeper chemical weathering with the advent of trees resulted in oceanic eutrophication. Evidence presented here shows that this was not a one-time event: fossil trees are found associated with deep calcic or noncalcareous paleosols of subhumid paleoclimatic spikes (fig. 8), which correspond precisely with marine black

shales (fig. 7). Geographic expansion of trees and humid climate, CO_2 greenhouse spikes, and black shale events are all likely consequences of extrinsic perturbations, such as large impacts or volcanic eruptions (Retallack and Huang 2011).

For most of the Late Devonian and Mississippian, however, the northern Appalachians had shallow calcic paleosols of aridlands, whose root traces and profile form indicate vegetation no larger than desert shrublands (Retallack 1985; Driese and Mora 1993). Desert shrubland paleosols alternating though time with paleosols of woodland expansions, as well as local mosaics of coastal-to-inland paleosols (Retallack 1985), and stream channel-to-floodplain paleosols (Retallack et al. 2009; Retallack and Huang 2011) are evidence for a variety of potential habitats against which to reconsider tetrapod evolution.

Paleoenvironments of Tetrapods

Twelve localities in Pennsylvania have yielded evidence of early tetrapods: Hazelton, Hometown, Hyner, Indian Run Reservoir, Jim Thorpe, Nescopeck, Pottsville (including Tumbling Run Dams and Mount Carbon), Lavelle, Saint Johns, Tamaqua, and White Haven (figs. 1, 9). Deep calcic paleosols as evidence for tetrapod paleoenvironments are known at all these localities, including localities for tetrapod bone (Daeschler et al. 1994; Daeschler 2000; Shubin et al. 2004; Retallack et al. 2009), footprints (Vrazo et al. 2007; Lucas et al. 2010b), body impressions (Lucas et al. 2010a), a large vertebrate burrow (Storm et al. 2010), nonmarine arthropod body fossils (Shear 2000; Wilson et al. 2005), and roots, stems, and leaves of trees such as *Archaeopteris* (Cressler 2006), *Triphyllopteris*, and *Adiantites* (Jennings 1985). In contrast, fish fossils and arthropod burrows are found in both deep and shallow calcic paleosols (fig. 8). Association with subhumid wooded paleosols is evidence that Late Devonian and Mississippian tetrapods of Pennsylvania preferred woodlands: none have been found in association with more abundant shallow calcic, aridland paleosols.

The precipitation requirements of early tetrapods in Pennsylvania can be estimated from the depth to carbonate in associated paleosols, using the relationship between depth to carbonate and mean annual precipitation in modern soils (Retallack 2005a), corrected for burial compaction of overlying rock (Sheldon and Retallack 2001). Comparable data on precipitation requirements of Devonian trees, whose height was estimated from diameter at breast height, showed that they re-

quired more water for the same height of tree than modern Australian trees (Retallack and Huang 2011). Similarly, body lengths of Devonian-Missisippian tetrapods can be estimated from key anatomical details (fig. 9A: measurements from Holmes et al. 1998; Smithson 1994; Ahlberg et al. 2005, Clack and Finney 2005; Lucas et al. 2010a). For completely known skeletons and body impressions of Devonian–Early Pennsylvanian tetrapods, length of body scales proportionally with length of jaw, scapulocoracoid, and pes. Regression equations derived from such data (table 2) yield total body length from isolated skeletal elements. Similar estimates of body size come from these regression equations applied to pes and glenoacetabular length measured from fossil footprints (though not all are yet described; table 1), assuming reptilian alternate gait (Lucas et al. 2010b). Secondary overstepping suggested as an alternative by Vrazo et al. (2007) was not assumed here because glenoacetabular measurements using that assumption consistently gave body sizes twice as large as estimates from pes length of the same trackway, and because the only known whole-animal impression from Pennsylvania (*Temnocorpichnus isaacleai*; Lucas et al. 2010a) was not unusually long bodied. Devonian-Missisippian tetrapods of Pennsylvania were mostly large animals (ca. 0.8 m long) and lived within the rainfall belt of Devonian-Mississippian trees (fig. 9B), which was wetter than 571 ± 72 mm mean annual precipitation (Retallack and Huang 2011).

