Delayed fungal evolution did not cause the Paleozoic peak in coal production

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Organic carbon burial plays a critical role in Earth systems, influencing atmospheric O_2 and CO_2 concentrations and, thereby, climate. The Carboniferous Period of the Paleozoic is so named for massive, widespread coal deposits. A widely accepted explanation for this peak in coal production is a temporal lag between the evolution of abundant lignin production in woody plants and the subsequent evolution of lignin-degrading Agaricomycetes fungi, resulting in a period when vast amounts of lignin-rich plant material accumulated. Here, we reject this evolutionary lag hypothesis, based on assessment of phylogenomic, geochemical, paleontological, and stratigraphic evidence. Lignin-degrading Agaricomycetes may have been present before the Carboniferous, and lignin degradation was likely never restricted to them and their class II peroxidases, because lignin modification is known to occur via other enzymatic mechanisms in other fungal and bacterial lineages. Furthermore, a large proportion of Carboniferous coal horizons are dominated by unlignified lycopsid periderm with equivalent coal accumulation rates continuing through several transitions between floral dominance by lignin-poor lycopsids and lignin-rich tree ferns and seed plants. Thus, biochemical composition had little relevance to coal accumulation. Throughout the fossil record, evidence of decay is pervasive in all organic matter exposed subaerially during deposition, and high coal accumulation rates have continued to the present wherever environmental conditions permit. Rather than a consequence of a temporal decoupling of evolutionary innovations between fungi and plants, Paleozoic coal abundance was likely the result of a unique combination of everwet tropical conditions and extensive depositional systems during the assembly of Pangea.

lignin | carbon cycle | wood rot | fungi | lignin degradation

Coal has been part of human civilization for thousands of years; it fueled the Industrial Revolution, ushered in our hydrocarbon dependence, and remains an important energy source (1, 2). Coal is largely derived from plant matter accumulated as peat in wetland ecosystems and subsequently compacted and converted to an organic-rich, combustible rock (3, 4). Land plants possess cell walls composed primarily of polysaccharides, such as cellulose; in vascular plants, the polyaromatic biopolymer lignin is deposited secondarily in some cell walls, notably those associated with biomechanical support and hydraulic transport. Cellulose and lignin are the two most abundant organic compounds on Earth, accounting for most modern terrestrial biomass; polysaccharides, however, are prone to greater rates of degradation, leading to lignin enrichment during diagenesis. Thus, coal is often thought to be composed largely of lignin derived from woody tissue (5). Coal deposits occur by the Early Devonian (6), but the most abundant, geographically extensive, and economically important are of late Paleozoic (Carboniferous–Permian) age (7, 8). Organic matter burial is an important feedback to the Earth system influencing atmospheric O_2 and CO_2, as well as global climate via its impact on CO_2. In particular, the peak in organic carbon sequestration during the late Paleozoic is linked to extensive glaciation and the highest concentrations of atmospheric O_2 in Earth history, with broad evolutionary ramifications (8).

Why is coal so abundant in late Paleozoic rocks? It has been speculated that plant decomposers, especially the saprotrophic fungi critical to modern ecosystems (9), were absent or inefficient during the Carboniferous, resulting in massive accumulations of organic matter (10). A subsequent argument further suggested Carboniferous plants possessed high lignin content, and fungal metabolism for lignin degradation was inefficient or had not yet evolved (11, 12). More recently, the evolution of lignin degradation in basidiomycete fungi was traced via phylogenomic methods and relaxed molecular clock estimates to the Permian (13, 14), offering support for a fungi-mediated decrease in coal formation following the Carboniferous (13). The wholesale or partial attribution of the Carboniferous–Permian peak in coal production to this evolutionary lag between lignin synthesis and fungal degradation of lignin has been widely promulgated (8, 15–22), reflecting the growing interest in life–Earth feedbacks over geological timescales (23–28). Such geobiological hypotheses sometimes persist based largely on the strength of their novelty, without sufficient predictive testing. Here, we compile data on the distribution of organic-rich sediments in the Phanerozoic of North America and synthesize arguments demonstrating that an evolutionary lag explanation for the waxing and waning of coal deposition (8, 10–13) is inconsistent with geochemistry, sedimentology, paleontology, and biology. Instead, the Carboniferous–Permian peak and subsequent decline in coal production most likely reflects a unique combination of tectonics

