Downloaded from geology.gsapubs.org on November 30, 2010

Geology

# Rainforest collapse triggered Carboniferous tetrapod diversification in Euramerica

Sarda Sahney, Michael J. Benton and Howard J. Falcon-Lang

*Geology* 2010;38;1079-1082
doi: 10.1130/G31182.1

**Email alerting services** click www.gsapubs.org/cgi/alerts to receive free e-mail alerts when new articles cite this article

**Subscribe** click www.gsapubs.org/subscriptions/ to subscribe to Geology

**Permission request** click http://www.geosociety.org/pubs/copyrt.htm#gsa to contact GSA

Copyright not claimed on content prepared wholly by U.S. government employees within scope of their employment. Individual scientists are hereby granted permission, without fees or further requests to GSA, to use a single figure, a single table, and/or a brief paragraph of text in subsequent works and to make unlimited copies of items in GSA's journals for noncommercial use in classrooms to further education and science. This file may not be posted to any Web site, but authors may post the abstracts only of their articles on their own or their organization's Web site providing the posting includes a reference to the article's full citation. GSA provides this and other forums for the presentation of diverse opinions and positions by scientists worldwide, regardless of their race, citizenship, gender, religion, or political viewpoint. Opinions presented in this publication do not reflect official positions of the Society.

**Notes**

© 2010 Geological Society of America

THE
GEOLOGICAL
SOCIETY
OF AMERICA

# Rainforest collapse triggered Carboniferous tetrapod diversification in Euramerica

Sarda Sahney[1], Michael J. Benton[1], and Howard J. Falcon-Lang[2]*
[1]Department of Earth Sciences, University of Bristol, Bristol BS8 1RJ, UK
[2]Department of Earth Sciences, Royal Holloway, University of London, Surrey TW20 0EX, UK

## ABSTRACT

**Abrupt collapse of the tropical rainforest biome (Coal Forests) drove rapid diversification of Carboniferous tetrapods (amphibians and reptiles) in Euramerica. This finding is based on analysis of global and alpha diversity databases in a precise geologic context. From Visean to Moscovian time, both diversity measures steadily increased, but following rainforest collapse in earliest Kasimovian time (ca. 305 Ma), tetrapod extinction rate peaked, alpha diversity imploded, and endemism developed for the first time. Analysis of ecological diversity shows that rainforest collapse was also accompanied by acquisition of new feeding strategies (predators, herbivores), consistent with tetrapod adaptation to the effects of habitat fragmentation and resource restriction. Effects on amphibians were particularly devastating, while amniotes ('reptiles') fared better, being ecologically adapted to the drier conditions that followed. Our results demonstrate, for the first time, that Coal Forest fragmentation influenced profoundly the ecology and evolution of terrestrial fauna in tropical Euramerica, and illustrate the tight coupling that existed between vegetation, climate, and trophic webs.**

## INTRODUCTION

During the latter part of the Carboniferous (318–299 Ma), Europe and North America (Euramerica) were positioned over the equator, and were covered, at times, by humid tropical rainforest (DiMichele et al., 2007). This biome, colloquially referred to as the Coal Forests, comprised a heterogeneous vegetation mosaic (Gastaldo et al., 2004) inhabited by a rich terrestrial fauna (Falcon-Lang et al., 2006). As climate aridified through the later Paleozoic, these rainforests collapsed, eventually being replaced by seasonally dry Permian biomes (Montañez et al., 2007). Collapse occurred through a series of step changes. First there was a gradual rise in the frequency of opportunistic ferns in late Moscovian time (Pfefferkorn and Thomson, 1982). This was followed in the earliest Kasimovian (cyclothem-calibrated age of 305.4 Ma; Heckel, 2008) by a major, abrupt extinction of the dominant K-selected lycopsids and a switch to tree-fern dominance (DiMichele and Phillips, 1996). In latest Kasimovian time, rainforests vanished (DiMichele et al., 2006).

