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Late Devonian tetrapod habitats indicated by palaeosols in Pennsylvania

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Abstract: Late Devonian (Famennian) tetrapods from the Duncannon Member of the Catskill Formation, near Hyner (Pennsylvania, USA) have been found within palaeosols that offer a new line of evidence for their ancient environments. Hyner has yielded at least two fossil tetrapod species, *Hynerpeton basseti* and *Densignathus rowei*. Subhumid Vertisol palaeosols and semiarid Aridisol palaeosols alternate at Hyner, as in other Catskill Formation sedimentary cycles attributed to Milankovitch-eccentricity periods (100 ka). Tetrapods were found in palaeosols of subhumid, not semiarid, phases of 100 ka palaeoclimate cycles. In addition, palaeosols at Hyner record an unusually warm and wet climatic episode compared with other palaeosols of the Catskill Formation, and correlated with the European *Annulata* black shale event. Tetrapod bones are cracked and disarticulated in red palaeosols of an oxbow lake margin, as if victims of dry-season death, decay, and subaerial weathering. Vegetation-choked swales and floodplains would have afforded shelter from 3–4 m long predatory fish (*Hyneria lindae*) of open water, and offered food of large dead fish, small live fish, arachnids, myriapods and scorpions. If these early tetrapods lived on land at all, it was during wet seasons of feeding and breeding, rather than fatally dry seasons.

Supplementary material: Chemical data are available at http://www.geolsoc.org.uk/SUP18373.

For many years, the 'desert pond' scenario for evolution of amphibians from fish postulated that limbs evolved from fins adapted to overland escape from shrinking ponds in dry climates or seasons (Romer 1933). Others have argued that desert ponds selected for evolution of limbs to dig aestivation burrows (Orton 1954) or clamber over a crowd of tadpoles (Warburton & Denman 1961). Subsequently discovered aquatic limbs and tails in Devonian tetrapods were interpreted as adaptations for reproduction and feeding in shallow water, rather than on land (Clack 2002). Other biotic models of selection argue for evolution of limbs and air-breathing to escape marine or lagoonal anoxia (Inger 1957; Clack 2007) or predation (Goin & Goin 1956). Testing such hypotheses requires not only tetrapod fossils close to the fish–amphibian transition and information on their adaptive features (Clack 2002; Long & Gordon 2004) but also independent evidence for their palaeoenvironment, such as palaeosols.

Palaeosols reveal formative factors of past soils, including climate, vegetation, palaeotopography, parent materials and time for formation (Retallack 2001). Palaeosols can be correlated to establish geological age from regionally significant attributes, such as degree of development (Rutter *et al*. 2006). Climatic variables such as mean annual precipitation also can be inferred from the degree of nutrient leaching from clayey subsurfaces of palaeosols (Sheldon *et al*. 2002), and from the depth of carbonate nodules in the profile (Retallack 2005). Palaeosols are also by definition in the place they formed, and so reveal the distribution of ancient ecosystems represented by root traces and burrows within ancient sedimentary environments (Retallack *et al*. 2000). We have studied palaeosols near Hyner, Pennsylvania (Fig. 1), as evidence for habitats of the fossil tetrapods found there (Daeschler *et al*. 1994; Daeschler 2000*a*; Shubin *et al*. 2004; Clack 2006). We also contrast other palaeosols in Pennsylvania lacking tetrapods, representing other palaeoenvironments and palaeoclimates available during the Late Devonian.

Geological setting

At least two species of early tetrapods and a variety of other fossil animals and plants (Table 1) have been found in a road cut near Hyner, in Clinton County, Pennsylvania (Fig. 1). These fossiliferous red and grey siltstones are within the Duncannon Member of the Catskill Formation (Woodrow *et al*. 1995). The Duncannon Member is widespread in Pennsylvania, although some authorities (Harper 1999), but not all (Cotter *et al*. 1993; Cotter & Driese 1998), merge it with underlying Sherman Creek Member into the Buddys Run Member at Selinsgrove, also reported here (Fig. 1c). A geological age of late Fammenian (late Fa2c), roughly 363–366 Ma (Gradstein *et al*. 2004), is suggested for the Hyner tetrapods by fossil spores of the VH (*Apiculatisporites verrucosa–Vallatisporites hystricosus*) zone (Marshall *et al*. 1999; Traverse 2003), consistent with this stratigraphic level (Sevon & Woodrow 1985; Harper 1999).

The sandstones at Hyner have been interpreted as former channels of large rivers, which drained high Acadian mountains (Woodrow *et al*. 1995) of a long southern promontory to Euramerica (Fig. 2). The most fossiliferous strata are within a broad swale-like feature filled with red and grey siltstone (see photomosaics of outcrop and panel diagrams of Woodrow *et al*. 1995; Cressler 2006), interpreted as a seasonally inundated oxbow lake formed in an abandoned meander of a large river (Woodrow *et al*. 1995), or as one of several swales within the 'avulsion belt' (proximal floodplain) of a meandering stream (R.L. Slingerland, pers. comm.).

Materials and methods

Geological sections at the Hyner locality were measured using the method of eye-heights, in which the Brunton compass is used as a levelling device (Compton 1985), but detailed sections of palaeosols were measured using a metric flexible tape. The

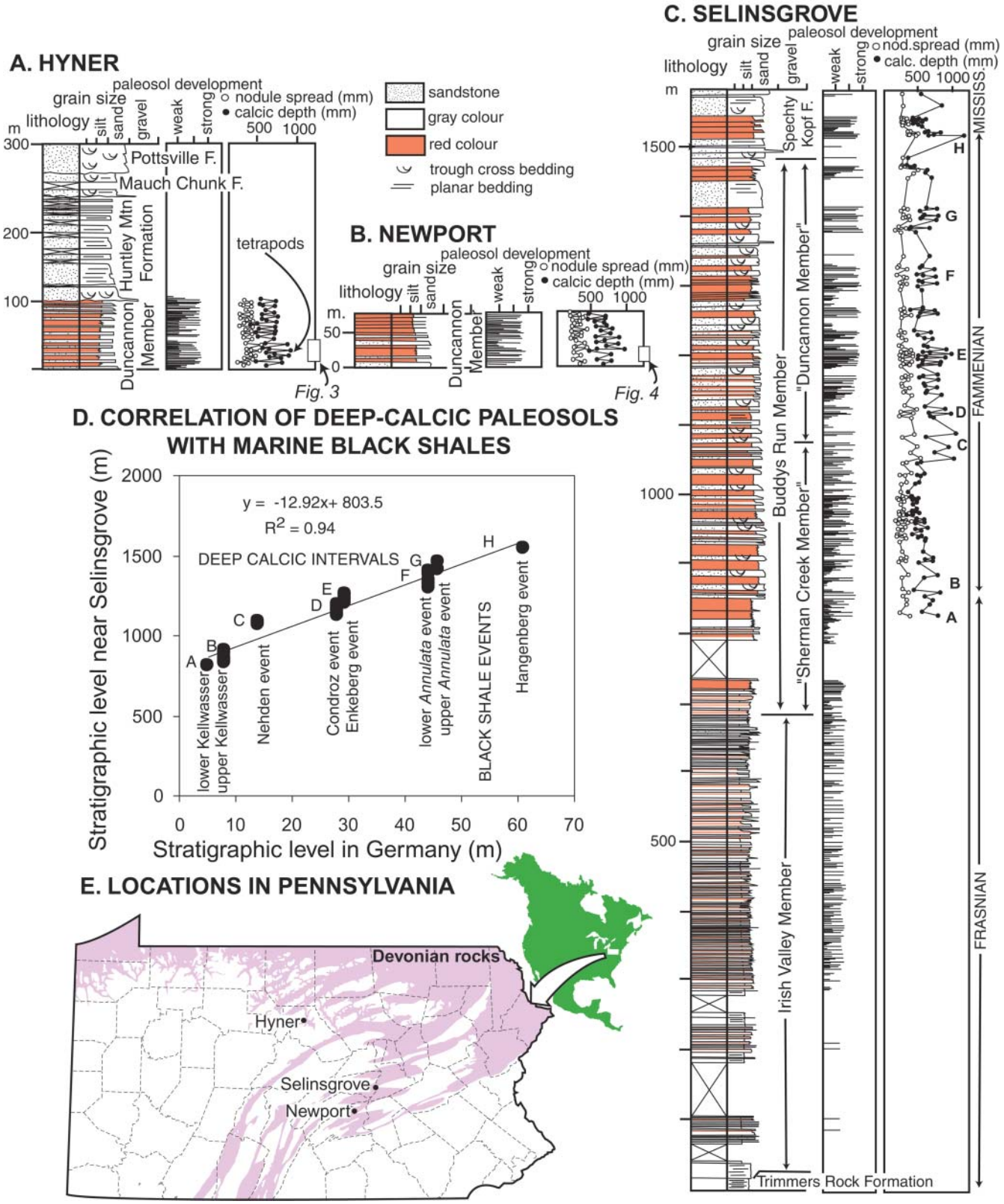

Fig. 1. Measured sections (**a**–**c**), their correlation (**d**) and location (**e**) in Pennsylvania: (**a**) fossil tetrapod locality in a road cut north of state highway 120, 3 km west of Hyner, Clinton County (41.29853°N, 77.81916°W); (**b**) correlative deep-calcic paleosols on state highway 322, 4 km NW of Newport, Perry County (40.50570°N, 77.12766°W); (**c**) near-complete section of Catskill Formation along US highway 11/15 south from 4 km south of Selinsgrove, Snyder County (40.76216°N, 76.86455°W); (**d**) correlation of deep-calcic (>650 mm) palaeosols in the Selinsgrove section with anoxic events in a composite section of Vogelsberg, Köstenhof and Drever quarries of Germany (Buggisch & Joachimski 2006); (**e**) locations and Devonian outcrop in Pennsylvania. Levels A–H in (**c**) are deep-calcic palaeosol intervals correlated with marine black shale events in (**d**).

