The diversification of Paleozoic fire systems and fluctuations in atmospheric oxygen concentration

Andrew C. Scott*†‡ and Ian J. Glasspool†§

*Department of Geology, Royal Holloway University of London, Egham, Surrey TW20 0EX, United Kingdom; and §Department of Geology, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605

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By comparing Silurian through end Permian [≈250 million years (Myr)] charcoal abundance with contemporaneous macroecological changes in vegetation and climate we aim to demonstrate that long-term variations in fire occurrence and fire system diversification are related to fluctuations in Late Paleozoic atmospheric oxygen concentration. Charcoal, a proxy for fire, occurs in the fossil record from the Late Silurian (≈420 Myr) to the present. Its presence at any interval in the fossil record is already taken to constrain atmospheric oxygen within the range of 13% to 35% (the "fire window"). Herein, we observe that, as predicted, atmospheric oxygen levels rise from ≈13% in the Late Devonian to ≈30% in the Late Permian so, too, fires progressively occur in an increasing diversity of ecosystems. Sequentially, data of note include: the occurrence of charcoal in the Late Silurian/Early Devonian, indicating the burning of a diminutive, dominantly rhyniophytoid vegetation; an apparent paucity of charcoal in the Middle to Late Devonian that coincides with a predicted atmospheric oxygen low; and the subsequent diversification of fire systems throughout the remainder of the Late Paleozoic. First, fires become widespread during the Early Mississippian, they then become commonplace in mire systems in the Middle Mississippian; in the Pennsylvanian they are first recorded in upland settings and finally, based on coal petrology, become extremely important in many Permian mire settings. These trends conform well to changes in atmospheric oxygen concentration, as predicted by modeling, and indicate oxygen levels are a significant control on long-term fire occurrence.

Earth system processes | global change | coal | charcoal | inertinite

Over geologic time, fluctuations in atmospheric oxygen (hereafter O_2) levels have influenced biological evolution and had an integral role in the feedback mechanisms governing Earth's biogeochemical cycles (1). During the Late Paleozoic when terrestrial vegetation underwent its greatest diversification and radiated into most of its current ecological niches (2) O_2 levels are predicted to have changed dramatically (Fig. 1). From a high in the Late Silurian–Early Devonian, O_2 levels are predicted to have fallen to ≈13% in the early Late Devonian before beginning to rise steadily by the end Devonian. This rise is predicted to have occurred more or less steadily, crossing the present atmospheric level (PAL) of 21% by the mid-Mississippian and continuing through the rest of the Carboniferous and Permian, peaking at 30% in the early Guadalupian. From then, O_2 levels are predicted to have crashed to <13% by the Early Jurassic (3). Such fluctuations are expected to have had a dramatic effect on the development of fire systems. Predictions of the degree to which O_2 fluctuated are based on data-driven models (3, 4). However, the complexity of the feedback mechanisms that govern O_2 levels results in a large degree of uncertainty in these models, as is evident in their frequent refinement (e.g., refs. 1, 3, and 4). Additional data sets are invaluable to these refinements.

Fire ignition requires a source of fuel, heat, and oxygen, whereas its propagation also depends on climate (weather) and topography (5). Experimental data (6–10) provide the following observations about O_2 levels and fire in the fossil record: At levels <13%, except under exceptional circumstances, wildfires will not ignite and spread irrespective of moisture content (7). Between 13% and 16% fires would be rare and would only burn very dry plant material. Ecologically, only vegetation growing in environments liable to drying would burn. Between 18% and 23% fire occurrences would be similar to those under the PAL of 21%, where plant matter (fuel) must have low moisture content; dry seasons help to effect this decline in fuel moisture and permit the rapid spread of the flame front and fire propagation (11). At >25% fires would become widespread, especially in wetter climatic areas, because of the prevalence of lightning strikes. At levels >30% fire activity would be globally distributed. However, at levels >35% plants have been predicted to burn irrespective of drying, resulting in an upper limit of O_2 beyond which fires could not be extinguished (8–10). These limits define the fire window (12), within which O_2 levels are constrained where charcoal, a pyrolysis product of fire, is found in the fossil record.

This article is presented in light of the recent increased interest in Paleozoic wildfires (e.g., refs. 5 and 13–15) and the recognition that most inertinite, a constituent component of many coals, is charcoal (16). The latter in particular, because of the great amount of coal quality data available, has affected the database from which fire occurrence and ecosystem distribution are assessed. In addition, there is increased data from charcoalified plant assemblages in both terrestrial and marine sediments that have provided data on the plants subjected to wildfire (5). Collectively, we aim to use these new data as a step in the extensive process of testing whether a long-term feedback mechanism exists between fire occurrence and O_2 levels and to provide a preliminary assessment of charcoal occurrence as an additional data set to test models of O_2 levels in the Late Paleozoic. To this end, we compare two models (3, 4) of Late Paleozoic atmospheric O_2 with charcoal occurrence over this interval (Fig. 1) to examine whether a relationship between the two is apparent. The models selected for comparison include the most recent predictions of Late Paleozoic O_2 fluctuations (3) and a prior, extensively cited and well accepted, set of predictions (4). The newer model (3) is significantly different in several respects. It predicts an O_2 high during the Late Silurian/earliest Devonian dropping to a more profound low in the early Late Devonian. Subsequently, O_2 levels are calculated to have increased more gradually and are predicted to have exceeded the PAL only in the Middle Mississippian, not the Late Devonian. From this point, a continued rise in O_2 levels is predicted to occur in both models before a steep decline into the Mesozoic. However, in the newer model (3) the acme of ≈30% O_2 in the Guadalupian is later and less than predicted by the older model.