Significance

The Carboniferous–Permian marks the greatest coal-forming interval in Earth's history, contributing to glaciation and uniquely high oxygen concentrations at the time and fueling the modern Industrial Revolution. This peak in coal deposition is frequently attributed to an evolutionary lag between plant synthesis of the recalcitrant biopolymer lignin and fungal capacities for lignin degradation, resulting in massive accumulation of plant debris. Here, we demonstrate that lignin was of secondary importance in many floras and that shifts in lignin abundance had no obvious impact on coal formation. Evidence for lignin degradation—including fungal—was ubiquitous, and absence of lignin decay would have profoundly disrupted the carbon cycle. Instead, coal accumulation patterns implicate a unique combination of climate and tectonics during Pangea formation.

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and climate with the particular details of the evolution of plant and fungal community composition bearing no direct relevance.

Results and Discussion

Central to the evolutionary lag model is the assumption that lignin is the dominant biochemical constituent of coal, following taphonomic enrichment (5, 8); alternative, nonlignitic sources of resistant organic matter include waxes from leaf cuticle, suberin from bark, or sporopollenin from reproductive propagules (2, 5, 29), but such sources are less abundant and more patchy in space and time. However, even where lignin is presumed to be the primary source, only ∼70% of the coal organic matter is consistent with the possibility of a lignin origin, the rest being broadly attributed to microbes or algae (30). Furthermore, this understanding was based on analyses of visually identified wood fragments in coal, from which progressive molecular transformations of lignin-derived organic matter were examined in coals of increasing thermal maturity (5, 31, 32); thus, these studies focused solely on lignin diagenesis, not on overall biochemical composition. Finally, such work has focused on Cenozoic coals, ensuring continuity and comparability with the modern flora (33); however, the wood-rich conifer and angiosperm-dominated source floras of these coals differ radically from the mostly nonwoody floras of the Carboniferous. Thus, certain assumptions undergirding lignin-based explanations for Paleozoic coal abundance are founded on studies of coals derived from plants with little meaningful overlap with the Paleozoic flora and with divergent research objectives not easily transferable to plants of that earlier time.

Carboniferous peat-forming environments were most frequently dominated by arborescent lycopsids: trees that were woody, but scantly so, with up to 80% of their peat biomass derived from secondary cortical tissues (i.e., periderm or "bark"), which lack extant homologs (34). Some bulk geochemical analyses of this tissue suggested periderm lignification (35), whereas others emphasized a greater abundance of aliphatics relative to aromatics (36), inconsistent with lignin but perhaps supporting suberin-like chemistry as in modern seed plant bark (37). This discrepancy may reflect the mixing of tissues during bulk analyses (36, 38) or stabilization of labile original biochemistry by the secondary production of more stable geopolymers during diagenesis (39, 40). Synchrotron-based analyses of individual cell walls has ensured sampling accuracy and demonstrated that periderm does indeed possess reduced aromaticity relative to, and contain aliphatics absent from, wood of the same fossil—together suggesting lycopsid periderm was not lignified and may well have been suberized (38). Thus, lignin would have been of secondary importance in many Carboniferous peats where lycopsid periderm was the single most abundant component and could represent a straight majority of the preserved biomass (41–43). In these materials, lags of largely intact lycopsid periderm often can be found amid a matrix of highly degraded plant debris (44). The preferential preservation of these nonlignified tissues—in contrast to lignified tissues of other taxa and, indeed, the lignified wood of the same lycopsids—sharply conflicts with and argues against elevated lignin content and the temporal absence of efficient lignin-degrading fungi as the prime factors responsible for Late Paleozoic coal formation.