Table 1. *Late Devonian fossils from Hyner*

Species	Higher taxa	Reference
Barinophyton obscurum	Zosterophyllopsida, Barinophytales	Cressler 2006
Barinophyton sibiricum	Zosterophyllopsida, Barinophytales	Cressler 2006
Otzinachsonia beerboweri	Lycopsida, Isoetales	Cressler & Pfefferkorn 2005
cf. *Lepidodendropsis* sp. indet.	Lycopsida, Isoetales	Cressler 2006
Rhacophyton ceratangium	Filicopsida, Zygopteridales	Cressler 2001, 2006
Gillespiea randolphensis	Filicopsida, Stauropteridales	Cressler 2006
Archaeopteris halliana	Progymnospermopsida, Archaeopteridales	Cressler 2006
Archaeopteris hibernica	Progymnospermopsida, Archaeopteridales	Cressler 2006
Archaeopteris macilenta	Progymnospermopsida, Archaeopteridales	Cressler 2006
Archaeopteris obtusa	Progymnospermopsida, Archaeopteridales	Cressler 2006
cf. *Aglaosperma quadripartita*	Gymnospermopsida, Pteridospermales	Cressler 2006
Cupulate ovules sp. indet.	Gymnospermopsida, Pteridospermales	Cressler 2006
Orcadesmus rubecollus	Arthropoda, Myriapoda, Diplopoda	Wilson *et al*. 2005
Millipede sp. indet.	Arthropoda, Myriapoda, Diplopoda	D. Murphy, pers. comm.
Gigantocharinus szatmaryi	Arthropoda, Arachnida, Trigonotarbida	Shear 2000
Scorpion sp. indet.	Arthopoda, Arachnida, Scorpiones	D. Murphy, pers. comm.
Groenlandaspis pennsylvanica	Placodermi, Groenlandaspidae	Daeschler *et al*. 2003
Turrisaspis elektor	Placodermi, Groenlandaspidae	Daeschler *et al*. 2003
Phyllolepis rossimontina	Placodermi, Phyllolepidae	Lane & Cuffey 2005
Ageleodus pectinatus	Chondrichthyes, Xenacanthidae	Downs & Daeschler 2001
Ctenacanthus sp. indet.	Chondrichthyes, Ctenacanthidae	Daeschler *et al*. 2003
Gyracanthus sp. indet.	Acanthodii, Gyracanthidae	Daeschler *et al*. 2003
Limnomis delaneyi	Actinopterygii, Chondrostei	Daeschler 2000*b*
Holoptychius sp.	Sarcopterygii, Porolepiformes	Daeschler *et al*. 2003
Dipnoi sp. indet.	Sarcopterygii, Dipnoi	Friedman & Daeschler 2006
Megalichthyid sp. indet	Sarcopterygii, Osteolepiformes	Daeschler *et al*. 2003
Hyneria lindae	Sarcopterygii, Osteolepiformes	Thomson 1968
cf. *Glyptopomus* sp. indet.	Sarcopterygii, Osteolepiformes	Friedman & Daeschler 2006
cf. *Sauripteris* sp. indet.	Sarcopterygii, Rhizodontiformes	Davis *et al*. 2001
Rhizodontid sp. indet.	Sarcopterygii, Rhizodontiformes	Daeschler *et al*. 2003
Densignathus rowei	Tetrapoda, Ichthyostegalia	Daeschler 2000*a*
Hynerpeton bassetti	Tetrapoda, Ichthyostegalia	Daeschler *et al*. 1994
Tetrapoda sp. indet	Tetrapoda, Ichthyostegalia	Shubin *et al*. 2004
Whatcheeriid sp. indet.	Tetrapoda, Ichthyostegalia	Clack 2006

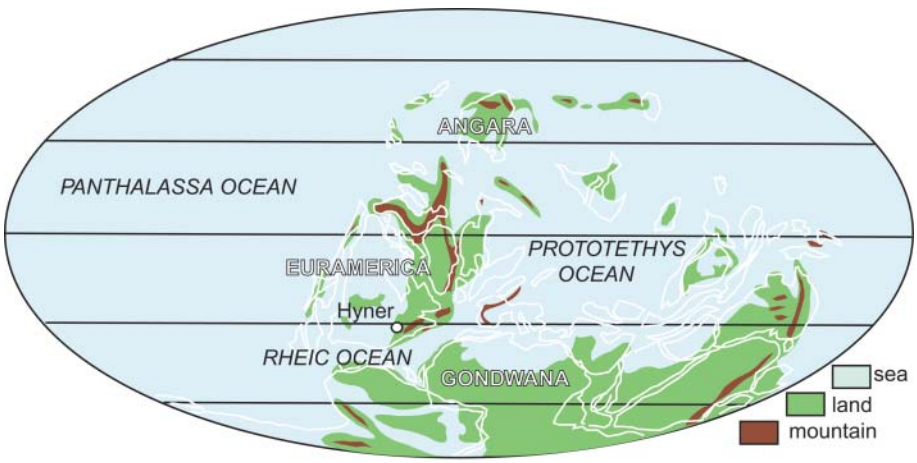

Fig. 2. Location of Hyner, Pennsylvania on a palaeogeographical map of the latest Devonian (Famennian) by J. Golonka for Joachimski *et al*. (2002). Reproduced with modification by permission of Elsevier Ltd license 2187800296438.

various palaeosols were classified into pedotypes, which are field categories of palaeosols (Retallack 2001). The overall section (Fig. 1a) was measured from the railway track below the main road to the top of the plateau. The upper part of a detailed section (Fig. 3) was measured at road level 200 m west of the western end of the 'plant layer' (Cressler 2006, figs 4 and 5), but the middle part of the section was measured 200 m west of the western end of the 'plant layer'. Fossil plants and vertebrates collected at Hyner were compared with collections of D. Rowe in North Bend, of E. Daeschler in the Philadelphia Academy of Sciences, and published information on fossil occurrence (Woodrow *et al*. 1995; Cressler 2001, 2006). Additional stratigraphic sections were measured in laterally equivalent sequences near Newport and Selinsgrove (Figs 1b, c and 5), where comparable palaeosols have been described (Cotter & Driese 1998; Cotter *et al*. 1993; Driese & Mora 1993; Driese *et al*. 1993). Petrographic thin sections of palaeosols were point-counted using a Swift® automated counter. Selected samples

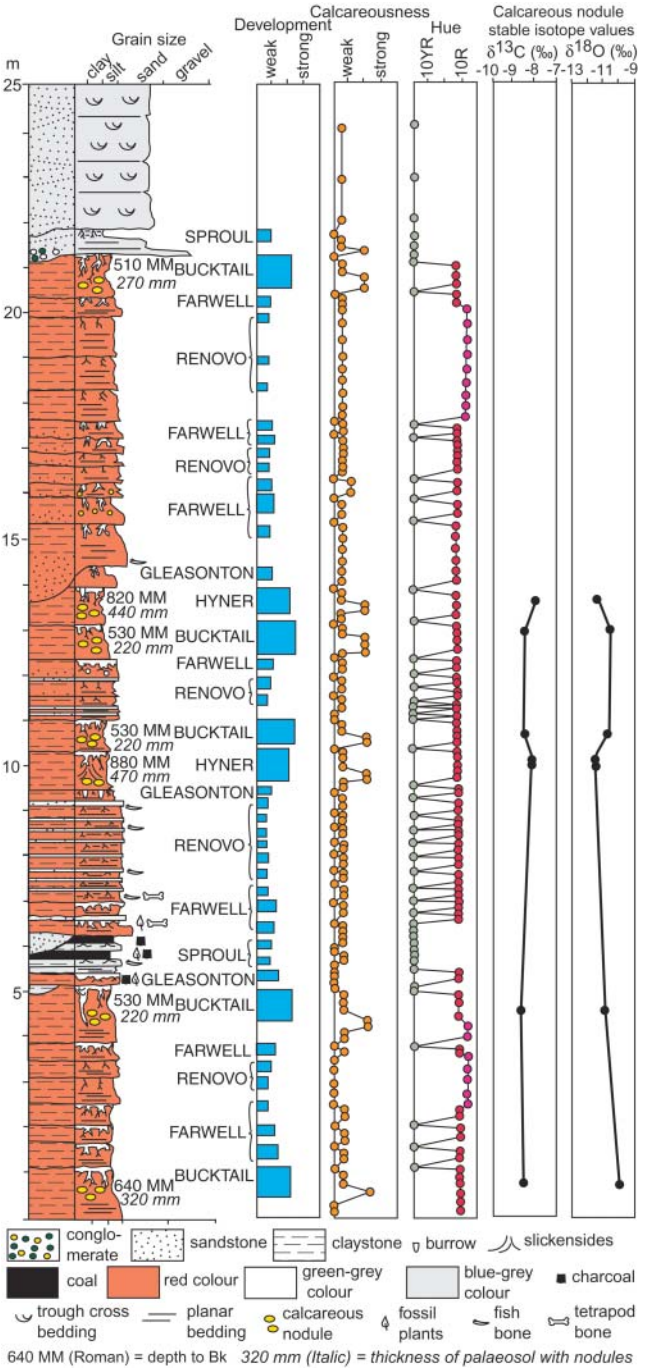

Fig. 3. Geological section of palaeosols at the Hyner tetrapod site (Fig. 1a), measured in 10 m increments at three stations 400 m laterally along the road. Filled boxes show position of palaeosols by height, and degree of development (Retallack 2001) by width. Calcareousness is degree of reaction (Retallack 2001) with 10% stock HCl, and colour from a Munsell chart.

