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C. R. Geoscience 335 (2003) 65–78

COMPTES RENDUS GEOSCIENCE

Geodynamics / Géodynamique

A methane fuse for the Cambrian explosion: carbon cycles and true polar wander

Un fusible de méthane pour l'explosion cambrienne : les cycles du carbone et dérive des pôles

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Received 6 July 2002; accepted 21 October 2002

Written on invitation of the Editorial Board

Abstract

The dramatic diversification of animal groups known as the Cambrian Explosion (evolution's 'Big Bang') remains an unsolved puzzle in Earth Science. The Vendian–Cambrian interval is characterized by anomalously high rates of apparent plate motion, interpreted as True Polar Wander (TPW), and by more than a dozen large, high-frequency perturbations in carbon isotopes that dwarf all others observed through the past 65 million years. We suggest that these biological, tectonic, and geochemical events are intimately related in the following fashion. First, tropical continental margins and shelf-slopes which formed during fragmentation of the supercontinent Rodinia accumulated massive quantities of isotopically-light organic carbon during Late Neoproterozoic time, as indicated by strikingly heavy isotope ratios in inorganic carbon during interglacial intervals. Second, an initial phase of Vendian TPW moved these organic-rich deposits to high latitude, where conditions favored trapping biogenic methane in layers of gas hydrate and perhaps permafrost. Continued sedimentation during Late Vendian time added additional hydrate/gas storage volume and stabilized underlying units until the geothermal gradient moved them out of the clathrate stability field, building up deep reservoirs of highly pressurized methane. Finally, a burst of TPW brought these deposits back to the Tropics, where they gradually warmed and were subjected to regional-scale thermohaline eddy variation and related sedimentation regime changes. Responding to the stochastic character of such changes, each reservoir reached a critical failure point independently at times throughout the Cambrian. By analogy with the Late Paleocene Thermal Maximum event, these methane deposits yield transient, greenhouse-induced pulses of global warming when they erupt. Temperature correlates powerfully with biodiversity; the biochemical kinetics of metabolism at higher temperature decrease generation time and maintain relatively rich and dense invertebrate populations. Repeated thermal pulses along with progressive disruption and alteration of global ocean circulation patterns by TPW could cause the increase in diversity that accompanied the radiation of metazoans. We suggest that a methane 'fuse' ignited the Cambrian Evolutionary Explosion.

Résumé

La diversification dramatique des groupes animaux connus sous le nom d'Explosion cambrienne (le *Big Bang* de l'Évolution) demeure un puzzle non résolu dans le domaine des Sciences de la Terre. L'intervalle Cambrien–Vendien est caractérisé par des

1631-0713/03/$ – see front matter
doi:10.1016/S1631-0713(03)00011-7

taux anormalement élevés de mouvements apparents de plaques, interprétés en tant que migration polaire « vraie » (*True Polar Wander*, TPW), et par plus d'une douzaine de grandes perturbations à haute fréquence au niveau des isotopes du carbone, qui éclipsent par leur ampleur toutes celles observées au cours des derniers 65 millions d'années. Nous proposons que ces événements biologiques, tectoniques et géochimiques soient intimement reliés de la manière suivante. D'abord, les marges et les talus continentaux tropicaux formés pendant la fragmentation du supercontinent de Rodinia ont accumulé des quantités massives de carbone organique isotopiquement léger pendant le Néoprotérozoïque supérieur, comme l'indiquent les rapports isotopiques étonnamment lourds du carbone inorganique pendant les intervalles interglaciaires. En second lieu, une première phase vendienne de TPW a déplacé ces dépôts riches en matière organique à des latitudes élevées, où les conditions ont favorisé le piégeage de méthane biogénique dans des couches d'hydrates de gaz et, peut-être, de pergélisol. La sédimentation continue pendant le Vendien supérieur a ajouté un volume additionnel de stockage des hydrates de gaz et a stabilisé les unités sous-jacentes jusqu'à ce que le gradient géothermique les eût déplacées hors du champ de stabilité des clathrates, accumulant des réservoirs profonds de méthane à haute pression. Enfin, un événement rapide de TPW a de nouveau apporté ces dépôts aux tropiques, où ils se sont graduellement réchauffés et ont été soumis à des variations de turbulence à l'échelle régionale de la couche thermohaline et à des changements de régime de sédimentation. En réponse au caractère stochastique de tels changements, chaque réservoir a, indépendamment des autres, atteint un point critique, et ce tout au long du Cambrien. Par analogie avec l'événement maximum thermique de la fin du Paléocène (LPTM), ces gisements de méthane déclenchent des épisodes transitoires de réchauffement global par effet de serre lorsqu'ils entrent en éruption. La température est fortement corrélée avec la biodiversité ; la cinétique biochimique du métabolisme à température élevée diminue le temps de génération et maintient des populations invertébrées relativement riches et denses. Les impulsions thermiques répétées, suivies de rupture et changements progressifs dans les itinéraires de la circulation globale des océans dus au TPW, pourraient être la cause de l'augmentation de la diversité qui a accompagné la radiation des métazoaires. Nous proposons qu'une « mèche au méthane » ait provoqué la mise à feu de l'Explosion cambrienne.