In contrast to what would be expected if coal deposition were driven by evolution of lignin metabolisms, there is no clear impact of the distinctly different biochemical signatures that successive Carboniferous swamp assemblages would have generated. Woody cordaitalean gymnosperms were secondary to equal elements with lycopsids in some peat-forming swamps, primarily during the early Middle Pennsylvanian (34). Such cordaitalean abundance would have elevated the lignin input to peat in these horizons; however, the derived coals are not thicker or more widespread than the earlier or later lycopsid-dominated coals. Furthermore, during the Kasimovian/Gzhelian transition of the Pennsylvanian, Euramerican communities lost most arborescent lycopsids and transitioned to dominance by nonwoody, *Psaronius* marattialean ferns (34, 45–47). Stems of these trees had multiple primary xylem cylinders in a parenchyma matrix with a peripheral sclerenchyma zone. The bulk of the aerial biomass was invested in a thick mantle of aerenchymatous roots, each with a small xylem strand and peripheral sclerenchyma sheath (48–50). Thus, this stratigraphic boundary also represents a major change in the biochemical inputs to Euramerican peats. Consequently, clear manifestations in the overall sedimentary and geochemical records of coal would be expected if an imbalance between lignin synthesis and degradation were the primary driver of Carboniferous coal accumulation. Instead, North American data from the Carboniferous demonstrate comparable levels of accumulation across each of these transitions, regardless of biochemical inputs (Fig. 1), as is consistent with global compilations (8, 51). Furthermore, coals are abundant and widespread in China, then at paleoequatorial latitudes, until the late Permian (52), with floral composition similar to that of Middle Pennsylvanian Euramerican coals (53, 54). These Permian coals occur after the supposed appearance of lignolytic fungi, and challenge the attribution of earlier deposits to the absence of fungal decay.

Whereas a post-Paleozoic increase in fungal abundance has been suggested (21, 55), Carboniferous fossils provide direct evidence that fungi were taxonomically and ecologically diverse (56–68). This is despite the recent recognition that fungal diversity and abundance is likely to be underestimated due to the selective loss of fungal fossils with standard fossil preparation techniques (68). Fossil wood and macrodetritus often exhibit signs of decay (61, 69–72), even specifically fungal decay, although the synapomorphies needed to link the fungi to specific lineages are not preserved (73–75). For example, basidiomycete white rot fungi are the most efficient modern lignin degraders, and their evolution is directly implicated in the decline of coal deposition (13). Although the earliest definitive fossil record of basidiomycete white rot is from Triassic conifer wood (76), an earlier evolution of fungal-mediated lignin degradation is indicated by Devonian-to-Permian woods infiltrated with fungi and possessing damage consistent with white rot decay or other forms of fungal degradation of lignified tissue (61, 76–79) (Fig. 2).

Inconsistencies between the fossil record and lignin/fungal-based explanations for Paleozoic coal abundance extend more broadly than documented fossil specimens of fungal rots. Carboniferous peat permineralizations (coal balls) generally contain low shoot:root ratios, suggesting decay of massive amounts of aerial plant tissue (34, 44, 80). This decay includes all tissue and organ types (61, 69–71), many decayed nearly to the point of unrecognizability, including wood. Also, in contravention to the evolutionary lag model, which is rooted in the synthesis and degradation of lignin, the tissue most resistant to decay was the unlignified periderm of arborescent lycopsids, which often built up in thick lag concentrations. In addition, there is strong contrast among barely compacted roots, often of multiple generations, penetrating highly degraded, aerially derived material—an indication of early and extensive decay of material above the water table during the accumulation process. Preservation of delicate aerial tissues, such as leaves, often in isolated concentrations, is consistent with deposition directly into local depressions, such as tree throws, where standing water would have been exposed at the surface (81). Thus, decomposition of all plant tissues was an integral part of Carboniferous ecosystems, and situations in which organic matter accumulated appear to reflect local environmental conditions, not the lignin content of the plant material.

In general, absence of lignin decay would be impossible by virtue of simple mass balance: Even if terrestrial productivity were only 25% of the modern levels (82, 83) of ∼55–60 gigatons per year (84) and lignin accounted for 20% of that production [lignin content generally ranges from 5% to 35% in most extant tracheophytes (85–87)], carbon deposition in the form of lignin would have amounted to ∼3 gigatons per year. The extremity of this number is placed in perspective by considering that modern