Studies of paleosols at many other localities of early tetrapods remain to be completed as evidence for their paleoenvironments and preservation, and important discoveries proceed apace (Niedźwiedzki et al. 2010; Storm et al. 2010, Lucas et al. 2010a, 2010b), but enough is known to assess paleoenvironments of tetrapods on a global basis (figs. 10, 11). The earliest tetrapods were large animals (fig. 9B) and, like modern crocodiles (Markwick 1994), were mainly at paleolatitudes of less than about 30° (fig. 11). The first tetrapods (Niedźwiedzki et al. 2010) and trees (Schweitzer 1999; Schweitzer and Giesen 2002) are associated with noncalcareous (humid climate) paleosols (app. C) of Eifelian age in the European-Baltic part of Euramerica (Old Red Continent). By the Frasnian, tetrapods and trees had spread to the south and east as far as the Australian part of Gondwana (Young 2007) and to China (Zhu et al. 2002). These tetrapod migrations are remarkable because the Eifelian-Givetian ptyctodont realm of fish in Laurentia (including Baltic, Armorican, Siberian, and Laurentian provinces) was very distinct from the phyllolepid-thelodont realm of fish with distinct east Gondwana, north
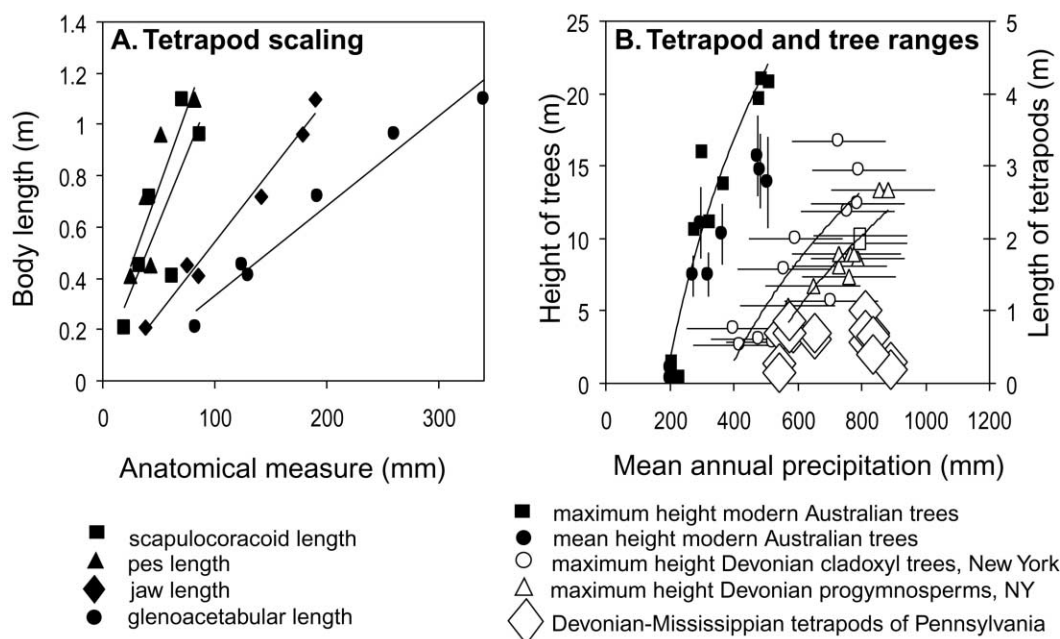
Figure 9. Relationships between body parts and total body length of Devonian-Mississippian tetrapods (*A*) and between size of Devonian-Mississippian trees and tetrapods and modern trees of Australia on a gradient of mean annual precipitation (*B*). Precipitation requirements of Devonian-Mississippian tetrapods and trees (>2 m) were comparable and greater than for modern Australian trees. Data for *A* is in table 2, and data for *B* is in table 1 and in an article by Retallack and Huang (2011).

Gondwana, and western Yunnan provinces (Lebedev and Zakharenko 2010; Lukševičs et al. 2010).