Keywords: Neoproterozoic; Cambrian; Paleomagnetism; True polar wander; Methane; Clathrate; Evolution

Mots-clés : Néoprotérozoïque ; Cambrien ; Paléomagnétisme ; Dérive « vraie » des pôles ; Méthane ; Clathrate ; Évolution

1. Introduction

1.1. The Cambrian Explosion

Early Cambrian time, punctuated by a unique and dramatic series of geological and biological events, has fascinated and puzzled geologists and paleontologists for more than a century [109,110]. Widespread preservation of a detailed animal fossil record was facilitated by the almost simultaneous evolution of the ability to precipitate biominerals such as calcium phosphates and carbonates in nearly forty phyletic-level groups of animals [6,58,71]. While this abrupt appearance of diverse bodyplans in the fossil record was once thought to be coincident with the radiation of animal phyla, recognition of the Late Precambrian, soft-bodied Ediacaran fauna first suggested a divergence of various lineages deeper in geologic time [38].

Today this divergence preceding radiation is further supported by the presence of putative Mesoproterozoic animal trace fossils [35,89,98,118]; however, the apparent lack of a continuous fossil record for these traces suggests that they did not survive for long, possibly experiencing population bottleneck or going extinct during global catastrophes such as "Snowball Earth" events. Molecular-clock analyses have not yet converged on a consistent and robust divergence date: estimates for the main divergence of lineages range from Paleoproterozoic to Vendian time [4,7,12,13,23,30,37,45,72,88,94,101,112,113].

Furthermore, as indicated in Fig. 1, a nearly 50-year investigation of the Ediacaran fauna has revealed only a low diversity of forms [82]. There is even some concern that many of these animals might not be related to extant phyla [96,97]. Either way, the low diver-