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Abbreviations: PAL, present atmospheric level; Myr, million years.

†A.C.S. and I.J.G. contributed equally to this work.

‡To whom correspondence should be addressed. E-mail: a.scott@gl.rhul.ac.uk.

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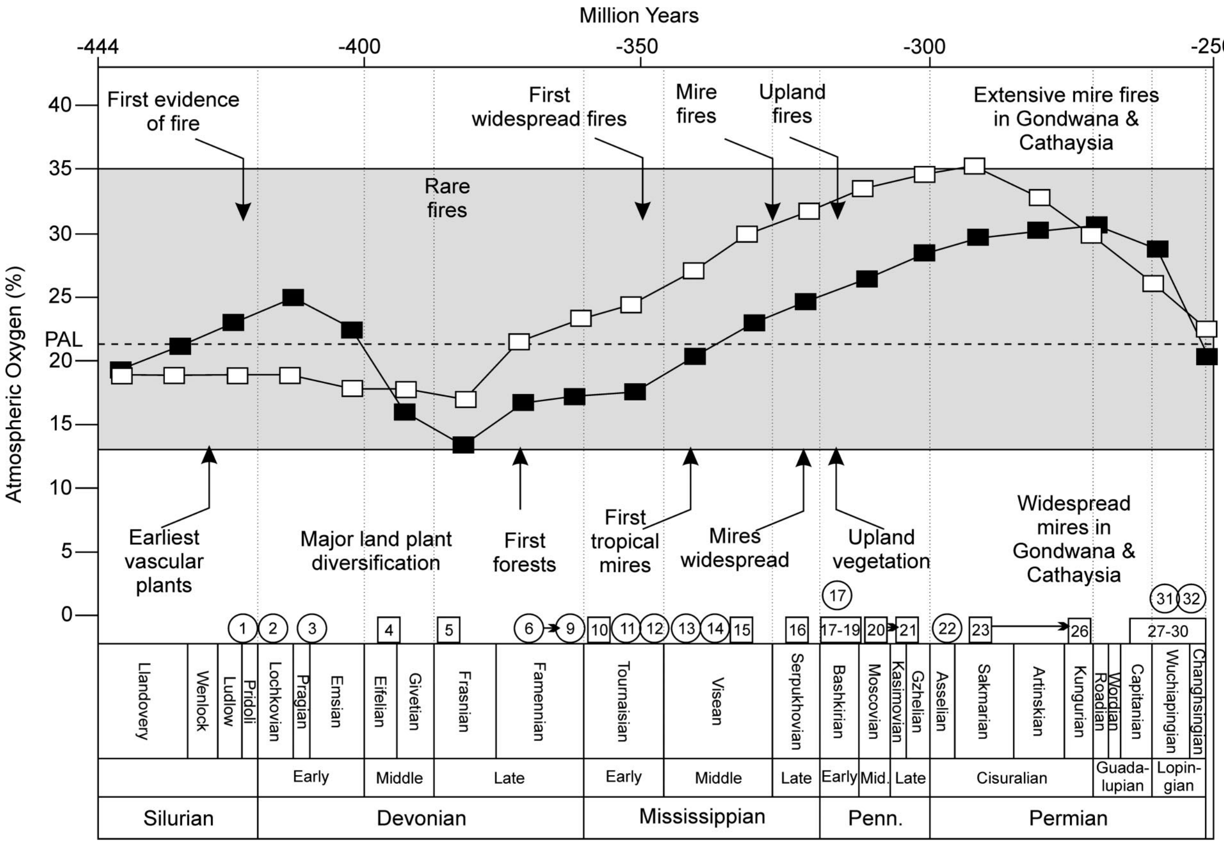

Fig. 1. Modeled fluctuations in Late Paleozoic atmospheric oxygen concentration (□, ref. 4; ■, ref.3) in context with the timing of key terrestrial ecological events (text and arrows toward base) and major trends in wildfire occurrence (text and arrows toward top). Shaded area indicates the fire window. The charcoal/inertinite data used to support our interpretations are differentiated into clastic sediments (numbered circles) and coals (numbered squares). The key to these numbered data and its referencing is as follows: 1, Prídolí (13); 2, Lochkovian (13, 20); 3, Pragian/Emsian (21, 22); 4, Givetian (27, 84); 5, Frasnian (27, 84); 6, Famennian (29); 7, Famennian (23, 84); 8, Famennian (30, 31); 9, Famennian/Tournaisian (Bear Island, this report); 10, Tournaisian (40, 41); 11, Tournaisian (36); 12, Tournaisian (refs. 32, 34, and 85, Foulden, this report); 13, Viséan (33–35, 85, 86); 14, Viséan (refs. 37–39, Pettycur, this report); 15, Viséan (41, 87); 16, Serpukhovian (ref. 44, Douglas Coalfield, this report); 17, Bashkirian (5, 34, 51, 54); 18, Bashkirian (36, 50, 56); 19, Bashkirian (52, 88); 20, Moscovian (89–93); 21, Kasimovian/Gzhelian (57, 58, 94); 22, Cisuralian (Asselian-Kungurian), Europe (95); 23, Cisuralian, Southern Africa (63, 96–99); 24, Cisuralian, India (67, 100, 101); 25, Cisuralian, South America (102, 103); 26, Cisuralian, China (61, 62, 94, 104, 105); 27, Guadalupian/Lopingian (Roadian-Changsingian), Antarctica (106); 28, Guadalupian/Lopingian, Australia (refs. 74, 107, and 108, Swansea Head, this report); 29, Guadalupian/Lopingian, India (68, 96, 109, 110); 30, Guadalupian/Lopingian, China (111); 31, Guadalupian/Lopingian, Europe (14); 32, Guadalupian/Lopingian, China (15).