Prototetrapods (*Elpisostege*, *Panderichthys*, *Livoniana*, *Tiktaalik*) with simplified fin lobes are known from coastal lagoon deposits of the early Frasnian but were widespread through floodplains by the upper Frasnian. The first aquatic tetrapods (footprints comparable with those of *Ichthyostega* and *Acanthostega*) appear around Eifelian coastal lagoons but were widespread in floodplains by the Givetian. By the latest Famennian, short-backed tetrapods appeared in coastal lagoons (*Tulerpeton*; Lebedev 1990). After Romer's Gap of the Tournaisian, terrestrial tetrapod habitats were comparable to those of amphibians today, reflecting a preference for swamp woodlands and forests (Holmes et al. 1998; Clack and Finney 2005), but there was also a Mississippian evolutionary radiation of long-bodied and snakelike aquatic tetrapods (Wellstead 1982; Godfrey 1989).

Romer's Gap and Other Taphonomic Biases

The rarity of early Missisppian tetrapods (Romer's Gap) would be explained by both the preservational environment and paleoenvironmental effects if they had the ecological preference for woodlands that is suggested here. The preservational environment would contribute to rarity because most humid woodland and forest soils are too acidic at the surface to preserve bone (Retallack 1998). Rarity would be paleoenvironmental because most paleosols of North America are desert shrubland soils, especially within the critical Tournaisian interval of Romer's Gap (fig. 8).

Woodland preference of early tetrapods continued during the Pennsylvanian, as indicated by trackways associated with swamp and forest paleosols (Keighley and Pickerill 1998; Falcon-Lang et al. 2007) and skeletons in rotted tree trunks (Falcon-Lang et al. 2006). The pattern is especially striking because sequences of shallow calcic paleosols preserve bone well, but only those of fossil fish and not tetrapods (33 fish localities in New York and Pennsylvania listed in app. B). Only by the Permian did reptiles and amphibians colonize aridlands, where they were preserved in shallow calcic paleosols of Texas and Oklahoma (Retallack 2005*b*).