were analysed by X-ray fluorescence, and potassium dichromate titration for major element composition, including redox state of iron, in the Vancouver (Canada) laboratories of ALS Chemex Inc. In addition, micrite nodules were analysed for carbon and oxygen isotope composition in the Paul H. Nelson Stable Isotope Laboratory of the University of Iowa. Powdered samples were roasted in a vacuum at 380 °C to remove volatile components, then reacted with anhydrous phosphoric acid at 75 °C in a Kiehl automated carbonate reaction device coupled to a Finnigan MAT 252 isotope ratio mass spectrometer. Isotope values are relative to the Vienna Peedee Belemnite Standard, with analytical precision better than 0.1‰ $\delta^{13}C$ and $\delta^{18}O$. Three samples were analysed from each stratigraphic level, showing that $\delta^{13}C$ varies ($\pm 2\sigma$) within a specific level by ± 0.3‰ and $\delta^{18}O$ by ± 0.6‰.

Palaeosols

Palaeosols are widely recognized in the Catskill Formation of Pennsylvania (Driese & Mora 1993; Driese *et al*. 1993) and New York (Retallack 1985; Cox *et al*. 2001), on the basis of drab-haloed and clayey root traces, hackly slickensided soil structure (peds and cutans), clay-enriched (Bt) and calcareous nodular (Bk) horizons, and geochemical variation such as alkali and alkaline earth depletion and low carbonate $\delta^{13}C$ values. The palaeosols have been altered by compaction as a result of burial under some 5.2 km of overlying rocks (Beaumont *et al*. 1987), and pervasive greenschist-facies metamorphism (Retallack 1985; Mora *et al*. 1998).

Field criteria such as root traces, soil horizons and soil structure were used to recognize 42 successive palaeosols of six pedotypes at Hyner (Fig. 3; Table 2) and comparable palaeosols at Newport and Selinsgrove (Figs 1 and 4). Bucktail and Hyner pedotypes (Figs 5 and 6) show little relict bedding, blocky to lenticular soil peds, slickensides and micritic carbonate nodules up to 46 mm in diameter. The depth to this pedogenic carbonate beneath the surface defined by drab-haloed root traces and sparry rhizoconcretions (Fig. 5c) in the Bucktail pedotype is shallow (Fig. 6a: mean 560 ± 30 mm), as in modern Aridisols (Soil Survey Staff 1999). In contrast, carbonate is deeper in the Hyner pedotype (mean 760 ± 80 mm), which also have clastic dykes, bowl-shaped slickensides (Fig. 6b), and surface palaeorelief as in modern Vertisols (Soil Survey Staff 1999), or equivalents in other soil classifications (Table 2; Food and Agriculture Organization 1974; Isbell 1996). Unlike these moderately developed pedotypes, Renovo, Farwell, Gleasonton and Sproul pedotypes, with their remnants of original sedimentary layering (Fig. 7), are uninformative of past climates and atmospheric carbon dioxide levels. The Sproul pedotype (Fig. 7) was measured at the western end of plant-bearing grey siltstone at road level where two levels are unusually carbonaceous and rooted. Sproul palaeosols do not extend laterally throughout the grey siltstone ('plant layer' of Cressler 2006).

Palaeoclimate

The semiarid climate of Bucktail versus subhumid climate of Hyner palaeosols implied by identification as Aridisols and Vertisols (Table 2) can be quantified by application of climofunctions, which are significant relationships between specific soil features and climatic variables in modern soils. Climofunctions can be used to interpret palaeoclimate from palaeosols, assuming that palaeosols formed under generally comparable conditions (floodplains and loess plains exposed to weathering for durations of less than 10 ka), and making adjustments for known alterations during burial. Depth to carbonate nodules in soils (D_o in mm) increases with mean annual precipitation (R in mm) following the equation

$$R = 137.24 + 0.6445 D_o - 0.00013 D_o^2 \qquad (1)$$

with $R^2 = 0.52$, and standard error ± 147 mm recalculated from Retallack (2005). Such depths in palaeosols could have been

Table 2. *Late Devonian palaeosol identification*

Pedotype	Diagnosis	US taxonomy (Soil Survey Staff 1999)	FAO World Map (Food and Agriculture Organization 1974)	Australian classification (Isbell 1996)
Bucktail	Red siltstone with drab-haloed root traces (A), blocky peds, and shallow (<650 mm) calcareous nodules (Bk) over bedded red siltstone (C)	Calcid	Calcic Xerosol	Calcic Calcarosol
Farwell	Red siltstone with drab-haloed root traces (A) and blocky peds, over slickensided red siltstone (Bw) and bedded siltstone (C)	Ochrept	Chromic Cambisol	Red-Orthic Tenosol
Gleasonton	Red siltstone with drab-haloed root traces (A) over bedded red siltstone (C)	Aquent	Eutric Fluvisol	Oxyaquic Hydrosol
Hyner	Red siltstone with drab-haloed root traces (A), slickensided peds, and deep (>650 mm) calcareous nodules (Bk) over bedded red siltstone (C)	Ustert	Chromic Vertisol	Red Vertosol
Renovo	Red siltstone with root traces (A) over bedded red siltstone (C)	Fluvent	Eutric Fluvisol	Stratic Rudosol
Sproul	Dark grey shale (O) over green–grey siltstone with carbonaceous root traces (A) over grey siltstone	Saprist	Humic Gleysol	Sapric Organosol

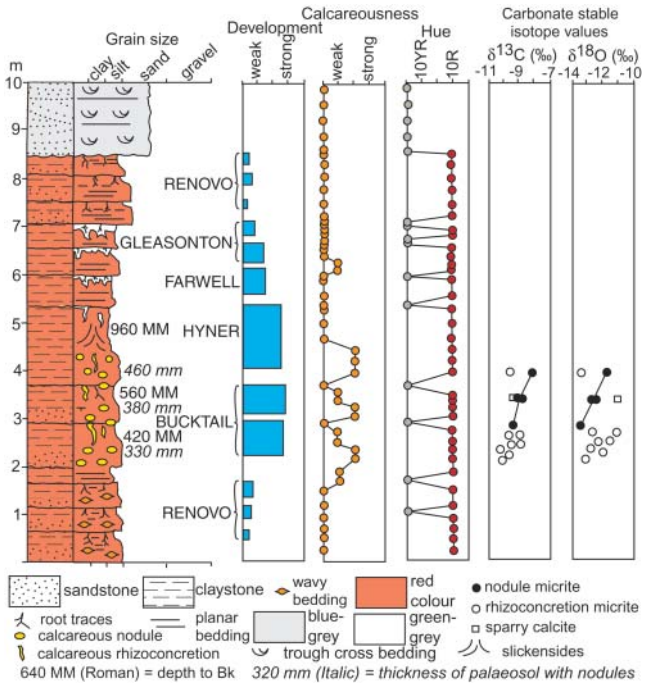

Fig. 4. Geological section of palaeosols near Newport (Fig. 1b), correlated with the Hyner deep-calcic interval because it is the first deep calcic level below the Spechty Kopf Formation capping the nearby plateau. Filled boxes show position of palaeosols by height, and degree of development (Retallack 2001) by width. Calcareousness is degree of reaction (Retallack 2001) with 10% stock HCl, and colour from a Munsell chart.