The nature and cause of late Moscovian-Kasimovian rainforest collapse have been the subjects of intense investigation. In cratonic areas of North America (where the effects of tectonics can be excluded), an abrupt shift to more arid climates has been linked to rainforest collapse (DiMichele et al., 2009, 2010), though the exact causal mechanism remains uncertain. One hypothesis is that aridification was triggered by a short-term but intense glacial phase. This is supported by earliest Kasimovian paleosols in the Lost Branch cyclothem that show that sea level dropped to its one of its lowest levels in the entire Pennsylvanian, if not its lowest level (Heckel, 1991, 2008), precisely coincident with the most abrupt phase of vegetation change (DiMichele et al., 2009). An alternative hypothesis is that medium-term greenhouse warming drove aridification, as supported by far-field records in Gondwana (Fielding et al., 2008) and evaporites in highstand deposits in western Euramerica (Bishop et al., 2010). However, regardless of what caused aridification, the consensus is that this climate shift led to the fragmentation of the Coal Forests into isolated rainforest islands surrounded by xerophytic scrub (Falcon-Lang, 2004; Falcon-Lang et al., 2009; Falcon-Lang and DiMichele, 2010).

At the time of peak levels of rainforest dieback in the earliest Kasimovian, terrestrial faunas had already become highly diversified, composing sophisticated interconnected communities (Falcon-Lang et al., 2006). Detritivory was the most common primary feeding strategy utilized by annelids, molluscs, and arthropods, including the giant litter-splitting arthropleurids (Shear and Kukaloveck, 1990; Labandeira, 2006). However, some insects had additionally evolved herbivorous and predatory forms (Labandeira and Sepkoski, 1993; Grimaldi and Engel, 2005). Terrestrial vertebrates (tetrapods), which included amphibians and basal amniotes ('reptiles'), were mostly piscivores, reflecting their dominantly waterside habitats, but some forms also had evolved insectivory (Benton, 2005; Coates et al., 2008). Here we analyze the effects of rainforest collapse on tetrapod communities. Specifically we test the hypothesis that population constriction into isolated rainforest islands exerted a major impact on tetrapod diversity, ecology, and the development of endemism. In doing so, we draw on the theory of island biogeography (MacArthur and Wilson, 1967), which was developed to explain patterns of diversification in oceanic islands, but is equally applicable to other kinds of islands, e.g., rainforest refugia.

## METHODS: LATE PALEOZOIC TETRAPOD DATABASE

In order to detect changes in tetrapod diversity across the Moscovian-Kasimovian interval, we constructed two late Paleozoic tetrapod databases, comprising records of global and alpha diversity over nine global stages (Visean, Serpukhovian, Bashkirian, Moscovian, Kasimovian, Gzhelian, Asselian, Sakmarian, and Artinskian) ranging from 346 to 270 Ma. We chose to restrict the analysis to this time span because the bracketing Tournaisian and Kungurian stages were times of very low diversity, which have been interpreted as mass extinctions or gaps in the record, i.e., Romer's gap and/or bottleneck (Ward et al., 2006) and Olson's gap and/or extinction, respectively (Sahney and Benton, 2008).

### Global Diversity Database

Initially 67 families from 163 tetrapod sites worldwide were tabulated to create the global diversity database. Analysis was run with all of the families and then was repeated after removing 14 monotypic families, those represented by only a single species. The inclusion or exclusion of singletons made no difference to the results as they are randomly distributed through the time bins and the overall diversity patterns remained the same. Stratigraphic ranges were assigned to each family and the associated dates were correlated with the Davydov et al. (2010) time scale.

Each family was also given an ecological assignment based on size (snout-vent length; small: <0.15 m, medium: 0.15–1.50 m, large: >1.50 m) and diet (fish, insects, tetrapods, plants), resulting in 12 ecological niches. Diet was inferred from jaw and tooth structure, patterns of tooth wear, body size, and whether the animal was adapted for a predominantly aquatic or terrestrial lifestyle (Benton, 1996). Occasionally, direct evidence in the form of gut contents was available, e.g., conifer and pteridosperm

---

*E-mail: h.falcon-lang@es.rhul.ac.uk.

---

*Geology*, December 2010; v. 38; no. 12; p. 1079–1082; doi: 10.1130/G31182.1; 3 figures; 1 table.

ovules in the Permian reptile, *Protorosaurus* (Munk and Sues, 1992).