The New York and Pennsylvania woodlands here regarded as preferred by tetrapods existed for only short intervals of time that were interrupted by
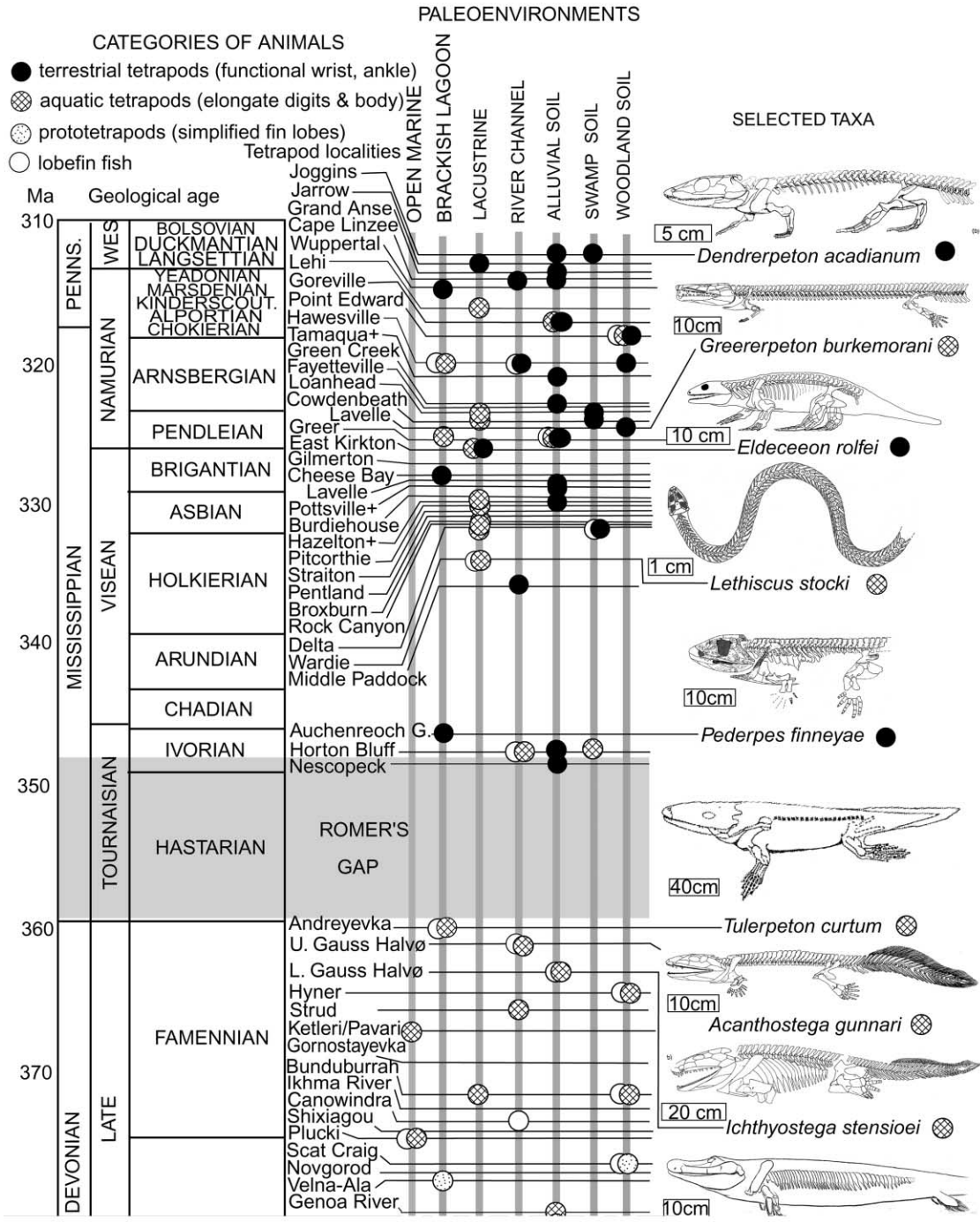
Figure 10. Summary of habitats of Devonian and Mississippian terrestrial and aquatic tetrapods, prototetrapods, and lobefin fish. Marine, lacustrine, and river channel habitats are inferred from associated fossils and sedimentary facies, but soil habitats are interpreted from paleosols in broad categories of alluvial soil (e.g., Farwell, Gleasonton, Renovo pedotypes), swamp soil (e.g., Sproul pedotype), and woodland soil (Hyner, Richard pedotypes; Retallack et al. 2009). Skeletal restoration sources include the following: *Eusthenopteron foordi* (Clack 2002), *Tiktaalik rosae* (Daeschler et al. 2006), *Ichthyostega stensioi* (Clack 2006), *Acanthostega gunnari* (Clack 2006), *Tulerpeton curtum* (Lebedev 1990), *Pederpes finneyae* (Clack and Finney 2005), *Lethiscus stocki* (Wellstead 1982), *Eldeceeon rolfei* (Smithson 1994), *Greererpeton burkemorani* (Godfrey 1989), and *Dendrerpeton acadianum* (Holmes et al. 1998).
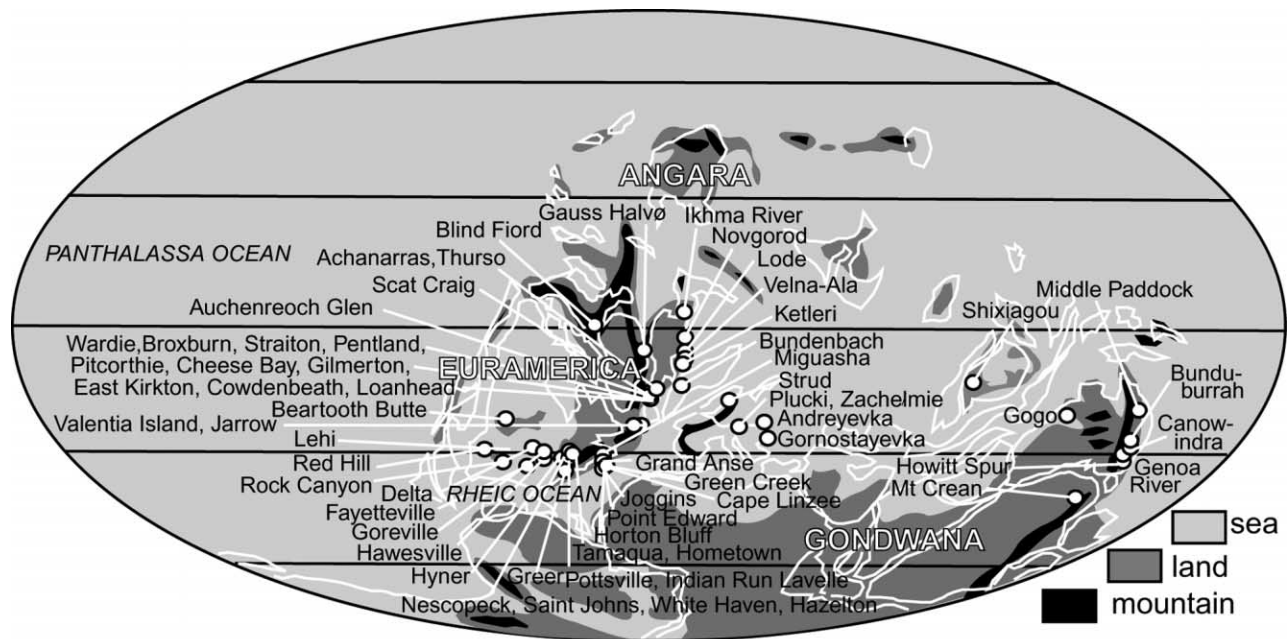
Figure 11.   Location of fossil fish and tetrapod localities on a palaeogeographic map of the latest Devonian (Famennian) by J. Golonka for Joachimski et al. (2002). Mount Crean, Thurso, Red Hill, Howitt Spur, Gogo, and Canowindra have not yielded prototetrapods or tetrapods, but they have important fish assemblages. This map is reproduced with modification by permission of Elsevier, license 2187800296438.