compromised by surficial erosion under palaeochannels (Cotter & Dreise 1998) or vertic displacement (Nordt *et al*. 2006; D. L. Miller *et al*. 2007), but these are not problems for palaeosols near Hyner with well-preserved soil surfaces defined by drab-haloed root traces showing no sign of microrelief formed by vertic displacement (Figs 3–5). An additional indication of palaeoprecipitation comes from chemical index of alteration ($C = 100 \times mAl_2O_3/(mAl_2O_3 + mCaO + mMgO + mNa_2O)$, in moles), which increases with mean annual precipitation (R in mm) in modern soils according to the equation

$$R = 221e^{0.0197C} \quad (2)$$

with $R^2 = 0.72$; SE $= \pm 182$ mm from Sheldon *et al*. (2002). Thickness of soil with carbonate, or distance between lowest and highest nodule in the profile (H_o in mm), also increases with mean annual range of precipitation, which is the difference in monthly mean precipitation between the wettest and driest month (M in mm), using the equation

$$M = 0.0786H_o + 13.71 \quad (3)$$

with $R^2 = 0.58$; SE $= \pm 22$ mm recalculated from Retallack (2005). Applying these climofunctions to palaeosols compacted by burial involves estimates of soil depth (D_o in equation (1)) and thickness (H_o in equation (3)) from measured palaeosol depth (D_p) and thickness (H_p), using a standard compaction algorithm

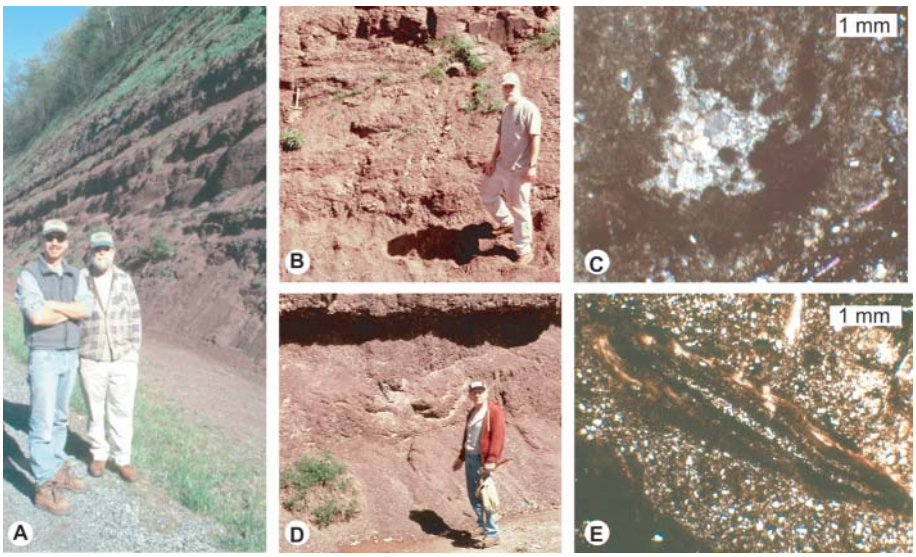

Fig. 5. Overall outcrop (**a**), with outcrop and petrographic thin sections of type Bucktail (**b**, **c**) and type Hyner pedotypes (**d**, **e**) at Hyner, Pennsylvania (Fig. 7). Bucktail palaeosols have shallow carbonate nodules (**b**) and common calcified roots (replaced by sparry calcite in (**b**)) as in Aridisols. Hyner palaeosols have bowl-shaped slickensides (**d**) and common clay skins (**e**) as in Vertisols. E. Daeschler (1.8 m) and D. Murphy (1.7 m) are scale in (**a**), D. Murphy in (**b**) and D. Rowe (1.6 m) in (**d**).

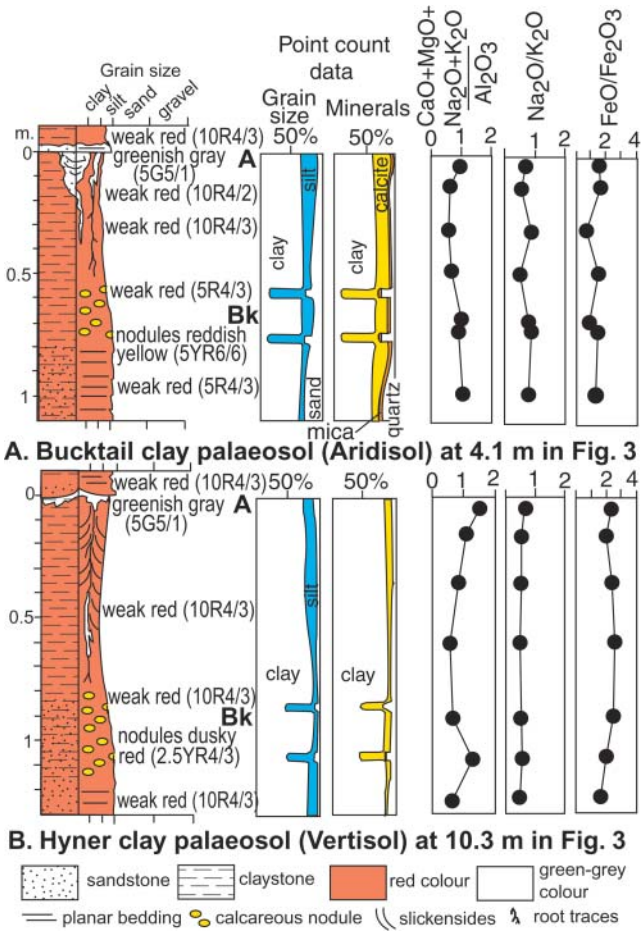

Fig. 6. Detailed sections of the type Bucktail (**a**) and type Hyner palaeosols (**b**) with selected petrographic and geochemical data indicative of subhumid to semiarid stable floodplain environments: grain size and mineral content by point counting petrographic thin sections, and chemical analyses by X-ray fluorescence with dichromate titration for ferrous iron.

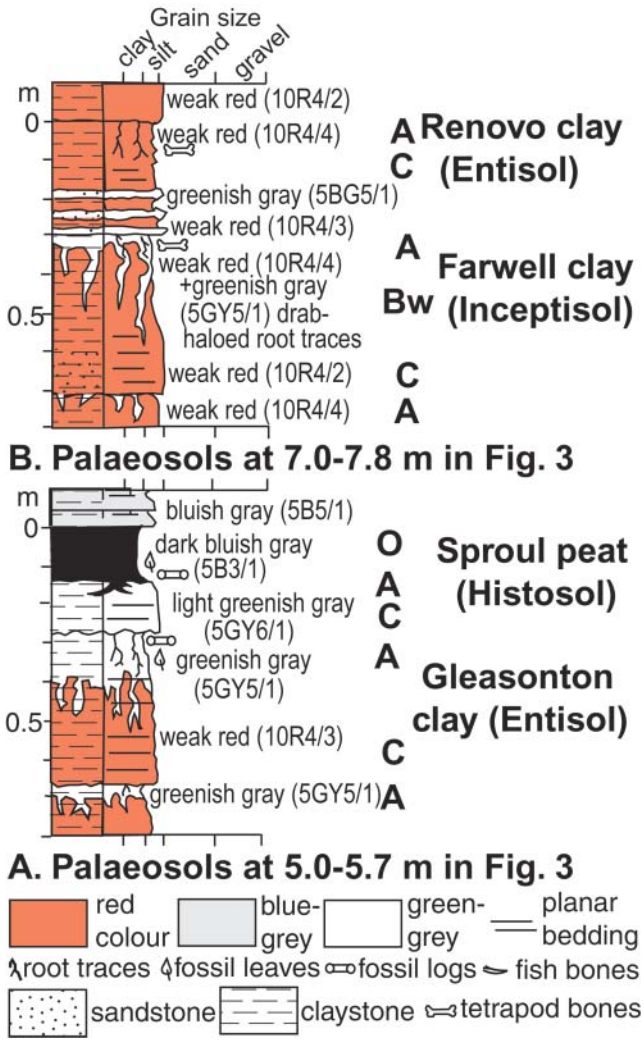

Fig. 7. Detailed sections of the Farwell, Gleasonton, Renovo and Sproul pedotypes at Hyner.

$$D_o = D_p / \left[-0.51 / \left(\frac{0.49}{e^{0.27K}} - 1 \right) \right] \quad (4)$$

(from Sheldon & Retallack 2001) for 5.2 km of overburden at Hyner (Beaumont *et al*. 1987). Higher than modern atmospheric CO_2 affects depth to carbonate nodules in soils, but an increase from 280 to 3080 ppmv modelled by McFadden & Tinsley (1985) increased depth to pedogenic carbonate only 50 mm. This correction was not made in this study.

Deriving palaeotemperature from isotopic composition of oxygen ($\delta^{18}O_c$) in soil carbonate (Veizer *et al*. 2000; Dworkin *et al*. 2005) is unreliable for these palaeosols because of metamorphic alteration of oxygen isotopic composition (Mora *et al*. 1998). A better palaeotemperature proxy for palaeosols is chemical index of clayeyness ($I = Al_2O_3/SiO_2$, as a molar ratio), which is related to mean annual temperature (T in °C) in modern soils by the equation

$$T = 46.94I + 3.99 \quad (5)$$

($R^2 = 0.96$; SE = ±0.6 °C; Sheldon 2006).