### Alpha Diversity Database

Community data, compiled in the alpha diversity database, were constructed as a subset of the global database, containing the most complete tetrapod assemblages available. Individual assemblages were selected based on the occurrence of >100 partial skeletons at a given site and, where possible, collector curves were used to assess completeness of these assemblages. After filtering, the database contained 22 well-sampled assemblages.

Although variably time averaged, we assumed that each assemblage was representative of a local community (sensu Begon et al., 2005). The number of families represented in each community was tabulated, based on published assignments (supplemental databases: global diversity database—http://www.fossilrecord.net/fossilrecord/download.html; alpha diversity database—http://palaeo.gly.bris.ac.uk/Sahney/pub/index.html) as a proxy for alpha (community) diversity. Communities were binned by stage, and assigned an average age (based on Davydov et al., 2010), to construct an alpha diversity curve.

### Data Distribution and Analysis

The global (n = 163) and alpha (n = 22) data sets were plotted on a Kasimovian paleogeographic map, demonstrating that ~97% of records derived from the paleoequatorial zone and therefore intensively sample a single region. Stratigraphic analysis shows that data sets are evenly spread through the study interval, and for each time bin, data sets are evenly distributed west and east of the Appalachians that divided the paleoequatorial zone (Fig. 1).

Global and alpha curves were plotted to analyze the separate diversification patterns as well as to calculate the degree of endemism (sometimes termed beta diversity, BD). Endemism is calculated by dividing global diversity ($T_t$) by mean alpha diversity ($\bar{T}$) (BD = $T_t/\bar{T}$; Sepkoski, 1988).

## RESULTS: TETRAPOD DIVERSIFICATION PATTERNS

Several patterns emerge from our analysis. First, global diversity steadily rose through the study interval from 6 to 7 families in the Visean and Serpukhovian to 39 families in the Artinskian (Fig. 2A). However, while alpha diversity closely tracked global diversity until the late Moscovian (i.e., Nyrany and Linton alpha sites), the two curves dramatically diverged across the Moscovian-Kasimovian boundary as alpha diversity collapsed from 20 families to 7 families (Fig. 2A).

Analysis of the rates of alpha and global diversification helps explain this divergence. Although the global diversification rate slowed across the Moscovian-Kasimovian boundary, the rate became strongly negative at the alpha (community) level, the only time when either rate of diversification became negative in the nine stages, reflecting the fact that communities shrank in size, i.e., an "alpha implosion" (Fig. 2B).

There is only one way to reconcile such a rise in global diversity at a time when alpha diversity was falling: the degree of endemism must have risen markedly between the Moscovian and Kasimovian-Gzhelian intervals. Calculations confirm that this is the case. The development of endemism peaked in Kasimovian-Gzhelian time, with the highest levels of endemism occurring in the following Asselian stage, before falling back to mid-Carboniferous levels by the Artinskian (Fig. 2C).

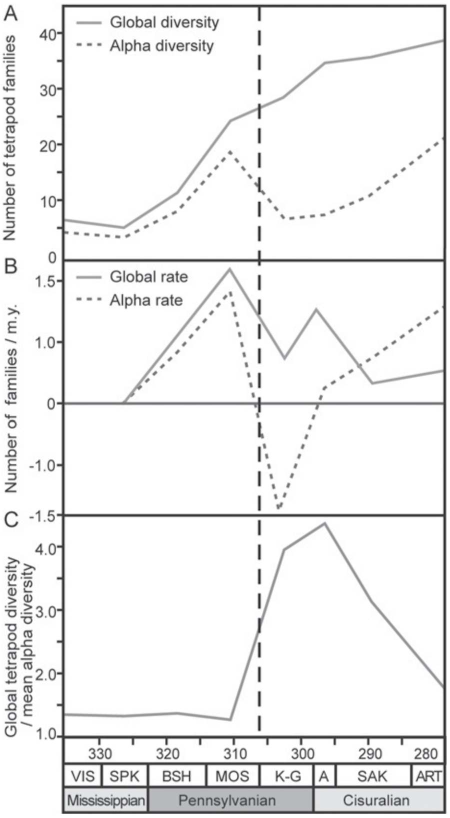

**Figure 2. Tetrapod diversification patterns from Visean (346 Ma) to Artinskian (270 Ma). A: Global diversity of tetrapods and alpha diversity. B: Alpha and global diversification rates measured as first derivative of values in A. C: Endemism measured as global diversity ($T_t$) divided by mean alpha diversity ($\bar{T}$) (Sepkoski, 1988). Vertical dotted line highlights Moscovian-Kasimovian boundary. Time scale after Davydov et al. (2010). Abbreviations as in Figure 1.**