We aim to investigate how charcoal occurrence reflects these predicted differences.

Late Paleozoic Charcoal Occurrence and Predicted Atmospheric Oxygen Levels

Prídolí–Emsian. Land plants had evolved by the Late Ordovician (17) but unequivocal evidence of vascular land plants does not exist until the Mid–Late Silurian (Wenlock–Prídolí) (18). These small plants had restricted environmental tolerances but could withstand some water stress (19). Charred plant fragments from the Prídolí (Late Silurian) constitute the earliest evidence of vegetation capable of propagating fire (13) (Fig. 1). Because of the restricted nature of the fuel load at this time it is unlikely that fires were widespread. However, charred plants have also been reported from the Lochkovian (20), Pragian, and Emsian (21–23) (Fig. 1). The fundamental requirements for fire ignition and propagation have been stated above. In light of these requirements and the diminutive size of the vegetation and its reproductive ties to moist environments, the comparatively frequent occurrence of wildfire-derived fossil deposits at this time is unexpected. These fires confirm that O_2 levels must have been $>13\%$ and, in consideration of the rarity of plant-bearing localities of this age, indicate levels in excess of the PAL. Berner's latest model (3) predicts high O_2 levels higher than PAL throughout this interval [23%, 420 mega-annum (Ma) (Ludlow); 25%, 410 Ma (Pragian); and 22%, 400 Ma (Emsian)] and may provide explanation for the charcoal occurrences recorded.

Late Emsian–Givetian. During the Early–Middle Devonian (Late Emsian–Givetian) plants diversified rapidly, evolving life strategies that allowed them to colonize previously unexploited lowland niches (18, 24). The maximum size of plants increased dramatically, and woody shrubs and small tree-sized plants have been reported by the Givetian (25). This development led to increased fuel loads. However, spore-producing reproductive strategies restricted these plants to predominantly wetland settings, although seasonal drying is indicated at this time (25). In light of this seasonality and increased biomass, evidence of frequent fires would be expected were O_2 levels higher than PAL, as appears probable in the Early Devonian. This evidence has not been found. Despite extensive mesofossil studies (e.g., ref. 26), evidence of charcoal is scant and corresponds well with modeled O_2 levels for this interval wherein a dramatic decline of $\approx 9\% > 20$ million years is predicted (3). This predicted decline of O_2 levels to $\approx 13\%$, and, if accurate, would offer a robust reason for the apparent paucity of charcoal in the fossil record during this interval (a "charcoal gap") despite increases in fuel load and drying of climate.

Frasnian–Famennian. *Archaeopteris*, the first large woody tree, evolved in the Late Devonian and spread rapidly. By the Mid–Late Frasnian, monospecific archaeopterid forests dominated lowland areas and coastal settings over a vast geographic range (25, 27). Despite this extensive biomass, charcoal occurrences are rare with only isolated fragments of charred *Callixylon* (archaeopterid) wood reported from this interval (23) and small amounts of inertodetrinite (microscopic charcoal fragments) preserved in early Late Devonian Canadian coals (28).

By the latest Devonian (Famennian) charcoal assemblages become more common and include a broad range of plant taxa (e.g., *Archaeopteris*, ferns, and some of the earliest seed plants) from fires in extra-basinal lowland settings (23, 29–30). Famennian/Tournaisian (Devonian–Carboniferous)-age coaly shales, with abundant lycopsid remains, from Bear Island, Svalbard, Norway, examined for this article, contain large amounts of charcoal (>50% by volume of the organic matter present; Fig. 2*g*, which is published as supporting information on the PNAS web site). Detailed analyses of Late Devonian marine sediments from Kentucky further confirm the data from terrestrial samples and show a rapid rise in the abundance of microscopic charcoal (inertinite), probably from coastal lowlands, toward the end of the Famennian (31).

These Devonian data reveal that the spread of forest vegetation preceded evidence of extensive wildfires (Fig. 1) by ≈20 million years and indicate that biomass alone does not necessitate high levels of charcoal in the fossil record. Widely accepted, prior predictions of O_2 levels (4) indicated a sharp rise of ≈6% during the Late Devonian (360 Myr) to 23%. These predicted levels, comparable to the present, would, with so much biomass, have resulted in extensive fires. As discussed, such evidence is absent. However, the charcoal data would be better explained by the most recent predictions of O_2 levels (3), which at about the beginning of the Frasnian (380 Myr) are estimated at ≈13%, subsequently throughout the Famennian (370–360 Myr) rising by only ≈4%. At such levels, suppression of fire activity during the Frasnian would be expected. The increase in charcoal occurrence toward the end of the Famennian could be explained if as predicted O_2 levels had risen to ≈17%, although we feel higher levels would more appropriate.