A mildly seasonal, warm temperate, semiarid to subhumid palaeoclimate can be inferred for Bucktail and Hyner palaeosols from these compaction-adjusted climofunctions (Table 3). The difference in seasonality of precipitation for Bucktail palaeosols was 32 ± 22 mm, and for Hyner palaeosols 39 ± 22 mm, from thickness of palaeosol with carbonate nodules (equation (3)). Mean annual temperature for a Bucktail palaeosol was 7.9 ± 0.6 °C, cooler than for a Hyner palaeosol (10.3 ± 0.6 °C), from clayeyness (equation (5)). Mean annual precipitation for Bucktail palaeosols was 680 ± 147 mm from depth to carbonate (equation (1)) and 822 ± 182 mm from chemical base depletion (equation (2)), but for Hyner palaeosols these values were 794 ± 147 mm and 952 ± 182 mm, respectively.

These palaeoclimatic estimates are averages for the duration of soil formation, not the traditional 30 year average used for climate. Comparison of palaeosol nodule size with that of radiocarbon-dated modern soils gives average soil-forming intervals of 4.7 ± 1.8 ka for four Bucktail palaeosols and 4.3 ± 1.8 ka for three Hyner palaeosols. These estimates are based on the relationship between carbonate-nodule diameter (S in mm) and soil age (A in ka) in modern soils from the equation

$$A = 1.799S^{0.34} \quad (6)$$

(with $R^2 = 0.57$; SE = ±1.8 ka recalculated from Retallack 2005). These were not strongly developed soils.

These palaeoclimatic estimates are neither monsoonal, nor tropical, contrary to former interpretations of the Catskill Formation (Barrell 1913; Woodrow *et al*. 1995). In contrast, temperate dry climate is evident from clayeyness of the palaeosols (Fig. 6), which indicates modest hydrolysis and gleization, but low salinization compared with that of soils in highly evaporative climates (Retallack 2001). During the latest Devonian Pennsylvania was located at a palaeolatitude of about 35°S (Fig. 2), at a time of initial Gondwanan continental glaciation (Caputo 1985).

Atmospheric CO_2

Late Devonian evolution of woodlands coincides with a long-term drawdown of atmospheric CO_2 inferred from carbon isotopic composition of pedogenic carbonate (Mora *et al*. 1996; Retallack 1997; Cox *et al*. 2001). Some local carbon isotopic variation is due to the kind of pedogenic carbonate analysed.

Table 3. *Late Devonian palaeosol interpretation*

Pedotype	Palaeoclimate	Palaeovegetation	Former animals	Palaeotopography	Parent material	Time for formation (ka)
Bucktail	MAT 7.9 ± 0.6 °C, MAP 822 ± 182 mm, MARP 32 ± 22 mm, CO_2 2009 ± 258 ppmv	Semiarid shrubland judging from root traces and profile: no plant fossils	No trace or body fossils	Dry floodplain	Quartzo-feldspathic silts	2–5
Farwell	No indication	Riparian woodland: *Archaeopteris halliana*, *Otzinachsonia beerboweri*	Myriapoda sp. indet., Scorpiones sp. indet., *Hyneria lindae*, *Ageleodus pectinatus*, *Groenlandaspis pennsylvanica*, *Hynerpeton bassetti*, *Densignathus rowei*	Fluvial levee	Quartzo-feldspathic silts	0.1–1
Gleasonton	Subhumid warm-temperate	Early successional scrub judging from root traces and profile: no plant fossils	No trace or body fossils	Fluvial levee	Quartzo-feldspathic silts	0.01–0.1
Hyner	MAT 10.3 ± 0.6 °C, MAP 952 ± 182 mm, MARP 39 ± 22 mm, CO_2 3742 ± 320 ppmv	Dry woodland judging from root traces and profile: no plant fossils	No trace or body fossils	Dry floodplain	Quartzo-feldspathic silts	2–8
Renovo	No indication	Dry early successional scrub judging from root traces and profile: no plant fossils	*Gyracanthus* sp., *Groenlandaspis pennsylvanica*, *Turrisaspis elektor*, *Phyllolepis rossimontina*, *Ageleodus pectinatus*, *Hyneria lindae*, *Sauripterus* sp.	Point bar swales and chutes	Quartzo-feldspathic silts	0.01–0.1
Sproul	No indication	*Rhacophyton ceratangium* or *Otzinachsonia beerboweri* fen, with *Archaeopteris macilenta* trees and gymnosperms	*Gigantocharinus szatmaryi*, *Orsadesmus rubecollus*, *Gyracanthus* sp., *Limnomis delaneyi*, *Hyneria lindae*, Rhizondontid sp.	Oxbow lake margin	Quartzo-feldspathic silts	0.1–0.2

MAT, mean annual temperature; MAP, mean annual precipitation; MARP, mean annual range of precipitation.

Nodular and rhizoconcretionary micrite, and spar all gave different values in the study by Driese & Mora (1993), who preferred rhizolith values. Here we analysed only micrite nodules, not spar fill (Fig. 5c), nor micritic rinds of rhizoconcretions, because nodules were the basis of the original model (Cerling 1991), and rhizolith isotopic values reported by Driese & Mora (1993) are more scattered than those of nodules near Newport (Fig. 4). Other carbon isotopic variation comes from different kinds of plants, and such isotopic heterogeneity is also known from Devonian plants (Peters-Kottig *et al*. 2006; Boyce *et al*. 2007). To evaluate this, we analysed three samples from each palaeosol. Our average isotopic values have little variance ($\pm 2\sigma$ of $\delta^{13}C$ per level of $\pm 0.3‰$), and are consistent with vegetation using the common C_3 photosynthetic pathway (Cerling 1991). A final consideration is alteration of isotopic composition during burial, judged for Devonian palaeosols of this region by Mora *et al*. (1998) to be likely for oxygen, but not for carbon isotopes.

Estimates of past atmospheric CO_2 (P_a in ppmv) come from the balance between isotopically light soil CO_2 ($\delta^{13}C_s$) compared with isotopically heavy atmospheric CO_2 ($\delta^{13}C_a$), given by the equation

$$P_a = P_r \frac{(\delta^{13}C_s - 1.0044\delta^{13}C_r - 4.4)}{(\delta^{13}C_a - \delta^{13}C_s)} \quad (7)$$

(Ekart *et al*. 1999). A variety of terms in this equation are derived from other analyses and transfer functions. The isotopic composition of soil CO_2 ($\delta^{13}C_s$) is derived from that of pedogenic carbonate ($\delta^{13}C_c$) using temperature (T in °C) dependent fractionation from the equation

$$\delta^{13}C_s = \frac{\delta^{13}C_c + 1000}{\frac{11.98 - 0.12T}{1000} + 1} - 1000 \quad (8)$$

($R^2 = 0.93$, SE= $\pm 0.28‰$; Romanek *et al*. 1992). The isotopic composition of associated soil organic matter ($\delta^{13}C_o$) is used as a proxy for respired soil CO_2 ($\delta^{13}C_r$) and also to calculate the isotopic composition of atmospheric CO_2 ($\delta^{13}C_a$) following the equation

$$\delta^{13}C_a = \frac{(\delta^{13}C_o + 18.67)}{1.1} \quad (9)$$

($R^2 = 0.91$, SE $= \pm 0.0039‰$; Arens *et al*. 2000). Finally, partial pressure of respired CO_2 in soil (P_r) is derived from its known relationship with depth to carbonate nodules (D_o, corrected for compaction in palaeosols using equation (4)) in modern soils expressed in the equation

$$P_r = 68.2D_o + 485 \quad (10)$$

($R^2 = 0.80$, SE= ± 914 ppmv; Retallack 2008).

Standard error of estimates of atmospheric CO_2 using equation (7) was calculated by Gaussian error propagation of the five component standard errors (for details of partial differential equations summed in quadrature see the Supplementary Material). The largest component of error comes from respired soil CO_2 partial pressure ($P_r \pm 914$ ppmv), but propagated error is less than that because dwarfed by averages of 10685 ppmv respired CO_2 in three Hyner pedotypes, and 7110 ppmv CO_2 in four Bucktail paleosols. Of the various carbon isotopic compositions ($\delta^{13}C$) needed for equation (7), the isotopic composition of carbonate ($\delta^{13}C_c$) was measured from the Hyner paleosols (Fig. 3). Two other quantities ($\delta^{13}C_a$ and $\delta^{13}C_r$) were derived from carbon isotopic composition of coexisting organic matter ($\delta^{13}C_o$) taken as $-27.2‰$ for the Duncannon Member of the Catskill Formation in Pennsylvania (Mora *et al*. 1996), which is lower than usual for late Devonian plants (Peters-Kottig *et al*. 2006). Palaeotemperatures and depth to carbonate were derived using equations (4) and (5).

Atmospheric CO_2 levels calculated using these equations from three Hyner palaeosols are 3742 ± 320 ppmv, but for four Bucktail palaeosols were 2009 ± 258 ppmv. These values at Hyner (Fig. 3) and comparable analyses from Newport (Fig. 4) demonstrate that atmospheric carbon dioxide levels fluctuated on Milankovitch frequencies by ± 1733 ppmV, with alternation of Hyner and Bucktail pedotypes. Furthermore, they demonstrate that atmospheric carbon dioxide levels were elevated during deposition of the tetrapod beds at Hyner compared with levels of CO_2 calculated by Mora *et al*. (1996) for the Duncannon Member of the Catskill Formation of 700–1275 ppmV.