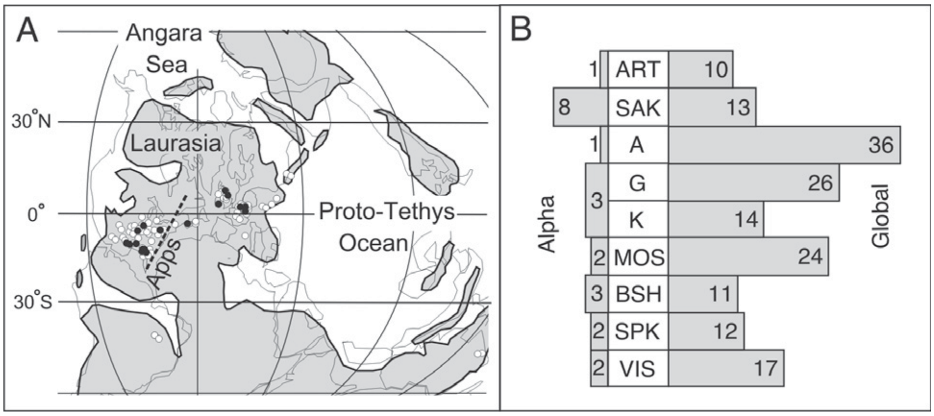

**Figure 1. Data distribution. A: By paleogeography (300 Ma; after Scotese and McKerrow, 1990). B: By stratigraphy. Open circles are global data and closed circles are alpha data. VIS—Visean; SPK—Serpukhovian, BSH—Bashkirian, MOS—Moscovian, K—Kasimovian, G—Gzhelian, A—Asselian, SAK—Sakmarian, ART—Artinskian, Apps—Appalachians.**

A complementary picture of diversification is expressed by the ecological diversity data. The number of ecological niches occupied by tetrapods increased from four in the Visean to nine by the Asselian and, although piscivores and insectivores of most sizes were diverse in pre-Kasimovian strata, there were no confirmed carnivores or herbivores. Following the Moscovian-Kasimovian boundary, a diversity of medium and large carnivores (9%) and herbivores (5%) evolved, resulting in a more modern proportioning of diet ratios (Fig. 3A). Ecological diversification was especially marked among reptiles, which occupied eight niches, seven of which were gained after the implosion, compared to only one gained by amphibians (Table 1).

## DISCUSSION: RAINFOREST COLLAPSE AND TETRAPOD EVOLUTION

It is now well established that climate fluctuations profoundly influenced Carboniferous Coal Forests (Montañez et al., 2007). In earliest Kasimovian time, an extreme glacial phase (Heckel, 1991) or greenhouse warming (Bishop et al., 2010) led to hyperconstriction of the Coal Forests and fragmentation into rainforest islands, a state from which they never fully

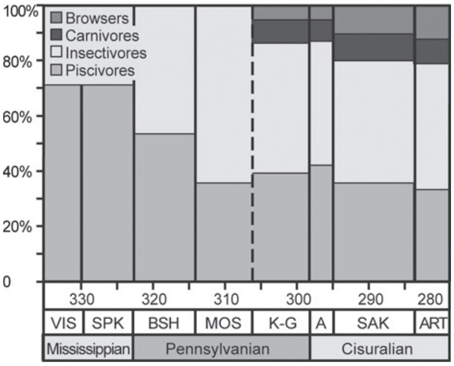

**Figure 3. Global ecological diversity of tetrapods from Visean (346 Ma) to Artinskian (270 Ma). Time scale after Davydov et al. (2010). Abbreviations as in Figure 1.**

recovered (DiMichele et al., 2009). By the end of the Kasimovian, Coal Forest remnants were restricted to tiny wet spots in a seasonally dry landscape (DiMichele et al., 2006). Patterns of tetrapod diversity identified here are best explained in terms of a population response to this habitat fragmentation.