Tournaisian–Viséan. Progressively, charcoal occurrences become more frequent in the fossil record of the Early–Middle Mississippian (Tournaisian–Viséan) (ref. 32 and Fig. 2 *a–d*). The first major charcoal deposits recording extensive fire activity are preserved in the Viséan of Ireland (33–36). As charcoal occurrence increases, so, too, do the range of sedimentological settings in which it occurs, and the diversity of vegetation burned (ferns, lycopsids, pteridosperms, calamites, and cordaites) (refs. 34 and 36–39 and Fig. 2 *e* and *f*). Thick, laterally extensive autochthonous peats first appear in the Viséan. An average charcoal (inertinite) content of ≈37%, based on data from four coals from two general regions (40–42), provides some of the earliest evidence of fires in mire settings. Collectively, these data suggest levels of O_2 modeled for this interval rising from 17% to 23.5% (3) are inappropriate and instead favor prior, higher levels modeled at ≈23–31.5% (4), values further supported by the occurrence of very large arthropods at this time (43).

Serpukhovian. Coals become increasingly abundant through the Late Mississippian (Serpukhovian) and provide most of our evidence of charcoal (e.g., Fig. 2*h*). Typically, coals of this age have average inertinite contents of ≈18% or more, whereas levels of up to 42% have been recorded (e.g., refs. 44–49). These values indicate major fire influence on peat-forming ecosystems and are in accord with modeled O_2 levels of ≈25% (3) that would be expected to have initiated fires even in wet mire settings.

Bashkirian–Moscovian. Charcoals are ubiquitous in lowland systems throughout the world by the Early–Middle Pennsylvanian (Bashkirian–Moscovian) and are found in fluvial, floodplain (34, 36, 50), lacustrine, mire, and marine facies (51). Bashkirian coals have been recorded with average inertinite (charcoal) contents of between 2% and 43% (e.g., refs. 47 and 52). The first upland floras also appear at this time (53), and many of the plants from these floras are found preserved as charcoal (54, 55). Cordaite trees and conifers from these upland settings provide evidence of regular burning throughout this period (34, 55, 56), and it is possible that fire systems affected the evolution of these plant groups. The diversification of fires into this range of ecosystem settings and the evidence of regular burning indicates O_2 levels in excess of 25%. Modeling supports such elevated O_2 concentrations, older data indicating >30% (4) and newer data indicating ≈25% (3).

Moscovian–Gzhelian. By the Middle–Late Pennsylvanian (Moscovian–Gzhelian) extensive peat facies occur, particularly in the tropical belt of Euramerica and China, and again provide the main source of charcoal data. Coals of this age show a decrease in charcoal content and often contain only 10–12% inertinite for whole coals (57, 58). However, this figure provides only a limited indication of the frequency of fire. Continuous profiles of Pennsylvanian coals show regular occurrences of charcoal, often comprising up to 40% (rarely 100%) of individual horizons in the coal (5). The regularity of fire throughout the history of these mires supports the interpretation of greatly elevated O_2 levels higher than PAL. Major climate fluctuations during the Pennsylvanian ice age (59, 60) complicate relating variations in the charcoal content of the coals to changes in O_2 rather than to climate. Past models predicted ≈32–35% O_2 for this interval (4), values that are challenged on the basis of experimental data that indicate at such levels wet plants would burn (9). However, new data predict oxygen levels of ≈28% at the end of the Pennsylvanian (3), values proportionate to charcoal occurrence.

Cisuralian–Lopingian. Charcoal deposits are recognized throughout the Permian from a variety of ecosystems spread across a great range of latitudes. Early Permian (Cisuralian) charcoal is known from coals in China and Gondwana. The former typically contain >20% charcoal (61, 62), whereas the latter from southern Africa (63, 64), Australia (refs. 65 and 66 and Fig. 2*i*), and India (67, 68) are often extremely charcoal-rich, even in seams >8 m thick. Charcoal assemblages are less common in the northern hemisphere, although they are known from Germany and the United States (14). This scarcity probably reflects a lack of vegetation resulting from widespread aridity at this time. Middle–Late Permian (Guadalupian–Lopingian) coals are common in Gondwana (Antarctica, Australia, and India) and Cathaysia, and most have high charcoal contents >20% but range from 7% to 81% (62, 66, 67, 69–74). End Permian sediments from China contain multiple horizons rich in lycopsid charcoal (15). Fires were therefore an important element in Permian peat-forming systems and would tend to support predictions of very high O_2 concentrations throughout this interval in which the decline below the PAL only occurs in the very latest Permian (3), rather than crashing immediately after the earliest Permian (4).