Milankovitch cycles

Alternation of Hyner and Bucktail pedotypes indicate alternations of warm–wet–high-CO_2 palaeoclimates with cool–dry–low-CO_2 palaeoclimates analogous to Quaternary glacial–interglacial palaeoclimatic variation. Milankovitch interpretation of sedimentary cycles in Late Devonian successions of Appalachia (van Tassell 1987) was criticized by Patzkowsky *et al*. (1988) for lack of an accurate time scale and unproven palaeoclimatic connections to what could have been due to autocyclic sedimentary processes. Variation demonstrated here in mean annual precipitation, range of precipitation, temperature and atmospheric CO_2 now removes that objection. Furthermore, spectral analysis (Weedon 2005; here using XLSTAT®) of depth to carbonate in palaeosols in the Selinsgrove section now finds power peaks at frequencies corresponding to intervals of 11.8, 2.1, 1.2, 0.55 and 0.46 m (Fig. 8), which are ratios compatible with 100 ka

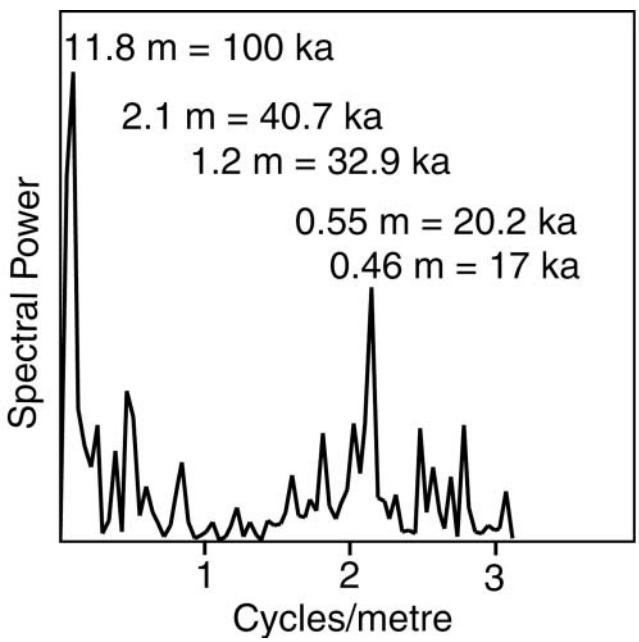

Fig. 8. Periodogram of palaeosol calcic horizon depths at Selinsgrove, Pennsylvania, interpreted as Milankovitch eccentricity (100 ka), obliquity (40.7 and 32.9 ka) and precession (20.2 and 17 ka) cycles.

eccentricity, 40.7 and 32.9 ka obliquity, and 20.2 and 17 ka precession cycles calculated for 350 Ma (by Berger *et al*. 1992). Uncertainties in these calculations back beyond 35 Ma were outlined by Laskar (1999), who regarded geological proportionalities as more reliable than theoretical calculations in deep time. Milankovitch periods are also evident from spectral analysis of gamma-ray logs of Late Devonian black shales (Algeo *et al*. 2006), although with thinner intervals in sediment-starved marine basins and in much more complete sections than the palaeochannel-rich Catskill Formation (Cotter & Driese 1998). These palaeosol-derived palaeoclimatic data confirm that Late Devonian sedimentary cycles were cued to climatic cycles on Milankovitch time scales (van Tassell 1987, 1994; Olsen 1994; Cotter & Driese 1998; Chen & Tucker 2003; Algeo *et al*. 2006), rather than purely sedimentary rhythms of stream meander or avulsion, or delta cutoffs unrelated to climatic rhythms.

Alternation of pedotypes is ubiqitous in the Catskill Formation. Among red, root-mottled, non-calcareous palaeosols of the Sherman Creek Member (Fig. 1), thick, slickensided, red Vertisols ('Irish Valley paleosol B' of Cotter *et al*. 1993: here called Selinsgrove pedotype) alternate with shallow, silty, red Inceptisols ('Irish Valley paleosol C' of Cotter *et al*. 1993: here called Durso pedotype). In the Irish Valley Member (Fig. 1), 'sandy rooted zones' (of Cotter & Driese 1998) are green–purple mottled, non-calcareous Inceptisols (described as Peas Eddy pedotype by Retallack 1985), which alternate with black lagoonal shales. This 'Irish Valley motif' was attributed by Walker & Harms (1971) and Cotter & Driese (1998) to sea-level oscillation on Milankovitch time scales. A fully developed astronomical cyclostratigraphy for the Catskill Formation would require more sections than examined (Fig. 1), as did the astronomical time scale for Plio-Pleistocene marginal marine sediments of the Wanganui Basin, New Zealand (Cooper 2004).

In addition to Milankovitch-scale palaeosol cycles there are unusual sets of palaeosols useful for regional pedostratigraphic correlation in a manner comparable with Pleistocene pedostratigraphy using geosols (Rutter *et al*. 2006). Hyner, Newport and Selinsgrove sections each have a distinctive interval of four palaeosols with medium-sized (20–50 mm diameter) and deep (650–960 mm) carbonate nodules over a considerable thickness of the palaeosol (310–440 mm), unusual for the Catskill Formation palaeosols, which mostly have smaller and shallower carbonate nodules in thinner horizons (open v. closed symbols in Fig. 1). These three attributes of carbonate horizons reflect more humid and seasonal climate and a longer time of soil formation (Retallack 2005) than usual for Catskill palaeosols. There are eight such deep-calcic intervals of 1–8 palaeosols in the unusually well-exposed Selinsgrove section (intervals A–H of Fig. 1c). Taking the upper Trimmers Rock Formation as early Frasnian and Spechty Kopf and Huntley Formation conglomerates as earliest Mississippian (Harper 1999), all the palaeosols with calcic horizon deeper than 650 mm are distributed through the Catskill Formation at Selinsgrove in clusters (A–H of Fig. 1) at unequal stratigraphic intervals, which match the spacing of Lower Kellwasser (5 m), Upper Kellwasser (8 m), Nehden (14 m), Condroz (28 m), Enkeberg (29.5 m), lower *Annulata* (44.4 m), upper *Annulata* (46 m) and Hangenberg (61 m) events (and black shales) in a composite section of the Vogelsburg, Köstenhof, and Drever quarries of Germany (Buggisch & Joachimski 2006). The coefficient of determination of this international graphic correlation is too high ($R^2 = 0.94$) to be due to chance (Fig. 1). Names of these black shale events come from European fossils and localities, but they are global in distribution (House 2002), and also are represented by splits of the Ohio and Sunbury Shales of the North American Midwest (Bjerstedt & Kammer 1988).

Our pedostratigraphic approach (Fig. 1d) correlates the Hyner tetrapod locality with the upper *Annulata* marine black shale event and its *Palmatolepis postera* conodont zone, roughly 366 Ma in the Gradstein *et al*. (2004) time scale or 363 Ma in the Buggisch & Joachimski (2006) time scale, in agreement with palynological estimates of Traverse (2003). Other temporal coincidences of deep-calcic palaeosols and black shales are at the Middle–Late and end-Permian, when high terrestrial precipitation and oceanic stagnation were consequences of transient carbon dioxide greenhouses (Retallack *et al*. 2006). Similarly, Late Devonian black shales may be consequences of short-lived ocean–atmospheric redox crises (Joachimski *et al*. 2002; Buggisch & Joachimski 2006), superimposed on long-term events such as oceanic eutrophication following the evolution and spread of forest ecosystems (Algeo *et al*. 1995; Algeo & Scheckler 1998; Ward *et al*. 2006). These redox crises were longer lived than Milankovitch-scale variation within them: the upper *Annulata* event lasted at least 4 × 100 ka beats (Figs 1 and 8), or 0.4 Ma, and was dated independently by Gradstein *et al*. (2004) at 365.8–366.1 Ma.