The impact of habitat fragmentation on diversification was first highlighted by MacArthur and Wilson's (1967) theory of oceanic island biogeography. However, this concept can be extended to explain any ecosystem surrounded by differing ecosystems, whether it comprises rainforest refugia or landscapes altered by humans (e.g., traffic island biogeography; Whitmore et al., 2002). The initial impact of fragmentation is usually devastating, with most life rapidly dying out from restrictions on resources. Then, as animals reestablish themselves, they adapt to their restricted environment to take advantage of the new allotment of resources. Thus, our data, which show elevated extinction rates, increased endemism, and ecological diversification, apparently represent a classic community-response to habitat fragmentation, as discussed in the following.

## Tetrapod Taxonomic Diversity

Taxonomic analysis of our data reveals important subtleties not evident from inspection of diversity curves alone. Ecosystems that developed prior to rainforest collapse were highly cosmopolitan and dominated by amphibian groups that had evolved in the Mississippian (Benton, 2005; Coates et al., 2008). Key taxa included temnospondyls (small- to large-sized fish eaters with broad, flat skulls), lepospondyls (small, aquatic nectrideans and terrestrial microsaurs, some of which fed on insects), and reptiliomorphs (mostly terrestrial anthracosaurs). In Bashkirian time, this latter clade also gave rise to the first amniotes ('reptiles').

The abrupt alpha implosion in the Kasimovian-Gzhelian interval (Fig. 2) appears to have been selective, with amphibians hardest hit. Globally, amphibians that became extinct at the Moscovian-Kasimovian boundary included the basal tetrapod families Baphetidae and Colosteidae, the microsaur families Microbrachidae, Hyloplesiontidae, and Odonterpetontidae, the temnospondyl family Dendrerpetontidae, and the reptiliomorph families Gephyrostegidae, Anthracosauridae, and Solenodonsauridae. Although three of these families were represented by a single taxon, the other six were more diverse. Origination of 10 new amphibian families in the Kasimovian-Gzhelian interval, including the temnospondyl families Eryopidae, Trematopidae, and Trimerorhachidae, balanced these losses, but the distribution of new taxa was endemic, not cosmopolitan, as earlier.

By contrast, amniotes underwent no loss of families, continuing to diversify into the Artinskian. In particular, the Ophiacodontidae, and related basal synapsid families, dominated Early Permian terrestrial red bed assemblages. The relative success of amniotes following rainforest collapse probably reflects their two unique adaptations, i.e., hard-shelled eggs that could be laid on dry land and protective scales that helped retain moisture; these key adaptations freed them from the aquatic habitats to which amphibians were tied and gave them ecologic advantage in the widespread drylands that developed, beginning in late Pennsylvanian time (Falcon-Lang et al., 2007).

## Tetrapod Ecological Diversity and Diet

The marked ecological diversification following rainforest collapse was also highly selective, with reptiles preferentially moving into new niches. Although global familial diversity of amphibians was several times larger than for reptiles (by the Artinskian this gap was less, but there were still 28 amphibian families compared to 11 reptile families), the ecological diversity of reptiles was much greater, with some families occupying multiple niches (Table 1). Amphibians maximally occupied six ecological niches after the alpha implosion, while reptiles occupied eight, seven of which were gained after the implosion, compared to only one by amphibians.

This ecological shift was primarily related to diet. Pre-Kasimovian amphibians and reptiles largely fed on fish (~70%), presumably reflecting the aquatic origin of tetrapods, while the proportion of insectivores gradually increased through this interval, reflecting greater insect abundance, size, and diversity. However, following rainforest collapse, diet ratios changed markedly. While amphibians continued to feed on fish and insects, reptiles began exploring two new food types, tetrapods (carnivory), and later, plants (herbivory). This ecological diversification reflected adaptations by tetrapods to maximize acquisition of limited resources in a fragmented habitat.