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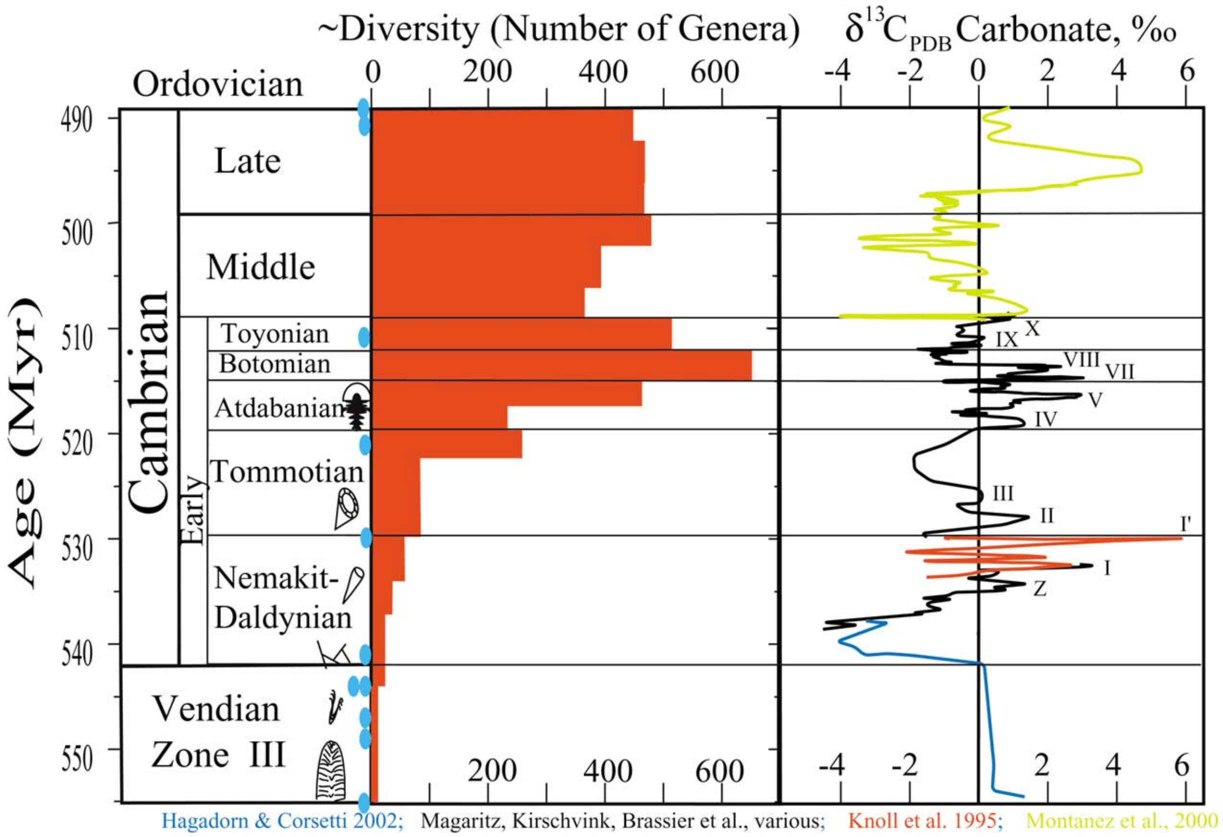

Fig. 1. Age constraints, biological diversity, and variations in inorganic carbon isotope ratios for Late Vendian and Cambrian time. Blue ovals along the left indicate the stratigraphic location of volcanic ashes that have been dated using U/Pb on zircon. Carbon isotope values from carbonate were compiled as follows: Blue curve from Corsetti and Hagadorn [18,19,42]; Black are the original data from Siberia [9,11,75,76]; red is the sub-Tommotian gap filled by Knoll et al. [65]; and Green is from the compilation of Montanez et al. [79].

Fig. 1. Contraintes d'âge, diversité biologique et variations dans les rapports isotopiques du carbone inorganique pour la période Vendien récent–Cambrien. Les ovales bleus sur la gauche indiquent la localisation stratigraphique des cendres volcaniques qui ont été datées par la méthode U/Pb sur zircon. Les valeurs isotopiques du carbone du carbonate ont été compilées comme suit : bleu, données de Corsetti et de Hagadorn [18,19,42] ; noir, données originales de Sibérie [9,11,75,76] ; rouge, lacune sous-tommotienne, comblée par Knoll et al. [65] ; vert, la compilation des données de Montanez et al. [79].

sity of Ediacaran fauna stands in stark contrast to the high morphological diversity displayed by Early Cambrian animals. Considering further the unexpected low diversity of forms preserved in otherwise appropriate and promising Neoproterozoic taphonomic settings [114–117], it seems likely that major changes in morphology and biochemistry actually took place during the Cambrian period. Hence, a major component of the massive diversification of life previously termed the 'Cambrian Explosion' does belong indeed to the Cambrian!