Taphonomy

The 41 successive palaeosols at Hyner (Figs 1a and 3), 32 palaeosols at Newport (Figs 1b and 4), and 494 palaeosols at Selinsgrove (Fig. 1c) each represent an ancient ecosystem, but not all palaeosols preserve fossils (Fig. 9). One possible factor contributing to fossil preservation at Hyner is its weakly developed palaeosols within a seasonally dry swale (Woodrow *et al*. 1995; R.L. Slingerland, pers. comm.), comparable with other productive fossil sites in Miocene fluvial deposits of Pakistan (Behrensmeyer 1987; Retallack 1991). This swale was created by avulsion, and filled with flood silt, intermittently exposed to

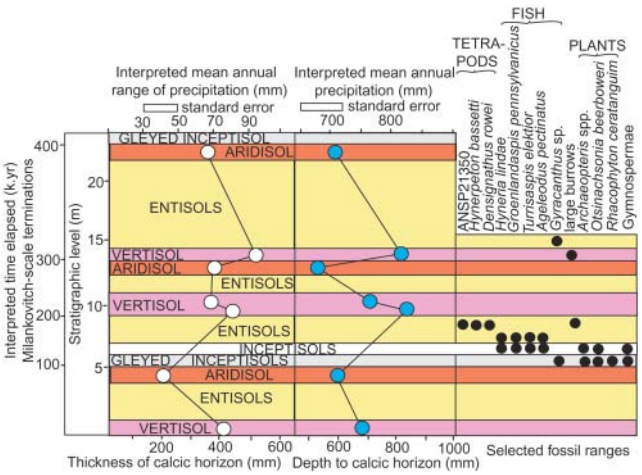

Fig. 9. Calcic horizon measurements of palaeosols at Hyner and their climatic and temporal implications, showing Milankovitch eccentricity (100 ka) palaeoclimatic fluctuation. Also shown (top axis) are estimated palaeoprecipitation and range of palaeoprecipitation, with standard error from transfer functions used. Fossil plants are partly decayed like leaf litter amid roots in growth position. Tetrapods lived here during the subhumid, not semiarid part of the palaeoclimatic cycle, in an oxbow lake (avulsion deposit) of a meandering stream system with Vertisol palaeosols.

allow formation of weakly developed palaeosols (Gleasonton, Sproul, Renovo and Farwell pedotypes). Meandering streams of wet phases of Milankovitch climate cycle alternated with braided streams of dry phases lacking such silty avulsion deposits.

Other plausible factors in fossil preservation are higher than usual seasonality of precipitation, mean annual precipitation, mean annual temperature, and atmospheric CO_2 indicated by Hyner pedotype, compared with other Catskill palaeosols (Figs 1, 3 and 9). Strongly seasonal climate and a steeper redoxocline in waterlogged soils at the greenhouse palaeoclimatic spike of the *Annulata* event would have promoted preservation of charcoal and other plant debris (Cressler 2001, 2006), and articulated arthropods (Shear 2000; Wilson *et al*. 2005) and fish (Daeschler *et al*. 2003; Friedman & Daeschler 2006) in chemically reducing and rapidly deposited increments of sediment.

Although Hyner is an exceptional fossil assemblage for the Catskill Formation (Table 1), fossil preservation within different pedotypes is typical for fossils preserved by attritional death and decay in palaeosols (Retallack 1998). Most vertebrates at Hyner are preserved within Renovo and Farwell palaeosols of the silty swale (Figs 3 and 9), with the red colour and deeply penetrating, clayey, root traces of well-drained soils (Retallack 2001). Farwell red palaeosols also preserve non-carbonaceous impressions of fossil plants. A few fossil fish in Renovo and Farwell palaeosols are articulated (Daeschler 2000*b*; Davis *et al* 2001), some partly disarticulated (Lane & Cuffey 2005), but most fish and tetrapods at Hyner are disarticulated (Thomson 1968; Downs & Daeschler 2001; Daeschler *et al*. 2003), with cracks, exposed spongy bone, and displaced splinters, like those formed by degreasing, trampling and decalcination of bone as a result of weathering on soils (Fig. 10). Stages of bone weathering have been devised for mammal bones (Behrensmeyer 1978; Cutler *et al*. 1999), which lack natural ornament (such as starburst ridges) and cartilaginous areas (Meckelian bone) of fossil fish and amphibians (Daeschler *et al*. 1994; Daeschler 2000*a*). Nevertheless, three of the four known tetrapod fossils show discernibly greater weathering on one side than the other (Fig. 10: see also colour illustrations of Clack 2006), as if they lay on the surface of a soil for months or years after death and dismemberment, and before burial. None of the tetrapods are preserved as if entombed by avulsion, flood, or other catastrophic burial.

Fossil plants (Cressler 2001, 2006) and some articulated spiders and millipedes (Shear 2000; Wilson *et al*. 2005) at Hyner

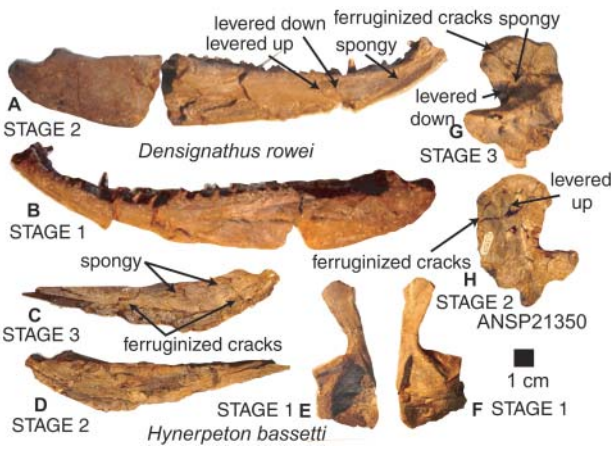

Fig. 10. Interpreted subaerial weathering features on fossil tetrapod bones at Hyner.

are preserved as carbonaceous compressions in and below the Sproul pedotype. These carbonaceous palaeosols have the drab colour and shallow carbonaceous root traces of poorly drained palaeosols (Retallack 2001). Articulated fish also have been found in Sproul palaeosols (Cressler 2006). Like fossil plants preserved in these palaeosols, these were probably buried rapidly and close to where they lived in swamps and marshes.

Palaeoecology

Detailed census of fossil plants in 'the plant layer' (5–6 m in Fig. 3) has been presented by Cressler (2006). The location of *Hynerpeton* (Farwell palaeosol at 6.8 m in Fig. 3 indicated by Woodrow *et al*. 1995) and other tetrapods (Farwell palaeosol at 7.2 m) are all from personal communication in the field with E. B. Daeschler and D. Rowe. Distributions of other fossils are from collecting by the authors and observations with D. Rowe of his local collection (Table 3).

The community of tetrapods and most other vertebrates at Hyner is represented by Farwell palaeosols, which are richly fossiliferous with curved vertical burrows 1 cm in diameter (ichnogenus *Macanopsis*), scorpions, millipedes, acanthodian fish (*Gyracanthus*), placoderm fish (*Groenlandaspis pennsylvanica*, *Turrisaspis elektor*, *Phyllolepis rossimontina*), sharks (*Ageleodus pectinatus*), lobefin fish (*Hyneria lindae*, *Sauripterus*), ray-finned fish (*Limnomis delaneyi*), and at least two tetrapod species (*Hynerpeton basseti*, *Densignathus rowei*, and an unassigned humerus). The small sharks were probably freshwater because there are no other hints of marine influence in the fauna (Downs & Daeschler 2001) or sediments, which are only locally and sparsely pyritic (Cressler 2006). Vegetation of the Farwell pedotype is represented by poorly preserved branches and leaves of progymnosperms with large leaves (*Archaeopteris halliana*) and trunks of lycopsids (*Otzinachsonia beerboweri*: Cressler & Pfefferkorn 2005). Farwell palaeosols are dark reddish grey like Renovo palaeosols, but differ in their drab-haloed root traces and less conspicuous bedding. These features reflect burial gleization of organic matter, and longer time for formation than for Renovo palaeosols (Retallack 2001). Farwell palaeosols supported broadleaf progymnosperm and swamp-lycopsid woodland of oxbow banks that were well drained and chemically oxidized for most of the year. Tetrapod-bearing Farwell palaeosols are not in themselves diagnostic of climate, but are within the wet part of the local Milankovitch-scale palaeoclimatic cycle, which extends from the base of the carbonaceous swale (Gleasonton pedotype) to the type Hyner palaeosol (Fig. 9).

Renovo palaeosols lack tetrapod and plant fossils, but contain fish fragments: acanthodian (*Gyracanthus*), placoderm (*Groenlandaspis pennsylvanica*, *Turrisaspis elektor*, *Phyllolepis rossimontina*), shark (*Ageleodus pectinatus*), and lobefin (*Hyneria lindae*, *Sauripterus*). The lamination of these weakly developed palaeosols indicates short periods of dry soil formation between floods. Their small root traces and red colour are evidence of seasonally drained, early successional vegetation, within and flanking the swale represented by the large cut-and-fill structure at Hyner (Woodrow *et al*. 1995; Cressler 2006).

Diverse, well-preserved, carbonized fossil plant impressions in Sproul palaeosols are dominated by charcoal and pyritized axes of fernlike plants (*Rhacophyton ceratangium*) of seasonally dry streamside marshes (Cressler 2001, 2006). Also found in these grey palaeosols were probably herbaceous plants (*Barinophyton obscurum*, *B. sibericum*, *Gillespiea randolphensis*) and rare woody seed ferns (cf. *Aglaosperma*). Larger plants include 3–4 mm wide lycopsid trunks (*Otzinachsonia beerboweri*) and

woody progymnosperm shoots (*Archaeopteris hibernica*, *A. obtusa* and *A. halliana*). Also found in Sproul palaeosols were spiders (*Gigantocharinus szatmaryi*) and millipedes (*Orsadesmus rubecollus*). Sproul palaeosols have the drab colour and sedimentary context of a low-lying margins of an oxbow lake that were perennially waterlogged.