longer periods of arid shrubland paleosols (fig. 8). These abundant shallow calcic paleosols have not yielded tetrapods. A prediction of the taphonomic hypothesis for Romer's Gap proposed here is that tetrapods will be found in other regions with deep calcic or noncalcareous paleosols, although because of their rarity, it will require extraordinary measures and luck for collection.

The prospect of future discoveries by focused search is good considering collection histories of other fossils. For example, Olsens' Gap in mid-Permian reptile evolution corresponds with deep calcic woodland paleosols in Texas and Oklahoma (Retallack 2005*b*), but there may be fossils of this age in Russia (Losovsky 2005). Mesozoic mammals are rare and poorly understood in red, shallow calcic paleosols with dinosaurs (Retallack 1997*b*) and better understood from extraordinary measures of microfossil sieving of noncalcareous sediments and large-scale quarrying of lake deposits (Luo 2007). The fossil records of Neogene great apes and of the transition between ape and human have required extraordinarily dedicated search, while in comparison, there is an abundance in shallow calcic paleosols of grassland creatures such as baboons and wildebeest (Retallack 1991). Similarly, Romer's

Gap is likely to yield fossils after focused and sustained search in and around deep calcic paleosols.

Alternatively, Romer's Gap has been taken as a reflection of genuine tetrapod rarity (Coates and Clack 1995) caused by recovery from an unusually profound mass exinction at the time of the terminal Devonian Hangenberg event (Sallan and Coates 2010). Prototetrapods and Devonian aquatic tetrapods disappeared during the Hangenburg turnover, and fully terrestrial tetrapods appear after this gap (Clack and Finney 2005). Nevertheless, some tetrapods survived in viable populations (Vrazo et al. 2007) and were widely distributed geographically (fig. 11). There is also no compelling evidence for Tournaisian aquatic hypoxia as argued by Ward et al. (2006), whose geochemical modeling yields 17% atmospheric O_2 for the Tournaisian but 13% O_2 for the Middle Devonian. The fossil charcoal record also does not support unusually low O_2 levels during Romer's Gap (Scott and Glasspool 2006).