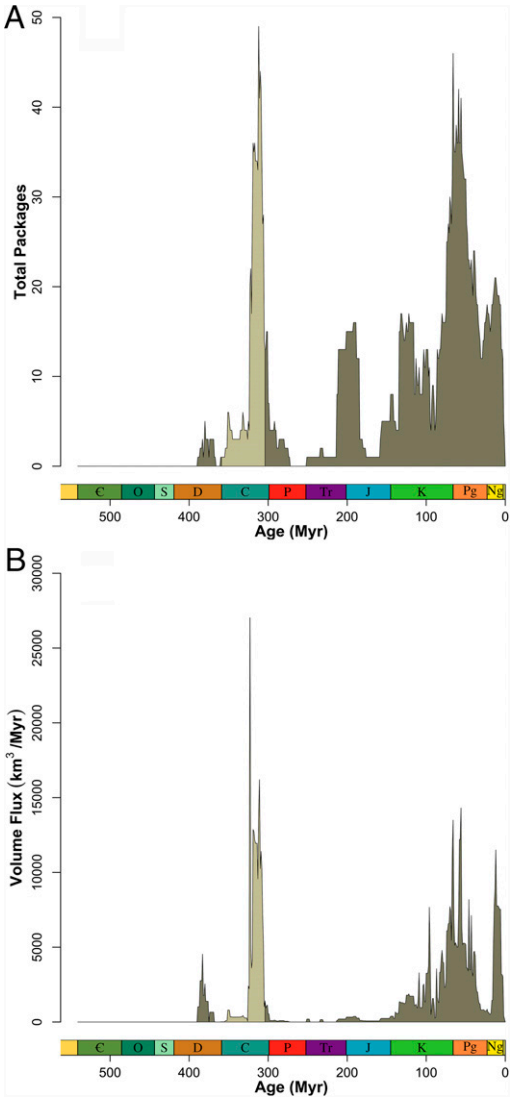

Fig. 1. Terrestrial, North American organic sediment (coal, peat, lignite, anthracite, and tar) accumulation through time. Data are from the Macrostrat database, and age estimates are derived from a continuous time age model. Sedimentation metrics include (*A*) total packages, i.e., the number of organic-rich sedimentary successions per million years, and (*B*) organic-rich sediment volume burial flux measured in cubic kilometers per million years (derived from stratigraphic thickness, depositional area, and deposition duration). The light-colored section under the curve indicates the time interval over which lycopsids played a dominant role in North American wetlands. Thus, lignin would have been of secondary importance during this period, aside from in a few interspersed floral assemblages in which woody cordaitalean seed plants with higher lignin contents were codominant. Consequently, lignin is expected to have been a greater contribution to coal formation both before and after this interval of lycopsid dominance. Coal production being the result of a temporal lag between the evolution of lignin synthesis by plants and lignin decay by fungi is inconsistent with (*i*) the lack of correspondence between coal production rates and transitions in biochemical inputs, (*ii*) the sharp, short-lived peaks in Carboniferous coal production, and (*iii*) the return to high levels of coal production in the last 100 million years.

global coal reserves spanning the entire 420-million-year history of lignified vascular plants are only on the order of a few thousand gigatons (88). Actual rates of organic accumulation are thought to be at least two orders of magnitude lower, even in the Carboniferous (89). Despite feedbacks with weathering rates, much smaller imbalances would have resulted in the complete removal of atmospheric CO_2 in less than a million years (90). Without evidence of such dire consequences, lignin production in the absence of lignin decay for more than 100 million years into the early Permian is untenable. Most organic matter decays, regardless of composition, and only accumulates where local stagnant waterlogging results in substrate anoxia (55, 81). Even if lignin were relatively less prone to decay in the Paleozoic, that would not impact the geographic extent of environments in which preservation could occur and, thus, should not be expected to have increased coal abundance. The evolution of trees and forested ecosystems over the Devonian and Carboniferous fundamentally altered sedimentary environments (91), but this environmental transition had no direct relationship with lignin because, as outlined above, lignin content of arborescent lineages varied considerably. Furthermore, this environmental restructuring was permanent and, thus, cannot account for a Paleozoic peak in coal production. Without question, decay is slower in certain biochemical constituents, such as lignin, cuticle, and sporopollenin; however, their accumulation is nonetheless confined to the subset of sedimentary environments that prevent their eventual degradation. Thus, reduced Paleozoic rates of lignin decay might, at most, have resulted in a greater fraction of the same amount of coal being sourced from lignin, not more coal overall.