Discussion and Wider Implications

Almost all charcoal in the fossil record is formed as a result of wildfire; a small amount is produced by entrainment in hot pyroclastic flow deposits or lava flows, but this charcoal is physically quite distinct (75). The distribution and abundance of wildfire-derived charcoal in the fossil record changes through the course of the Late Paleozoic. Although we can use the stratigraphic, geographic, and ecosystem spread of charcoal in

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sediments and inertinite in coal to provide a general test of atmospheric oxygen level we cannot compare quantitative data from different sedimentary settings, including coals, to provide "inertinite/charcoal curves" to match oxygen curves as there are too many unknown controls on the data (taphonomic, operator bias, etc.).

The occurrence of Late Silurian/earliest Devonian charcoal can almost certainly be explained by oxygen levels elevated above PAL. The paucity of charcoal throughout the Middle and much of the Late Devonian, despite the spread of large woody vegetation (increased fuel load) growing under seasonally dry climates, is most probably explained by low atmospheric oxygen levels at this time, as are predicted by current models. Similarly, the timing of fire system diversification into mire and upland settings is coincidental with predictions of pronounced increases in O_2 levels, rising to well above PAL. It is proposed that this fire system diversification and the high levels of charcoal recorded in various ecosystem settings were predominantly driven by atmospheric oxygen levels elevated above PAL throughout the much of the Carboniferous and most of the Permian. Therefore, based on these preliminary data, charcoal appears to track closely the predictions made by Berner's latest O_2 model (3).

The increase of fire activity in the Late Paleozoic in a range of environmental settings would have had far-reaching significance for the Earth system. Increased charcoal production and burial would have enhanced carbon sequestration; charred plant material is much less readily broken down than noncharred organic matter (76) and hence may have contributed to carbon dioxide draw down. Upland fires would have had particular significance. These fires may have been a trigger for the evolution and diversification of several plant groups, particularly the conifers, but they would also have resulted in extensive postfire erosion. Increased charcoal production after frequent and widespread fires would have resulted in the burial of more inert carbon. Systems analysis (4) suggests there is a positive feedback loop where if O_2 rises there are more fires, leading to increased charcoal production and burial, and further increased levels of O_2 (4). However, it has been suggested that there is also a positive relationship between increasing fire and the rise of atmospheric carbon dioxide (77). Wildfire, we propose, has had an important effect on the evolution of the biosphere throughout the late Paleozoic.

Conclusions

Paleozoic charcoal data support the predictions of Berner's most recent atmospheric oxygen model (3). Calculations of elevated oxygen levels during the Late Silurian/earliest Devonian are coincident with the preservation of rhyniophytoid charcoal, whereas a predicted profound oxygen low during the Middle and early Late Devonian is contemporaneous with a paucity of charcoal (a charcoal gap). Remodeling of the Phanerozoic oxygen high predicts a shift from the Carboniferous–Permian boundary to the Middle–Late Permian, estimates that are supported by charcoal occurrences in coals of this age. This increase in Late Paleozoic fire activity would have affected the evolution of terrestrial ecosystems and altered the balance of the whole Earth system.

Materials and Methods

Additional material was prepared for this article to provide further information on charcoal abundance during key intervals. Quantitative reflectance data were gathered for four additional coal samples. Qualitative scanning electron microscope data were collected for samples from two terrigenous settings. The four coal samples are: (*i*) Famennian–Tournaisian coal (78) from Bear Island, Svalbard, Norway, obtained from the Naturhistoriska Rijksmuseet, Stockholm; (*ii*) Pyramidian, Viséan coal from the Høbybreen Formation of Spitzbergen, Norway (40); (*iii*) Serpukhovian coal from the Douglas Coalfield, Scotland (79); and (*iv*) Late Permian, coal from Swansea Head in the Newcastle Coal Measures of the Sydney Basin, Australia (80). The two terrigenous samples are: (*i*) Calcareous mudstones from the Late Tournaisian, Kinnesswood Group at Foulden, Berwickshire, United Kingdom (81); and (*ii*) limestones from the late Viséan of Pettycur, Fife, Scotland (37). Fig. 2 illustrates the charcoal identified in these materials.

The coal samples were prepared as polished blocks following standard protocols (82). The blocks were analyzed at ×200 magnification by using a Nikon Microphot reflected light microscope linked to a Leica QWin image analysis system. Maceral analyses were counted by using a cross-hair graticule and a traverse distance of 0.5 mm, recording 500 data points per block. Mesofossil charcoal was isolated from the sediment samples by using standard techniques (83) then sputter-coated with gold by using a Polaron (Watford, U.K.) Sputter Coater E5100 and viewed with a Hitachi (Tokyo) S3000N scanning electron microscope.