Woodland Hypothesis for Tetrapod Evolution

These new regional data and global review of early tetrapod paleoenvironments present a different picture than the desert (Romer 1941, 1958; Orton

1954; Warburton and Denman 1961) or intertidal hypotheses (Blieck et al. 2007; Niedźwiedzki et al. 2010), and suggest a new hypothesis (fig. 12) that the evolutionary transition to land was a matter of opportunity rather than escape. The opportunity was a geologically new habitat appearing during the mid-Eifelian (395 Ma; Schweitzer 1999) and then spreading around the world: flooded woodlands and oxbow lakes without effective terrestrial predators other than themselves. Flash floods are common today in desert regions and were widespread before the Devonian evolution of trees and woodland soils (Retallack 1997a). In contrast, flash floods are mitigated in woodlands, where floodwaters impeded by trees formed ponds (Darby 1999). Flash flooding of desert regions also promotes braided streams with low-sinuosity anabranches, but the Early Devonian evolution of trees coincided with increased frequency of lateral accretion deposits, oxbow lakes, and meandering streams (Davies and Gibling 2010). There were no large fish-eating terrestrial predators during the Devonian; it was a world without egrets, herons, bears, and humans (Feunteun and Marion 1994; Crowder et al. 1997; Jennings et al. 1999; Quinn et al. 2001). The Devonian was a unique time in Earth history, when newly evolved woodlands ponded floodwaters and oxbow lakes of meandering streams but terrestrial and aerial fishing had not evolved (Zimmer 1998). Devonian prototetrapods swimming in floodwaters avoided predation in shallow water and also found food of fish, myriapods, scorpions, arachnids, and the first true seeds (Cressler 2006). As flood-waters subsided, these foods continued to be available in oxbow lake and stream margins and were supplemented by carcasses of large stranded fish on land. Limbs, necks, and ankles evident from the evolution of Late Devonian tetrapods would have aided scavenging after floods (Clack 2002; Long and Gordon 2004). Such twist-feeding is indicated by suture patterns in the skull of the otherwise aquatically adapted *Acanthostega* (Markey and Marshall 2007).

The outgroup of the tetrapod evolutionary trajectory were lobe-finned fish such as *Eusthenopteron* from Miguasha, functionally comparable with living lungfish and coelacanths, which today, as in the Devonian, live in a variety of marine and floodplain environments. The coelacanth of the Comoro Islands does not use its lobed fins to negotiate rocky marine sea floors and caves, as was once thought, but rather to hover and head-stand for electroreception in deep water (Weinberg 2000). The living Australian lungfish (*Neoceratodus forsteri*) is nocturnal and capable of limited land excursions, but its lobe-fins are mostly used for nav-

igating slow, vegetation-choked water (Allen et al. 2002). Lobe-fins are not required for such a lifestyle, because the living ray-fin bichir (*Polypterus bichir*) of Africa nests and spawns in flooded swamps during the wet season and can negotiate small exposed obstacles with its fins (Greenwood 1986). Other ray-fin fish such as the "walking catfish" (*Clarias batrachus*) of Borneo, also come onto land to eat grain, but only on wet nights in rain forest (Inger 1957).

Load-bearing limbs, ankles, and digits are advantages in waters shallower than body height and on slippery or vegetated ground, as can be seen readily from the poor performance of fish out of water compared with salamanders. The thick, deep neck of fish was poorly suited to body-twisting motions needed to rip flesh and scales from stranded carcasses that were as big as or bigger than early tetrapods. Narrow, flexible, and laterally braced necks would have been selected for such twist feeding. Simplified fin-rays in lobefins appeared with *Elpistostege* at Miguasha, more flexible necks with *Tiktaalik* in Blind Fiord, and digits in trackways at Zachełmie, Valentia Island, and Genoa River. Nevertheless, tetrapods remained aquatic, like *Acanthostega*, until the appearance of tracks without tail drags at Nescopeck and stout limb bones at Horton Bluff (fig. 10).

Paleoenvironmental conditions of the woodland hypothesis for tetrapod origins are different from hypotheses of desert pond escape (Romer 1941, 1958), estivation (Orton 1954), larval competition (Warburton and Denman 1961), anoxia survival (Inger 1957; Clack 2007), predator avoidance (Goin and Goin 1956; Shubin 2008), or basking on land (Carroll 2009). The desert pond, estivation, basking, and larval competition hypotheses predict evolution of tetrapods in semiarid and highly seasonal climates unlike those demonstrated here (figs. 8, 9).