Modern analogue

The suite of palaeosols near Hyner is comparable with soils of the Murray River floodplain in New South Wales, Australia, where eastern Vertisols (map unit Vc52-3a of Food and Agriculture Organization 1981) like the Hyner pedotype grade downstream to the west into Calcic Xerosols (map unit Xk40-1/2b) like the Bucktail pedotype. In Australian terminology these are Red Vertosols near Albury to the east and Calcic Calcarisols to the west of Corowa (McKenzie *et al*. 2004). Albury to the east has a mean annual temperature of 14.8 °C, a mean annual precipitation of 737 mm, and a mean annual range of precipitation of 54 mm; whereas the comparable figures for Corowa to the west are 15.7 °C, 537 mm, and 23 mm, respectively (from the website http://www.bom.gov.au/climate/averages). Vertisols near Albury to the east support woodland of yellow box (*Eucalyptus melliodora*) but Xerosols from Corowa to the west support low open woodland of green mallee (*Eucalyptus viridis*; Beadle 1981; Carnahan & Bullen 1990). Palaeoenvironments at Hyner oscillated between comparable extremes on Milankovich time scales (Fig. 9).

Although well south of monsoonal northern Australia, the Murray River before damming showed marked changes in water level, from flooding of montane snow-melt in spring to sluggish streams and ponds in summer and winter (Humphries *et al*. 1999). Late summer fires are common throughout Australia (McKenzie *et al*. 2004), and a comparable spring flush and summer burn of *Rhacophyton* is likely for carbonaceous Sproul palaeosols at Hyner (Cressler 2001). This was not the harsh, monsoonal, tropical desert envisaged for the origin of tetrapods by escape from shrinking, anoxic, or warming ponds (Romer 1933; Orton 1954; Inger 1957; Warburton & Denman 1961; Clack 2007).

Wet-season wooded floodplains would have offered Hyner tetrapods food, shelter and spawning grounds (Martin 2004). In the Australian Riverina, small (up to 0.8 m) yellow perch (*Macquaria ambigua*) spawn on seasonally flooded plains, whereas large (up to 1.8 m), predatory Murray cod (*Maccullochella peeli*) breed and live their entire life within deep river channels (Humphries *et al*. 1999; Allen *et al*. 2002). Similarly, Hyner tetrapods some 1 m long faced even larger predators of open water: 4 m long lobefins (*Hyneria lindae*: Thomson 1968) and 2 m long acanthodians (*Gyracanthus* sp.: Warren *et al*. 2000). Dry-season aquatic refuges included deep oxbow lakes and isolated reaches and swales of the main channel, which were also frequented by large predators, judging from *Hyneria* scales and *Gyracanthus* spines found with the Hyner tetrapods. Dry-season creeks in Indiana, USA, have pools with either sunfish (*Lepomis cyanellus*) or salamanders (*Ambystoma barbouri*), but seldom both, so heavy is predation from larger and faster swimming sunfish (Sih *et al*. 2000). Hyner tetrapods may have suffered this lottery of dry-season refuges, but carcasses of large predators stranded by dry-season low-water would have provided a bounty of food, in addition to larval fish, millipedes, and scorpions among the herbaceous plants of oxbow and river margins.

Preservation of tetrapods in sequences of palaeosols is not unique to Hyner. A jaw of *Metaxygnathus* was found in bone breccia overlying a floodplain palaeosol (Campbell & Bell 1977) rather than more typical fish habitats of palaeochannels, lakes and lagoons. Observations (by G.J.R.) of specimens and field photographs (J. H. Miller *et al*. 2007) of the *Tiktaalik* locality (Daeschler *et al*. 2006) confirms preservation of these skeletons in red palaeosols with drab-haloed root traces. This habitat does not necessarily indicate that these creatures crawled out on land, because Renovo and Farwell palaeosols at Hyner and floodplains of Australia also contain remains of fish stranded after floods.

Conclusions

Within the dynamic ancient landscapes revealed by palaeosols at Hyner, all the known fossil tetrapods died and were disarticulated on seasonally dry oxbow soils (Farwell pedotype), which supported wet-season herbaceous vegetation, with spiders and millipedes, and dry woodland (Fig. 11). These early tetrapod bones weathered on land along with other fish remains (Fig. 10). There is no evidence of fossil tetrapods in palaeochannels or dry floodplain soils, nor during the dry part of the Milankovitch-scale climate cycle, when vegetation was open and sparse (Fig. 12), nor in even drier conditions before and after the *Annulata* greenhouse and black shale event (Fig. 1). Thus tetrapods were found only in the first of the following four climates–ecosystems represented by Catskill palaeosols near Hyner: (1) subhumid greenhouse; (2) semiarid greenhouse; (3) semiarid non-greenhouse; (4) arid non-greenhouse.

Theories of tetrapod origins have for many years been guided by evidence from Euramerica (Fig. 2), which was interpreted as

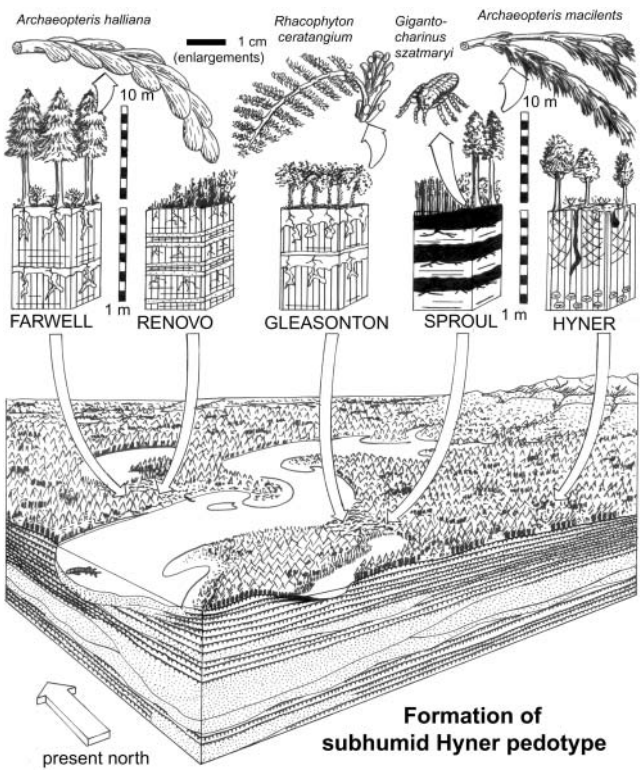

Fig. 11. Interpreted palaeosols and palaeoenvironments at Hyner during humid palaeoclimatic phases of Milankovitch eccentricity cycle: woodlands with tetrapods and other fossils preserved. Lithological symbols are as for Figure 3.

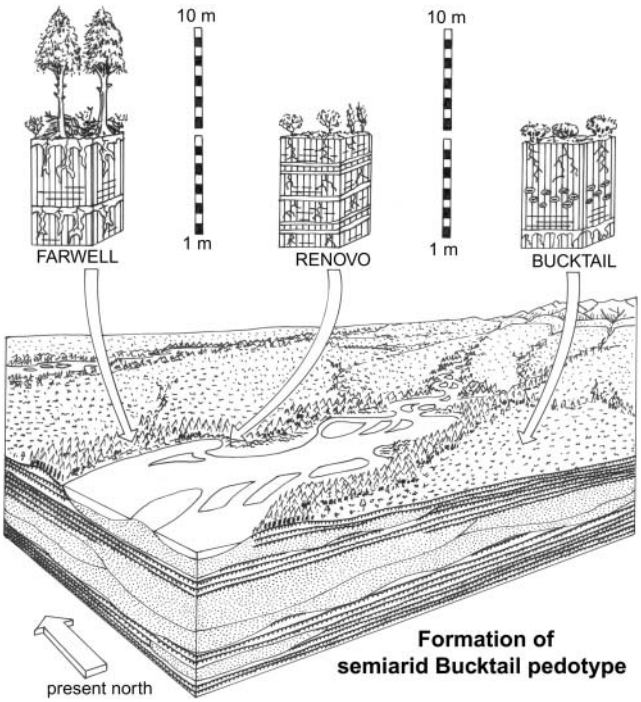

Fig. 12. Interpreted palaeosols and palaeoenvironments at Hyner during semiarid palaeoclimatic phases of Milankovitch eccentricity cycle: shrublands and riparian woodlands but few fossils of any kind preserved. Lithological symbols are as for Figure 3.

dry, monsoonal, subtropical (Barrell 1913: Woodrow *et al*. 1995). Such hot landscapes and seasonal climates were seen as selection pressures by various theories of tetrapod selection for escaping shrinking ponds (Romer 1933), digging aestivation burrows (Orton 1954), clambering over tadpoles (Warburton & Denman 1961), escaping anoxia (Inger 1957; Clack 2007) or avoiding predation (Goin & Goin 1956). Doubts about such theories came from discovery that tetrapods such as *Acanthostega* retained laterally flattened tails and other aquatic adaptations, so that their limbs were presumably used for negotiating waters choked by abundant trees and other vegetation (Clack 2002). Now evidence from palaeosols shows that at least two species of tetrapods at Hyner died and decayed in wooded floodplains of extratropical, moderately seasonal (non-monsoonal), subhumid climate, and high-CO_2 times and places (Fig. 11), not in the semiarid soilscapes of most Catskill Formation palaeosols (Fig. 12).

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