1.2. Geochronology

An age estimate of ∼610 million years ago (Ma) for the first appearance of trilobites [16] once implied that the Cambrian radiation event might span an interval of nearly 100 million years. However, an interbedded, zircon-bearing volcanic ash in the pre-trilobite sediments of Morocco (collected by JLK in 1988) yielded a U/Pb age of less than 525 Ma ([17], but see earlier hints for a shorter Cambrian duration [84]). Numerous U/Pb dates from stratigraphically bound zircon-bearing ash units now confirm that only ∼30 million years separate the first appearance of trilobites and the first appearance of graptolites as indicated in Fig. 1 [8, 17,26,41,49,69,70]. Concern that the continued contraction of Cambrian time might lead it to vanish entirely prompted the IUGS/IGCP working group on the Precambrian–Cambrian boundary to define the Cambrian Series base over 6 km stratigraphically below the first trilobites, at the present GSSP in Newfoundland [21]. This revised position, marked by the first appearance of a vertically-burrowing trace fossil, *Treptichnus pedum*, is now dated, in Namibia, at $\sim$543 Ma [41].

Compared to the duration of evolutionary events later in Earth history, this 'shrinking' of the Cambrian geologic timescale indicates an intrinsic background rate of speciation approximately twenty times higher than the average speciation rate for all Mesozoic time – well in excess of the $\sim$five-fold increase estimated by earlier studies [31]. Such recognition, based on recent, new constraints on the geologic timescale, demands re-examination and evaluation of possible relationships between several geologically unique events that occurred coincident with the Cambrian Explosion.

1.3. Cambrian carbon cycles

As compiled here in Fig. 1, one of the most puzzling and as yet unexplained features of the Cambrian Explosion is the sequence of over a dozen accompanying oscillations in inorganic δ^{13}C values preserved in carbonate, with typical negative-shift magnitudes of $\sim 4‰$ and sometimes larger [9–11,20,61,65,75,76, 91,107]. The composite record shows a large negative drop starting at the base of the first Cambrian biozone, coincident with the appearance of *T. pedum* [19,42], followed by a general rise to positive values of about $+6‰$ near the base of the Tommotian (carbon cycle I′ [65]). This trend is punctuated by several abrupt and sharp negative excursions (e.g., "Z", etc.). The following series of oscillations (II through X) extend into Middle Botomian time and span the classic interval of the Cambrian Explosion. Several more oscillations including a sharp negative swing at the Early Cambrian–Middle Cambrian boundary and a large positive excursion punctuate the Middle and Upper Cambrian [79]. In all, the revised geologic timescale indicates that each of these swings lasts approximately a few hundred thousand to perhaps a million years each. Frequently the excursions are asymmetric, with a sharp, $\sim$ten- to $\sim$hundred-thousand-year negative 'spike', followed by a more gradual return to more positive values.

No other set of multiple, high-frequency carbon-isotope perturbations of comparable magnitude, frequency, and duration ($\sim$15 to 20 million years) has been documented in all Earth history. The dominant cause of most of these oscillations is as yet unknown; they represent one of the major puzzles associated with the Cambrian explosion.

We must emphasize here that the Cambrian carbon cycles are robust features of the geological record. After their discovery in the mid 1980s [75,107], they subsequently correlated stratigraphic sequences between various Early Cambrian sections worldwide, thereby solving a long-standing problem of faunal provinciality that had inhibited selection of a Precambrian/Cambrian boundary stratotype [21]. Fig. 2 shows a typical example of this correlation ability for three sections of Tommotian and Atdabanian age on the Siberian platform, demonstrating the robust ability of these carbon cycles to provide detailed stratigraphic correlation.

Where local or regional paleo-environmental factors render absolute isotopic values different in magnetostratigraphically defined but spatially separated, synchronous sections, the position and sense of isotopic swings, maxima, and minima remain constant. Coexisting organic carbon (kerogen) records show expected fractionation with respect to inorganic carbon-isotope values [36,64,103,104]; where kerogen is absent, implied C-isotope correlation schemes are supported by other, independent tests (for a discussion, see [100]).