The anoxia-escape hypothesis would be supported if tetrapods were found in or near black shales, but the earliest fossil prototetrapods and tetrapods are preserved in red, well-aerated paleosols (Miller et al. 2007) or known from subaerial foot prints (Niedźwiedzki et al. 2010), with the exception of the poorly known Plucki locality (Szrek 2008). Times of woodland expansion in New York and Pennsylvania do coincide with marine and lacustrine anoxic events that created some famous fossil fish beds that lack tetrapods, such as Achanarras and Thurso, Scotland (Marshall et al. 2007). Having limbs or a snakelike body to allow escape from anoxia evidently did not save the tetrapods preserved in black shales at Plucki, Wardie, Strai-
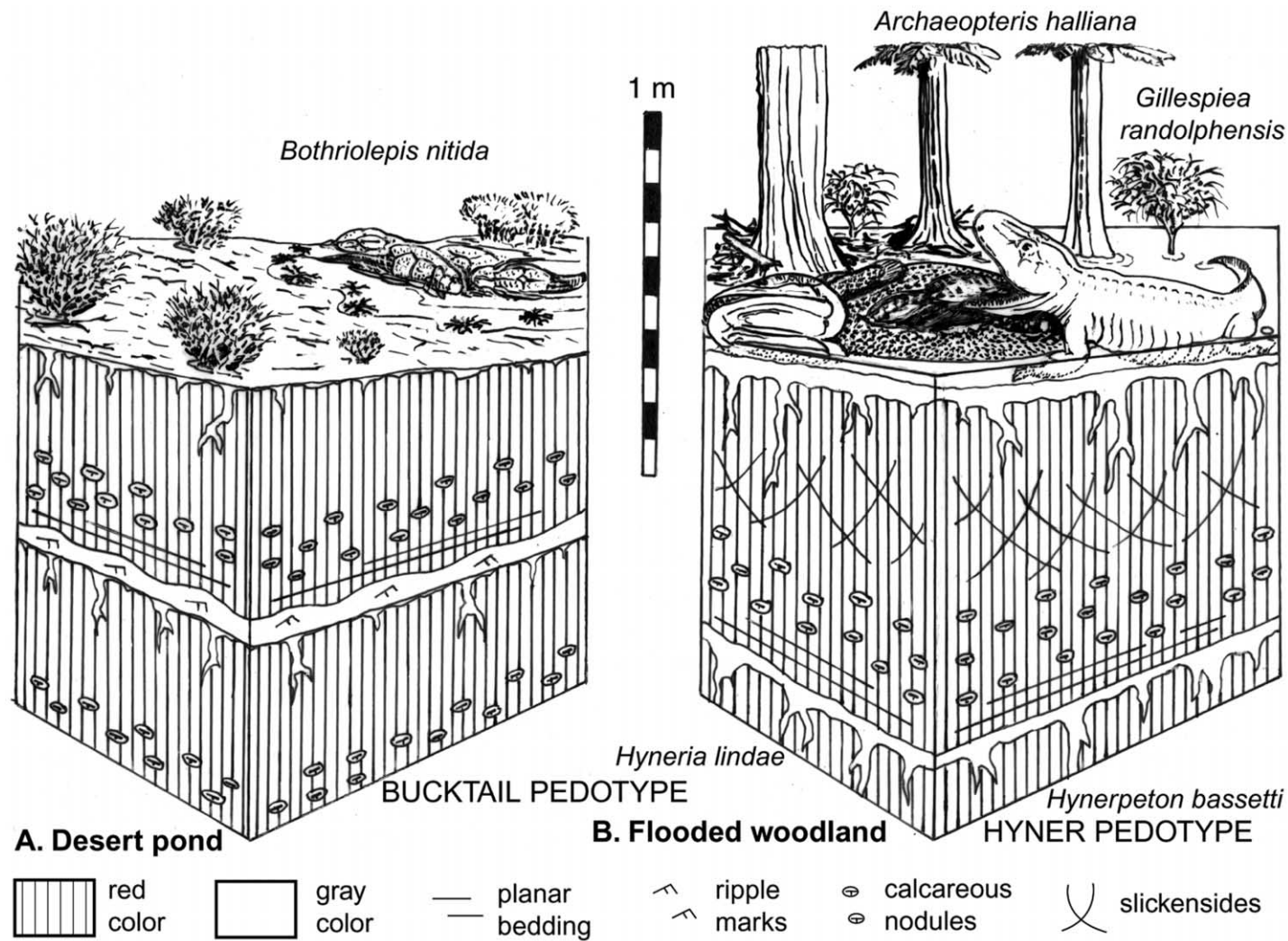
Figure 12. "Woodland hypothesis" (this article; *right*) and "desert hypothesis" (Romer 1941, 1958; *left*) for tetrapod evolution contrasted, using restorations of shallow calcic (Bucktail pedotype) paleosols at Port Matilda and deep calcic (Hyner pedotype) paleosols at Hyner, both Duncannon Member of the Catskill Formation (Famennian), in Pennsylvania (Retallack et al. 2009). The paleosols are not restored but shown with current field appearance, including drab-haloed root traces and burial reddening.