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1. Berner, R. A. (1999) *Proc. Natl. Acad. Sci. USA* **96,** 10955–10957.
2. Bateman, R. M., Crane, P. R., DiMichele, W. A., Kenrick, P., Rowe, N. P., Speck, T. & Stein, W. E. (1998) *Annu. Rev. Ecol. Syst.* **29,** 263–292.
3. Berner, R. A. (2006) *Geochim. Cosmochim. Acta*, in press.
4. Berner, R. A., Beerling, D. J., Dudley, R., Robinson, J. M. & Wildman, R. A. (2003) *Annu. Rev. Earth Planet. Sci.* **31,** 105–134.
5. Scott, A. C. (2000) *Palaeogeog. Palaeoclimatol. Palaeoecol.* **164,** 281–329.
6. Wildman, R. A., Hickey, L. J., Dickinson, M. B., Berner, R. A., Robinson, J. M., Dietrich, M., Essenhigh, R. H. & Wildman, C. B. (2004) *Geology* **32,** 457–460.
7. Chaloner, W. G. (1989) *J. Geol. Soc. (London)* **146,** 171–174.
8. Watson, A. J., Lovelock, J. E. & Margulis, L. (1978) *Biosystems* **10,** 293–298.
9. Lenton, T. M. (2003) *Global Change Biol.* **7,** 613–629.
10. Lenton, T. M. & Watson, A. J. (2000) *Global Biogeochem. Cycles* **14,** 249–268.
11. Pyne, S. J., Andrews, P. L. & Laven, R. D. (1996) *Introduction to Wildland Fire* (Wiley, New York).
12. Jones, T. P. & Chaloner, W. G. (1991) *Palaeogeog. Palaeoclimatol. Palaeoecol.* **97,** 39–50.
13. Glasspool, I. J., Edwards, D. & Axe, L. (2004) *Geology* **32,** 381–383.
14. Uhl, D., Lausberg, S., Noll, R. & Stapf, K. R. G. (2004) *Palaeogeog. Palaeoclimatol. Palaeoecol.* **207,** 23–35.
15. Wang, Z.-Q. & Chen, A.-S. (2001) *Rev. Palaeobot. Palynol.* **117,** 217–243.
16. Scott, A. C. & Glasspool, I. J. (2006) *Int. J. Coal Geol.*, in press.
17. Wellman, C. H., Osterloff, P. L. & Mohiuddin, U. (2003) *Nature* **425,** 282–285.
18. Edwards, D. & Wellman, C. (2001) in *Plants Invade the Land: Evolutionary and Environmental Perspectives*, eds. Gensel, P. G. & Edwards, D. (Columbia Univ. Press, New York), pp. 3–28.
19. Edwards, D. & Richardson, J. B. (2004) *Geol. J.* **39,** 375–402.
20. Edwards, D. & Axe, L. (2004) *Palaios* **19,** 113–128.
21. Pflug, H. D. & Prössl, K. F. (1989) *Naturwissenschaften* **76,** 565–567.
22. Pflug, H. D. & Prössl, K. F. (1991) *Sci. Drill* **2,** 13–33.
23. Rowe, N. P. & Jones, T. P. (2000) *Palaeogeog. Palaeoclimatol. Palaeoecol.* **164,** 331–338.
24. Hotton, C. L., Heuber, F. M., Griffing, D. H. & Bridge, J. S. (2001) in *Plants Invade the Land: Evolutionary and Environmental Perspectives*, eds. Gensel, P. G. & Edwards, D. (Columbia Univ. Press, New York), pp. 179–203.
25. Algeo, T. J., Scheckler, S. E. & Maynard, J. B. (2001) in *Plants Invade the Land: Evolutionary and Environmental Perspectives*, eds. Gensel, P. G. & Edwards, D. (Columbia Univ. Press, New York), pp. 213–236.
26. Gensel, P. G., Johnson, N. G. & Strother, P. K. (1990) *Palaios* **5,** 520–547.
27. Meyer-Berthaud, B., Scheckler, S. E. & Wendt, J. (1999) *Nature* **398,** 700–701.
28. Gentzis, T. & Goodarzi, F. (1991) *Bull. Soc. Géol. Fr.* **162,** 239–253.
29. Cressler, W. L. (2001) *Palaios* **16,** 171–174.
30. Fairon-Demaret, M. & Hartkopf-Fröder, C. (2004) *Cour. Forschungsinst. Senckenb.* **251,** 89–121.