TABLE 1. NICHES, A COMBINATION OF DIET AND BODY SIZE OCCUPIED BY AMPHIBIANS AND "REPTILES" BEFORE AND AFTER THE ALPHA IMPLOSION

| | Piscivores | | | Insectivores | | | Browsers | | | Predators | | | Total niches | Total families |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | S | M | L | S | M | L | S | M | L | S | M | L | | |
| BAS-MOS amphibians | Y | Y | Y | Y | Y | | | | | | | | 5 | 23 |
| K-G amphibians | Y | Y | Y | Y | Y | | | | | | | Y | 6 | 24 |
| BAS-MOS reptiles | Y | | | | | | | | | | | | 1 | 2 |
| K-G reptiles | Y | Y | | | Y | | Y | Y | Y | | Y | Y | 8 | 5 |

*Note:* S—small; M—medium; L—large; BAS-MOS—Bashkirian-Moscovian; K-G—Kasimovian-Gzhelian.

Carnivory was a natural transition from insectivory for medium and large tetrapods, and it required minimal adaptation. In contrast, a complex set of adaptations was necessary for feeding on highly fibrous plant materials, requiring structural modifications to the teeth, jaws, and digestive tract as well as formation of endosymbiotic relationships with microbes to aid in digestion (Sues and Reisz, 1998). Only a small proportion of extant tetrapods are obligate herbivores. Many extant carnivores also consume low-fiber plant material as well as insects and fish (e.g., bears), so it could be that early tetrapods made the transition to fully fledged herbivory by way of omnivory.

Kasimovian-Gzhelian tetrapods that fed on high-fiber plants include *Diadectes* and *Edaphosaurus*. In Early Permian time, several distantly related lineages of amniotes were completely herbivorous, including the Caseidae and the widespread Captorhinidae. Herbivory emerged independently in several lineages in the Kasimovian-Gzhelian and Permian (Sues and Reisz, 1998), which is consistent with convergent evolution within a fragmented habitat. A similarly marked increase in the incidence of herbivory is also seen among arthropods in the Kasimovian-Gzhelian, and an additional factor governing this change may have been the rise to dominance by tree ferns, which were relatively cheaply constructed and therefore more digestible (Labandeira, 2006).

## Paleoenvironmental Data

Our hypothesis that Coal Forest collapse drove tetrapod diversification is confirmed by facies analysis of tetrapod-bearing sites. The most complete assemblages preceding the earliest Kasimovian event (Joggins, Jarrow, Newsham, Linton, and Nyrany) are all associated with coal-bearing successions. Specifically, all occur in sedimentary deposits formed under humid interglacial climates when Coal Forests were at their maximum areal extent (Falcon-Lang and DiMichele, 2010), comprising a new continuous belt from Kansas to Kazakhstan. In contrast, the only substantially represented late Kasimovian tetrapod community (Hamilton) is associated with a rainforest island surrounded by seasonally dry biomes, following initial Coal Forest fragmentation. Gzhelian and Early Permian environments comprised even more widespread seasonally dry areas with highly fragmentary habitats in which communities were restricted to small isolated wet spots (DiMichele et al., 2006).

## ACKNOWLEDGMENTS

Sahney appreciates Paul Ferry's continued technical support. Benton is supported by Natural Environment Research Council (NERC) grant NE/C518973/1, and Falcon-Lang by NERC Advanced Postdoctoral Fellowship NE/F014120/2.

## REFERENCES CITED

Begon, M., Townsend, C.R., and Harper, J.L., 2005, Ecology: From individuals to ecosystems: Oxford, UK, Blackwell Publishing, 752 p.

Benton, M.J., 1996, Testing the roles of competition and expansion in tetrapod evolution: Royal Society of London Proceedings, ser. B, v. 263, p. 641–646, doi: 10.1098/rspb.1996.0096.

Benton, M.J., 2005, Vertebrate palaeontology (third edition): Oxford, UK, Blackwell, 472 p.