The unique style and pattern of these carbon oscillations, their detailed agreement with both paleontological and magnetostratigraphic constraints across nearly 400 km on the Siberian platform, and their invariance with dolomite/calcite ratios and other lithological factors argue persuasively that they record a primary signal of the Cambrian oceans [61]. When viewed in detail, individual Cambrian carbon cycles do bear some relation to biological evolution. For example, Hagadorn and Corsetti [19,42] note that the first sharp drop at the basal Cambrian (Nemakit–Daldynian stage) is followed closely by the initial evolution of vertical burrowing behavior. The subsequent

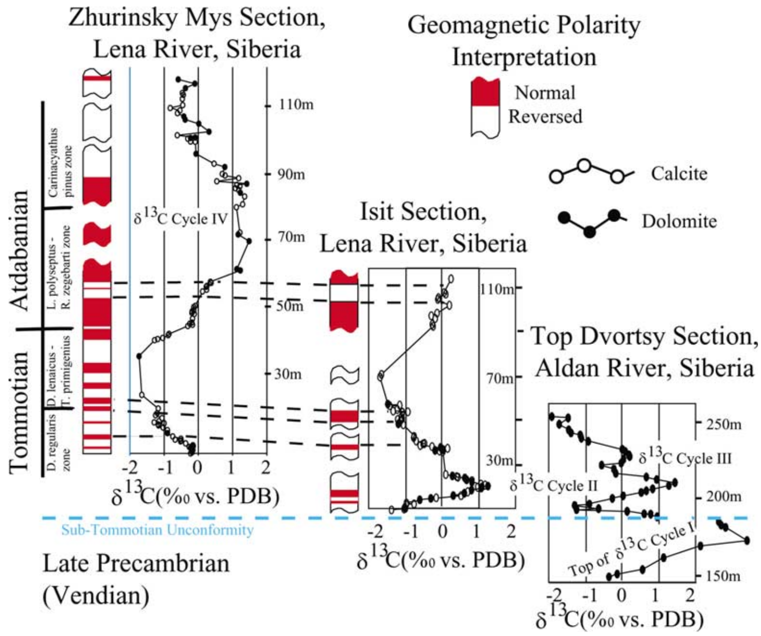

Fig. 2. Example of stratigraphic correlation using combinations of carbon isotope, paleontology, and magnetostratigraphy during Early Cambrian time. Note that the tie-in between the carbon data and magnetostratigraphy is exact, because selected fine-grained end-chips from the paleomagnetic samples of Kirschvink and Rozanov [60] were used by Magaritz et al. [75] and Kirschvink et al. [61] as the discovery samples which define the first five Cambrian Carbon Cycles. Figure is updated from [61].

Fig. 2. Exemple de corrélation stratigraphique utilisant des combinaisons entre rapports isotopiques du carbone, données paléontologiques et magnétostratigraphiques pendant le Cambrien ancien. À noter que la liaison entre les données relatives au carbone et magnétostratigraphiques est exacte, car des termes à grain fin, sélectionnés dans les échantillons paléomagnétiques de Kirschvink et Rozanov [62] ont été utilisés par Magaritz et al. [75] et Kirschvink et al. [61] en tant qu'échantillons de recherche définissant les cinq premiers cycles du carbone du Cambrien. Figure d'après [61], mise à jour.

global rise in δ^{13}C values is associated with the progressive radiation of molluscan-type fauna [65]. Similarly, sharp drops in δ^{13}C following carbon cycles II, III, and IV are followed by radiation of the archeocyathids, arthropods, and echinoderms, respectively, during Tommotian and Atdabanian time [61]. The sharp drop at the end of the Toyonian [79] is associated with the extinction of the archeocyathid fauna.

Historically, two general hypotheses propose biological association with these carbon cycles. In one, carbon cycles are driven by expansion and contraction of the biosphere itself [74,76]. In the other, carbon shifts directly fingerprint major climatic and geologic (physical) events on Earth's surface [79]; the biosphere presumably responds in accordance with observation, though specific selection pressures are not explicated [62].

1.4. Paleomagnetic data and true polar wander

Many investigators note that Cambrian time appears to be characterized by high dispersion among paleomagnetic pole positions determined for most major continental blocks [55,56,61,63,106,108]. Prior to 1997, few, if any, new age and stratigraphic-correlation constraints were integrated into the existing paleomagnetic database. Attempts to resolve the Cambrian dispersion problem by using numerical smoothing techniques yielded Apparent Polar Wander (APW) paths in disagreement with both geological observations and the best-constrained subsets of the data itself (see the discussion in Kirschvink et al. [62] and analysis in Evans et al. [33] comparing the uncorrected, temporally and spatially-smeared database for the Gondwanaland continents with that corrected for recent age and tectonic constraints).