Genomic evidence used to support delayed fungal lignin degradation can be readily reconciled with the direct evidence of pre-Permian lignin decay. The evolutionary origin of lignin-degrading fungal class II peroxidases (PODs) involved in white rot has been traced to the most recent common ancestor (MRCA) of Auriculariales and all other Agaricomycetes (excluding Cantharellales and Sebacinales) in the Early Permian, thus conforming to the evolutionary lag model (13). However, lignin modification is not restricted to lignin-degrading PODs; alternate enzymes, such as dye-decolorizing PODs, H_2O_2-generating oxidases, and certain laccase-like multicopper oxidases, also are used by basidiomycetes for lignin modification (92–94). Furthermore, Agaricomycotina lineages outside of this clade, such as Cantharellales and Dacrymycetes, are capable of degrading lignin and/or producing macroscopic decay patterns similar to white rot (93, 95–97). The presence of gene families and/or enzymes associated with lignin degradation has also been suggested from these lineages (14, 93, 98, 99), although lignin-degrading POD genes have not been detected in genome-sequencing studies of Dacrymycetes thus far (13, 14). Additionally, reconciliation analyses suggest the presence of some gene families associated with lignin modification, albeit in low abundance, before the evolution of the white rot decay mode

Fig. 2. Modern white rot, and Upper Devonian fossil specimens of *Callixylon newberryi* wood containing fungal hyphae or exhibiting patterns consistent with fungal decay. (*A*) Modern wood exhibiting macroscopic white rot decay pattern with patches of degraded tissue. (Scale bar, 5 mm.) (*B*) Acetate peel of *C. newberryi* illustrating extensive macroscopic decay consistent with fungal decay to the left of the arrow. Specimen from Kettle Point, Ontario, United States National Museum number 618400. (Scale bar, 1 cm.) (*C*) Longitudinal thin section of *C. newberryi* wood and associated fungal hyphae previously described and recognized as consistent with white rot decay, although without documentation of clamp connections necessary for placement in Basidiomycota (77, 138). Specimen is from the New Albany Shale of Indiana, University of Michigan Museum of Paleontology Paleobotany number 13834. (Scale bar, 25 μm.)

in Agaricomycotina (14). Thus, although it has been suggested that the white rot type of lignin decay evolved in the MRCA of Auriculariales and more derived Agaricomycetes in the Permian, alternate mechanisms of lignin degradation may well have evolved deeper in the phylogeny. Furthermore, although white rot Agaricomycetes are the most studied group of wood decay fungi, other fungal (100–107) and bacterial (101, 102, 108–114) lineages are either known lignin degraders or show some enzymatic capability for lignin decay, although the phylogenetic breadth, evolutionary origins, and degradative capacities of these lineages are far less understood. Taken together, there appears to have been no shortage of options available for the decomposition of lignified tissue in the pre-Permian world. Finally, an earlier evolution of POD-mediated lignin degradation in the Agaricomycetes themselves is still consistent with taking the molecular dating analysis at face value: Although a Permian mean age is recovered for this node, evolution as early as the Devonian is directly indicated by the 95% highest posterior density, and perhaps earlier if the stem lineage is included (13). Although a ∼120-Ma gap between Silurian lignin synthesis and Permian lignin degradation had been deemed most likely with genomic data taken in isolation, age range estimates encompass the possibility of closer temporal association between the evolutionary origin of lignin (∼420 Ma) and POD-mediated lignin decay—suggesting a more rapid evolutionary response by fungi to the evolution of this recalcitrant, defensive compound and highlighting the adaptive capacity of fungi.

If the waxing and waning of the massive coal deposits of the Late Paleozoic was not a consequence of delayed fungal evolution, then what was responsible for their abundance? An alternative explanation for Paleozoic coal production is indicated by two aspects of the North American history of organic accumulation rates (Fig. 1): (*i*) the sharp Carboniferous peaks in depositional rates and (*ii*) Paleogene rates of accumulation approximating Carboniferous rates. Neither is consistent with the evolution of novel fungal metabolisms permanently slowing peat accumulation rates, but both are instead consistent with physical, abiotic drivers (115–118). Organic matter can accumulate only where productivity outstrips decay (119, 120). Productivity is maximized in the wet tropics, and decay is reduced in the anoxic environments accompanying a stagnantly waterlogged substrate (4, 121, 122). During the Carboniferous, a massive amount of organic debris accumulated in warm, humid–perhumid equatorial wetlands formed during glacial periods, which was subsequently buried during interglacial phases (47). However, long-term preservation further requires crustal subsidence to ensure continued deposition instead of erosion (119, 123). Continental flexures formed in response to crustal thickening in active orogens (i.e., foreland basins) provide such a setting and are commonly associated with coal-bearing deposits, as their rates of subsidence and coal accumulation can be roughly comparable, permitting the formation and preservation of thick peats (124–126). Extensive foreland and cratonic basins, formed in association with the Pennsylvanian–Permian coalescence of Pangea and were positioned in the humid–perhumid, equatorial zone, ensuring the cooccurrence of both the subsidence requisite for long-term preservation of organic deposits and the climate necessary for promoting high water tables and biological productivity.