Bishop, J.W., Montanez, I.P., and Osleger, D.A., 2010, Dynamic Carboniferous climate change, Arrow Canyon, Nevada: Geosphere, v. 6, p. 1–34, doi: 10.1130/GES00192.1.

Coates, M.I., Ruta, M., and Friedman, M., 2008, Ever since Owen: Changing perspectives on the early evolution of tetrapods: Annual Review of Ecology Evolution and Systematics, v. 39, p. 571–592, doi: 10.1146/annurev.ecolsys.38.091206.095546.

Davydov, V.I., Crowley, J.L., Schmitz, M.D., and Poletaev, V.I., 2010, High-precision U-Pb zircon age calibration of the global Carboniferous time scale and Milankovitch-band cyclicity in the Donets Basin, eastern Ukraine: Geochemistry, Geophysics, Geosystems, v. 11, Q0AA04, doi: 10.1029/2009GC002736.

DiMichele, W.A., and Phillips, T.L., 1996, Climate change, plant extinctions and vegetational recovery during the Middle-Late Pennsylvanian transition: The case of tropical peat-forming environments in North America, *in* Hart, M.B., ed., Biotic recovery from mass extinction events: Geological Society of London Special Publication 102, p. 201–221.

DiMichele, W.A., Tabor, N.J., Chaney, D.S., and Nelson, W.J., 2006, From wetlands to wet spots: Environmental tracking and the fate of Carboniferous elements in Early Permian tropical floras, *in* Greb, S.F., and DiMichele, W.A., eds., Wetlands through time: Geological Society of America Special Paper 399, p. 223–248, doi: 10.1130/2006.2399(11).

DiMichele, W.A., Falcon-Lang, H.J., Nelson, J., Elrick, S., and Ames, P., 2007, Ecological gradients within a Pennsylvanian forest: Geology, v. 35, p. 415–418, doi:10.1130/G23472A.1.

DiMichele, W.A., Montanez, I.P., Poulsen, C.J., and Tabor, N., 2009, Climate and vegetational regime shifts in the late Paleozoic ice age earth: Geobiology, v. 7, p. 200–226, doi: 10.1111/j.1472-4669.2009.00192.x.

DiMichele, W.A., Cecil, B., Montanez, I.P., and Falcon-Lang, H.J., 2010, Cyclic changes in Pennsylvanian paleoclimate and it effects on floristic dynamics in tropical Pangaea: International Journal of Coal Geology, v. 83, p. 329–344, doi: 10.1016/j.coal.2010.01.007.

Falcon-Lang, H.J., 2004, Pennsylvanian tropical rainforests responded to glacial-interglacial rhythms: Geology, v. 32, p. 689–692, doi: 10.1130/G20523.1.

Falcon-Lang, H.J., and DiMichele, W.A., 2010, What happened to the Coal Forests during glacial phases?: Palaios, v. 25, p. 611–617, doi: 10.2110/palo.2009.p09-153r.

Falcon-Lang, H.J., Benton, M.J., Braddy, S.J., and Davies, S.J., 2006, The Pennsylvanian tropical biome reconstructed from the Joggins Formation of Canada: Geological Society of London Journal, v. 163, p. 561–576, doi: 10.1144/0016-764905-063.

Falcon-Lang, H.J., Benton, M.J., and Stimson, M., 2007, Ecology of earliest reptiles inferred from basal Pennsylvanian trackways: Geological Society of London Journal, v. 164, p. 1113–1118, doi: 10.1144/0016-76492007-015.

Falcon-Lang, H.J., Nelson, J., Elrick, S., Looy, C., Ames, P., and DiMichele, W.A., 2009, Incised valley-fills containing conifers imply that seasonally-dry vegetation dominated Pennsylvanian lowlands: Geology, v. 37, p. 923–926, doi: 10.1130/G30117A.1.

Fielding, C.R., Frank, T.D., Birgenheier, L.P., Rygel, M.C., Jones, A.T., and Roberts, J., 2008, Stratigraphic imprint of the Late Palaeozoic Ice Age in eastern Australia: A record of alternating glacial and nonglacial climate regime: Geological Society of London Journal, v. 165, p. 129–140, doi: 10.1144/0016-76492007-036.