Such application of updated age constraints reveals intrinsic rates of Cambrian apparent polar wander exceeding those expected from normal plate tectonics. A major part of these plate motions occurs during the time interval encompassing major Early Cambrian biological diversification [62].

Contentious suggestions that the Siberian APW path does not show such Cambrian motion [105] seemed to belie both that paleomagnetic data and its possible import for evolution. Ultimately, erroneous and arbitrary classification criteria used in the former Soviet database [59] obscured recognition of rapid Siberian APW. Furthermore, Early Ordovician tectonic deformation on the Siberian platformal margin completely or partially overprinted characteristic magnetic components, challenging simple determination of primary directions. Subsequent reinvestigations using experimental and statistical approaches designed to resolve such superimposed components demonstrate that large Early Cambrian APW motions comparable to those found on all other continents [54,87] do indeed exist in Siberia, confirming earlier investigation [61]. Kirschvink et al. [62] suggest that this burst of Early Cambrian, apparently rapid plate motion is reasonably explained by an episode of True Polar Wander resulting from an interchange event in Earth's moment of inertia tensor (termed an Inertial Interchange True Polar Wander, or 'IITPW', event).

All planets must spin about their principal moment of inertia [39,40]. Since inertial axes are determined by geodynamic processes on and within a planet, over time the magnitude of the principal moment of inertia (the largest eigenvector of the inertial tensor, defining one of three mutually perpendicular inertial axes) may weaken and eventually become equal to the intermediate moment of inertia, producing instability. Relative to its spin axis, the solid part (the mantle and crust) of such a planet can decouple from the remainder (the core) of the planet at a viscosity discontinuity (such as D$''$) and move relatively freely around the axis of the minimum eigenvector, which is always located on the equator. Thus relatively small changes in inertial configuration can lead to large shifts in the entire solid Earth relative to its geomagnetic field (produced in the liquid outer core). Angular jumps may reach 90° over time intervals as short as 5–15 million years [2,62,90].

IITPW events also predict consequent, non-eustatic sea-level fluctuations that agree to first-order with the geological record of Cambrian relative sea level changes [80]. Cross-continent comparison in an IITPW reference frame furthermore deduces an absolute paleogeography (both paleolatitudes and paleolongitudes constrained by paleomagnetic data to within $\sim 10^3$ km [62]). Such calculated paleogeography comfortingly yields a close approach between North America and the South American margin of Gondwanaland in Early Paleozoic time, supporting earlier suggestions [24,25].

Evans [32] notes that when Earth's principle and intermediate inertial moments are nearly equal, relatively small geological perturbations can induce IITPW events. In such a case, a single, isolated IITPW event is not any less conceivable than a series of multiple events in which the Earth pivots to and from about the minimum inertial axis. Intriguingly, the locus of Vendian and Cambrian paleomagnetic poles for North America (which, of all continents, displays the best-resolved APW dataset) describes an untrended, great-circle swath: time-sequential poles alternate between low and high paleolatitude. Such a pattern, if founded on reliable and well-time-resolved paleomagnetic data, is expected for multiple IITPW events but as yet unexplained by other scenarios. As detailed below, such motion of Laurentia from equatorial latitudes during Cryogenian glaciations [57] to a position near the South Pole during Mid-Vendian time, and back to the Equator during the Early Cambrian provides a mechanism for creating, storing, and 'exploding' methane 'time bombs' capable of producing the observed carbon cycles.

2. Methane-clathrate release and the Cambrian: A testable hypothesis

2.1. The Late-Paleocene thermal maximum (LPTM)

The LPTM event coincides with a sudden negative spike in inorganic δ^{13}C of magnitude comparable to that of the smaller Cambrian carbon cycles. Many exquisitely preserved deep-sea sediment cores span this interval and record both shallow-water and deep-sea carbon- and oxygen-isotope profiles. Zachos et al. [119] provide an excellent review of the globallyaveraged stable isotope trends, rhythms, and aberrations from the Cretaceous–Tertiary mass extinction event 65 million years ago to the present – a time interval comparable in length to that of the Late Vendian through Cambrian interval.