31. Rimmer, S. M., Thompson, J. A., Goodnight, S. A. & Robl, T. L. (2004) *Palaeogeog. Palaeoclimatol. Palaeoecol.* **215,** 125–154.
32. Scott, A. C., Galtier, J. & Clayton, G. (1985) *Rev. Palaeobot. Palynol.* **44,** 81–99.
33. Nichols, G. J. & Jones, T. P. (1992) *Sedimentology* **39,** 487–502.
34. Scott, A. C. & Jones, T. P. (1994) *Palaeogeog. Palaeoclimatol. Palaeoecol.* **106,** 91–112.
35. Falcon-Lang, H. J. (1998) *Palaeogeog. Palaeoclimatol. Palaeoecol.* **139,** 121–138.
36. Falcon-Lang, H. J. (2000) *Palaeogeog. Palaeoclimatol. Palaeoecol.* **164,** 339–355.
37. Scott, A. C., Meyer-Berthaud, B., Galtier, J., Rex, G. M., Brindley, S. & Clayton, G. (1986) *Rev. Palaeobot. Palynol.* **48,** 161–180.
38. Rex, G. M. & Scott, A. C. (1987) *Geol. Mag.* **124,** 43–66.
39. Brown, R., Scott, A. C. & Jones, T. P. (1994) *Trans. R. Soc. Edinburgh Earth Sci.* **84,** 267–274.
40. Abdullah, W. H., Murchison, D. G., Jones, J. M., Telnaes, N. & Gjelberg, J. (1988) *Org. Geochem.* **13,** 953–964.
41. Michelsen, J. K. & Khorasani, G. K. (1991) *Bull. Geol. Soc. Fr.* **162,** 385–397.
42. Potter, J., Richards, B. C. & Cameron, A. R. (1993) *Int. J. Coal Geol.* **24,** 113–140.
43. Rolfe, W. D. I., Durant, G., Fallick, A. E., Hall, A. J., Large, D., Scott, A. C., Smithson, T. R. & Walkden, G. (1990) *Geol. Soc. Am. Spec. Publ.* **244,** 13–24.
44. Nowak, G. J. (1996) *Geol. Soc. Spec. Publ.* **109,** 261–286.
45. Varma, A. K. (1996) *Int. J. Coal Geol.* **30,** 327–335.
46. Masalerz, M. & Wilks, K. R. (1992) *Int. J. Coal Geol.* **20,** 243–261.
47. Dopita, M. & Kumpera, O. (1993) *Int. J. Coal Geol.* **23,** 291–321.
48. Sachsenhofer, R. F., Privalov, V. A., Izart, A., Elie, M., Kortensky, J., Panova, E. A., Sotirov, A. & Zhykalyak, M. V. (2003) *Int. J. Coal Geol.* **55,** 225–259.
49. Cmiel, S. R. & Fabianska, M. J. (2004) *Int. J. Coal Geol.* **57,** 77–97.
50. Falcon-Lang, H. J. (1999) *J. Geol. Soc. (London)* **156,** 137–148.
51. Scott, A. C., Galtier, J., Mapes, R. H. & Mapes, G. (1997) *J. Geol. Soc. (London)* **154,** 61–68.
52. Marques, M. (2002) *Int. J. Coal Geol.* **48,** 197–216.
53. Leary, R. L. (1981) *Ill. State Mus. Rep. Invest.* **37,** 1–88.
54. Scott, A. C. (1978) *Proc. Yorkshire Geol. Soc.* **41,** 461–508.
55. Scott, A. C. & Chaloner, W. G. (1983) *Proc. R. Soc. London B* **220,** 163–182.
56. Falcon-Lang, H. & Scott, A. C. (2000) *Palaeogeog. Palaeoclimatol. Palaeoecol.* **156,** 225–242.
57. Renton, J. J. & Bird, D. S. (1991) *Int. J. Coal Geol.* **17,** 21–50.
58. DiMichele, W. A., Eble, C. F. & Chaney, D. S. (1996) *Int. J. Coal Geol.* **31,** 249–276.
59. Calder, J. M. & Gibling, M. R. (1994) *Palaeogeog. Palaeoclimatol. Palaeoecol.* **106,** 1–21.
60. Cleal, C. J. & Thomas, B. A. (2005) *Geobiology* **3,** 13–31.
61. Sun, Y., Püttmann, W., Kalkreuth, W. & Horsfield, B. (2002) *Int. J. Coal Geol.* **49,** 251–262.
62. Yang, Y., Zou, R., Shi, Z. & Jiang, R. (1996) *Atlas for Coal Petrography of China* (China Univ. Mining Technol. Press, Beijing).
63. Glasspool, I. J. (2003) *Int. J. Coal Geol.* **53,** 81–135.
64. Semikwa, P., Kalkreuth, W., Utting, J., Mpanju, F. & Hagemann, H. (2003) *Int. J. Coal Geol.* **55,** 157–186.
65. Le Blanc Smith, G. & Mory, A. J. (1995) *Geol. Surv. West. Aust. Rep.* **44,** 1–60.
66. Mishra, H. K. (1996) *Palaeogeog. Palaeoclimatol. Palaeoecol.* **125,** 199–216.
67. Mishra, H. K., Chandra, T. K. & Verma, R. P. (1990) *Int. J. Coal Geol.* **16,** 47–71.
68. Singh, M. P. & Shukla, R. R. (2004) *Int. J. Coal Geol.* **59,** 209–243.
69. Marchioni, D. L. (1980) *Int. J. Coal Geol.* **1,** 35–61.
70. Kojima, K., Sugia, T. & Hara, Y. (1985) *C. R. Congr. Int. Strat. Geol. Carbonifere* **9,** 501–509.
71. Diessel, C. F. K. & Smyth, M. (1995) *Geol. Soc. Aust. Coal Geol. Grp. Spec. Publ.* **1,** 63–81.
72. Gray, R. L. & Bowling, C. M. (1995) *Int. J. Coal Geol.* **27,** 279–298.
73. Semikwa, P., Kalkreuth, W., Utting, J., Mayagilo, F., Mpanju, F. & Hagemann, H. (1998) *Int. J. Coal Geol.* **36,** 63–110.