Gastaldo, R.A., Stevanovic-Walls, I.M., Ware, W.N., and Greb, S.F., 2004, Community heterogeneity of Early Pennsylvanian peat mires: Geology, v. 32, p. 693–696, doi: 10.1130/G20515.1.

Grimaldi, D., and Engel, M.S., 2005, Evolution of the insects: New York, Cambridge University Press, 772 p.

Heckel, P.H., 1991, Lost Branch Formation and revision of upper Desmoinesian stratigraphy along midcontinent Pennsylvanian outcrop belt: Kansas Geological Survey Geology Series, v. 4, 67 p.

Heckel, P.H., 2008, Pennsylvanian cyclothems in Midcontinent North America as far-field effects of waxing and waning of Gondwana ice sheets, *in* Fielding, C.R., et al., eds., Resolving the late Paleozoic ice age in time and space: Geological Society of America Special Paper 441, p. 275–289, doi: 10.1130/2008.2441(19).

Labandeira, C.C., 2006, The four phases of plant-arthropod associations in deep time: Geológica Acta, v. 4, p. 409–438.

Labandeira, C.C., and Sepkoski, J.J., Jr., 1993, Insect diversity in the fossil record: Science, v. 261, p. 310–315, doi: 10.1126/science.11536548.

MacArthur, R.H., and Wilson, E.O., 1967, The theory of island biogeography: Princeton, New Jersey, Princeton University Press, 203 p.

Montañez, I.P., Tabor, N.J., Niemeier, D., DiMichele, W.A., Frank, T.D., Fielding, C.R., Isbell, J.L., Birgenheier, L.P., and Rygel, M.C., 2007, CO$_2$-forced climate and vegetation instability during late Paleozoic deglaciation: Science, v. 315, p. 87–91, doi: 10.1126/science.1134207.

Munk, W., and Sues, H.-D., 1992, Gut contents of *Parasaurus* (Pareiasauria) and *Protorosaurus* (Archosauromorpha) from the Kupferschiefer (Upper Permian) of Hessen, Germany: Paläontologische Zeitschift, v. 67, p. 169–176.

Pfefferkorn, H.W., and Thomson, M.C., 1982, Changes in dominance patterns in Upper Carboniferous plant fossil assemblages: Geology, v. 10, p. 641–644, doi:10.1130/0091-7613(1982)10<641:CIDPIU>2.0.CO;2.

Sahney, S., and Benton, M.J., 2008, Recovery from the most profound mass extinction of all time: Royal Society of London Proceedings, ser. B, v. 275, p. 759–765, doi: 10.1098/rspb.2007.1370.

Scotese, C.R., and McKerrow, W.S., 1990, Revised world map and introduction, *in* McKerrow, W.S., and Scotese, C.R., eds., Palaeozoic palaeogeography and biogeography: Geological Society of London Memoir 12, p. 1–21.

Sepkoski, J.J., 1988, Alpha, beta, or gamma—Where does all the diversity go?: Paleobiology, v. 14, p. 221–234.

Shear, W.A., and Kukaloveck, J., 1990, The ecology of Paleozoic terrestrial arthropods: The fossil evidence: Canadian Journal of Zoology, v. 68, p. 1807–1834, doi: 10.1139/z90-262.

Sues, H.D., and Reisz, R.R., 1998, Origins and early evolution of herbivory in tetrapods: Trends in Ecology & Evolution, v. 13, p. 141–145, doi: 10.1016/S0169-5347(97)01257-3.

Ward, P., Labandeira, C., Laurin, M., and Berner, R.A., 2006, Confirmation of Romer's Gap as a low oxygen interval constraining the timing of initial arthropod and vertebrate terrestrialization: National Academy of Sciences Proceedings, v. 103, p. 16,818–16,822, doi: 10.1073/pnas.0607824103.

Whitmore, C., Crouch, T.E., and Slotow, R.H., 2002, Conservation of biodiversity in urban environments: Invertebrates on structurally enhanced road islands: African Entomology, v. 10, p. 113–126.

Manuscript received 3 March 2010
Revised manuscript received 30 June 2010
Manuscript accepted 1 July 2010

Printed in USA