ton, and Broxburn (fig. 10). Strong swimmers to the surface are more likely to avoid aquatic anoxia than animals with clumsy limbs. Low atmospheric oxygen for the entire Middle-Late Devonian (Clack 2007) or early Mississippian (Ward et al. 2006) has been invoked as an explanation of early tetrapod evolution and preservation, but these hypotheses are based on paleoclimatic models with 10-m.yr. time steps, and paleosols are now evidence of short-term climatic transients (figs. 6, 8).

Larval competition is compatible with likely pedomorphic origins of limbs (Long and Gordon 2004) aiding return of hatchlings overland to water. However, studies of juvenile and adult humeri and their muscle attachments in *Ichthyostega* now show that those animals became more active on land as they grew older, unlike *Acanthostega* (Callier et al. 2009). Furthermore, the distribution of tetrapods outlined here is evidence that returns to water at any stage of life were in the shade and slime of wooded floodplains and oxbow lakes (Clack 2002), not to shrinking desert ponds, as envisaged by Warburton and Denman (1961).

Limbs as claspers during amplexus (mating) would be more useful either in water or freshly emergent than on land (Martin 2004). However, the forelimb is used for amplexus in frogs, yet hindlimbs developed further in early tetrapods, and neither limb had a large grasp (Carroll 2009).

Avoidance of predation also is compatible with evidence of enormous predators in Devonian rivers (Shubin 2008), but Devonian predation differed from modern predation, which comes from both air and water (Zimmer 1998). Early tetrapods were large (0.8 m or more long) and rare, not small and common like modern mudskippers, blennies, and other fish adapted for predator avoidance in shallow water (Feunteun and Marion 1994; Crowder et al. 1997; Jennings et al. 1999; Quinn et al. 2001). Early tetrapods had only themselves to fear.

The woodland hypothesis shares with the intertidal hypothesis (of Niedźwiedzki et al. 2010) the idea that excursions onshore were facilitated by high water: tides and floods. A key argument for the intertidal hypothesis is the presumed greater array of stranded and resident food on tidal flats than on floodplains (Niedźwiedzki et al. 2010). These arguments are not supported by the abundance of large nonmarine mollusks and invertebrate burrows in Early to Middle Devonian paleosols (Gordon 1988; Friedman and Chamberlain 1995; Retallack and Huang 2011). Many of the earliest cladoxyl woodlands of the Devonian were marine-influenced (Schweitzer and Giesen 2002; Mintz et al. 2010) woodlands, ecologically comparable with modern mangroves. Modern mangrove communities include oysters, crabs, and other marine creatures at their oceanward limit but range to freshwater estuarine communities in their landward, tidally influenced limit (Pool et al. 1977). Normal marine salinities and seashells are essential criteria differentiating woodland and intertidal hypotheses for tetrapod evolution, and such evidence of marine conditions is lacking for the oldest tetrapods (Niedźwiedzki et al. 2010) and all known Devonian-Mississippian tetrapod occurrences of New York and Pennsylvania (Vrazo et al. 2007; Retallack et al. 2009; Storm et al. 2010; Lucas et al. 2010*a*, 2010*b*). While this article falsifies the desert hypothesis and offers little support for the intertidal hypothesis, intertidal and woodland hypotheses overlap within brackish mangrove communities and deserve further evaluation as more fossils within the evolutionary transition from fish to amphibian and associated paleosols are discovered.

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