74. Glasspool, I. J. (2000) *Palaeogeog. Palaeoclimatol. Palaeoecol.* **164,** 357–380.
75. Scott, A. C. & Glasspool, I. J. (2005) *Geology* **33,** 589–592.
76. Schmidt, M. W. I. & Noack, A. G. (2000) *Global Biogeochem. Cycles* **14,** 777–793.
77. Carcaillet, C., Almquist, H., Asnong, H., Bradshaw, R. H., Carrion, J. S., Gaillard, M. J., Gajewski, K., Haas, J. N., Haberle, S. G., Hadorn, P., *et al.* (2002) *Chemosphere* **49,** 845–863.
78. Heafford, A. P. (1988) in *Geological Evolution of the Barents Shelf Region*, eds. Harland, W. B. & Dowdswell, E. K. (Graham and Trotman, London), pp. 89–108.
79. Scott, A. C. (1999) *Palynology* **23,** 3–14.
80. Diessel, C. F. K. (1985) *Proc. 10th Int. Congr. Carb. Strat. Geol. Madrid 1983* **4,** 197–210.
81. Scott, A. C. & Meyer-Berthaud, B. (1985) *Trans. R. Soc. Edinburgh Earth Sci.* **76,** 13–20.
82. Taylor, G. H., Teichmüller, M., Davis, A., Diessel, C. F. K., Littke, R. & Robert, P. (1998) *Organic Petrology* (Gebrüder Borntraeger, Berlin).
83. Pearson, T. & Scott, A. C. (1999) in *Fossil Plants and Spores: Modern Techniques*, eds. Jones, T. P. & Rowe, N. P. (Geological Soc., London), pp. 202–225.
84. Goodarzi, F. & Goodbody, Q. (1990) *Int. J. Coal Geol.* **14,** 175–196.
85. Scott, A. C. (1989) *Int. J. Coal Geol.* **12,** 443–475.
86. Scott, A. C. & Collinson, M. E. (1978) in *SEM in the Study of Sediments*, ed. Whalley, W. B. (Geoabstracts, Norwich, U.K.), pp. 137–167.
87. Dvorak, J., Honek, J., Pesek, J. & Valterova, P. (1997) *Geol. Soc. Spec. Publ.* **125,** 179–193.
88. Hower, J. C., Calder, J. H., Eble, C. F., Scott, A. C., Robertson, J. D. & Blanchard, L. J. (2000) *Int. J. Coal Geol.* **42,** 185–206.
89. Calder, J. H., Gibling, M. R., Eble, C. F., Scott, A. C. & MacNeil, D. J. (1996) *Int. J. Coal Geol.* **31,** 277–313.
90. Hower, J. C., Eble, C. F. & Pierce, B. S. (1996) *Int. J. Coal Geol.* **31,** 195–215.
91. Hower, J. C., Ruppert, L. F., Eble, C. F. & Clark, W. L. (2005) *Int. J. Coal Geol.* **62,** 167–181.
92. Kalkreuth, W. D., Marchioni, D. L., Calder, J. H., Lamberson, M. N., Naylor, R. D. & Paul, J. (1991) *Int. J. Coal Geol.* **19,** 21–76.
93. Rimmer, S. M., Hower, J. C., Moore, T. A., Esterle, J. S., Walton, R. L. & Helfrich, C. T. (2000) *Int. J. Coal Geol.* **42,** 159–184.
94. Querol, X., Alastuey, A., Lopez-Soler, A., Plana, F., Zeng, R., Zhao, J. & Zhuang, X. (1999) *Int. J. Coal Geol.* **42,** 63–88.
95. Uhl, D. & Kerp, H. (2003) *Palaeogeog. Palaeoclimatol. Palaeoecol.* **199,** 1–15.
96. Falcon, R. M. S. (1989) *Int. J. Coal Geol.* **12,** 681–731.
97. Faure, K., Willis, J. P. & Dreyer, J. C. (1996) *Int. J. Coal Geol.* **29,** 147–186.
98. Glasspool, I. J. (2003) *Fuel* **82,** 959–970.
99. Oesterlen, P. M. & Lepper, J. (2005) *Int. J. Coal Geol.* **61,** 97–118.
100. Navale, G. K. B. & Saxena, R. (1989) *Int. J. Coal Geol.* **12,** 553–588.
101. Mukherjee, B. C. (1984) *Commun. Serv. Geol. Portugal* **70,** 269–275.
102. Holz, M., Kalkreuth, W. & Banerjee, I. (2002) *Int. J. Coal Geol.* **48,** 147–179.
103. Kalkreuth, W., Holz, M., Kern, M., Machado, G. Mexias, A., Silva, A. M., Willett, J., Finkleman, R. & Berger, H. (2006) *Int. J. Coal Geol.*, in press.
104. Liu, G., Yang, P., Peng, Z. & Chou, C.-L. (2004) *J. Asian Earth Sci.* **23,** 491–506.
105. Liu, G., Zheng, L., Gao, L., Zhang, H. & Peng, Z. (2005) *Energy* **30,** 1903–1914.
106. Holdgate, G. R., McLoughlin, S., Drinnan, A. N., Finkleman, R. B., Willet, J. C. & Chiehowsky, L. A. (2005) *Int. J. Coal Geol.* **63,** 156–177.
107. Hunt, J. W. (1989) *Int. J. Coal Geol.* **12,** 589–634.
108. Smyth, M. (1989) *Int. J. Coal Geol.* **12,** 635–656.
109. Navale, G. K. B. & Mishra, B. K. (1984) *Commun. Serv. Geol. Portugal* **70,** 56–63.
110. Singh, M. P. & Singh, P. K. (1996) *Int. J. Coal Geol.* **29,** 93–118.
111. Dai, S., Chou, C.-L., Yue, M., Luo, K. & Ren, D. (2005) *Int. J. Coal Geol.* **61,** 241–258.