Through the later Permian and the Mesozoic, seasonally dry, savannah-like conditions pervaded most—although not all (e.g., China)—of the tropics (118, 127). Equatorial rainforests have been common in the Cenozoic, but the passive continental margins of the post-Pangean tropics led to more localized accumulations, such as in Southeast Asia and at higher latitudes in North America during the super greenhouse conditions of the earlier Cenozoic. These warm wet conditions during the Cretaceous–Paleogene permitted the formation of woody seed plant-dominated mire ecosystems in tectonic basins along the Western Interior Seaway of North America formed in association with the Laramide Orogeny, which ultimately gave rise to the thick coal beds of western North America (80, 124, 125, 128–131). Regional coal accumulation rates during this time approximated those of the Carboniferous (Fig. 1), albeit those coal accumulation rates were not integrated over so extensive a geographic area globally as in the Carboniferous. The occurrence of these substantial coal deposits 200 million years after the undisputed evolution of wood-rotting fungi sharply conflicts with the evolutionary lag model (132). Although at least some coal has accumulated at nearly all times since the evolution of vascular plants (133), the only time a wet tropics has coincided with globally extensive low-latitude foreland basin-like depositional systems over the last 400 million years has been during the Carboniferous assembly of Pangea. The magnitude of Carboniferous–Permian coal production was not a product of increased plant lignin content coupled with the delayed evolution of lignin-degrading fungi but rather a unique confluence of climate and tectonics.

Feedbacks between life and the Earth's surface over geological timescales are a growing scientific focus. The coupling of genomics and phylogenetics is a tremendously useful tool to expand geobiology to lineages and physiological capacities that might otherwise be invisible in deep time, as long as it is considered in the full geological context. In the present case, coal can be the most fossiliferous of fossil fuels, and, thus, the Carboniferous can speak for itself in demonstrating the role of decomposition and other environmental factors in the terrestrial carbon cycle. A variety of organisms and genomic pathways could have been involved in Paleozoic lignin degradation before the evolution of POD-mediated lignin decay by agaricomycete white rot fungi. Even if agaricomycete white rot fungi are considered exclusively, genomic data are directly consistent with the evolution of lignin degradation between the Devonian and Jurassic (13). Just as the original molecular clock calibrations of the phylogeny were based on different fossil constraints, the fossil record can then be used in an iterative process to determine what proportion of that temporal range is actually viable. Thus, the geobiological utility of phylogenetics and genomics is strongly supported here as long as they are treated as being among several equal constraints alongside the geochemical, sedimentological, and fossil records.

Methods

Data on organic-rich Phanerozoic sediments (peat, lignite, anthracite, coal, and tar) were extracted from the Macrostrat database (https://macrostrat.org) for continental North America [consisting of 23,813 mostly lithostratigraphic geological units representing 949 geographic subregions (134)]. Ages of all organic-rich sediments were estimated on the basis of general chronostratigraphic correlations to Phanerozoic time intervals (e.g., international stages) and stratigraphic superposition of geological units within those time intervals. Two metrics for organic-rich sediments were derived: (*i*) the total number of packages (Fig. 1*A*), which corresponds to the total number of sedimentary successions containing organic-rich sediment in each region in each 1-My time increment, and (*ii*) organic-rich sediment volume burial flux measured in cubic kilometers per million years (Fig. 1*B*). Volumes of organic-rich sediments required for volume flux calculations were based on sediment coverage area, unit thickness, and proportional abundance of organic-rich sediment within each unit (i.e., proportional lithological abundance was used to determine the thickness of the organic-rich component of a single Macrostrat unit). Our overall approach to volume flux calculation is comparable to that of Halevy et al. (135). Raw data are available at the following Macrostrat application program interface (API): https://macrostrat.org/api/v2/units?lith_type=organic&project_id=1&format=csv. Summarized data were plotted using the geoscale package (136) in R (137), and are available in Dataset S1.

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