Characteristically, the LPTM event records a sudden drop in bulk carbonate δ^{13}C by $\sim -3‰$ [27], with a larger drop in shallow water Foraminifera than in deeper-water species. Orbital chronology calibration confines this event to at most a few 10^5 years [92]. Oxygen isotopes suggest that temperatures of Late Paleocene surface waters rose by as much as four to eight degrees Celsius [119], preceding turnover in the marine fauna [3] and a massive evolutionary radiation of mammalian fauna [14]. At present, the most robust hypothesis explaining the LPTM event involves rapid release of a large volume of methane stored originally as, or trapped under, gas clathrate [27–29,66,77].

Biogenic methane is produced by a group of Archaea (the methanogenic Archaeobacteria) during anaerobic metabolism of organic compounds; this biochemistry gives it isotopically light δ^{13}C values of ~ -60 to $-80‰$. Hence, quantifiable perturbation of the oceanic carbon-isotope balance requires volumetrically smaller amounts of organic carbon in methane than in other phases. Such perturbation does not necessarily require massive changes in net oceanic productivity or in biomass.

Methane hydrate at 0 °C is stable in the oceans at depths below ∼300 m; with increasing pressure, this stability temperature rises to ∼24 °C at 4 km [29,67]. Methane clathrates are found on most continental shelves where bottom waters are chilly and where methanogens are active in underlying sediment. Methane hydrate remains stable in these sedimentary reservoirs for long periods of time, but, with increasing burial depth, heating from the geothermal gradient will eventually move deeper layers out of the clathrate stability field (at ∼2 km water depth, the critical sediment burial is ∼500 m).

Until an entire clathrate field passes through burial inversion to free gas, a dynamically unstable situation persists, in which deeper sediments are overpressurized with gas, but are covered by hundreds of meters of clathrate-cemented sediment. Small seismic events or other physical disruption such as erosion can lead to sudden and dramatic sediment failure, releasing large volumes of methane gas. Such events may even be responsible for generation of destructive tsunamis [68].

Estimates from carbon-cycle models suggest that $\sim 10^{18}$ g of methane are needed to produce the observed LPTM isotopic signal in a modern-ocean model [28], a quantity we approximate by a clathrate 'ice cube' ∼20 km on edge. Although this quantity represents about 8% of conservative modern estimates of methane clathrate reserves, it is only a small fraction of the global carbon budget (including carbon locked in sediments and rocks; e.g., [67]).

Data from seismic stratigraphic studies provide strong support for this hypothesis: extensive volumes of Latest Paleocene sediment have been identified as disrupted by methane release. ODP drillcore at site 1051 on the Blake Nose penetrates the seismically disturbed interval; a disrupted mud-clasts lithology is intimately associated with the LPTM event [50,51].

2.2. *Cambrian comparison*

Carbon isotope variations during the Tertiary are much smaller in amplitude and fewer in number than analogous variations during the Neoproterozoic–Cambrian interval. The largest long-wavelength Tertiary oscillation (from Mid-Paleocene through Early Eocene) has an amplitude of only about 2.5‰ [119], whereas some of the Cambrian oscillations (e.g., I′) have swings of up to 8 to 10‰. In terms of shorter, faster excursions, the LPTM event is within a factor of two or so of the duration of some of the highest-frequency Cambrian cycles (e.g., II, III, V through X).

Hence, if deposits of methane clathrate are responsible for the Cambrian carbon cycles, several conditions must be satisfied: (1) Vendian–Cambrian time must support larger source areas for methane formation than the Cenozoic; (2) a plausible geological situation should lead to the conversion and accumulation of methane as gas hydrates; and (3) some global process must facilitate the episodic release of these overpressurized reservoirs over a long interval of time (randomly 'detonating' the methane 'bombs').

2.2.1. *Evidence suggesting massive production of methane*

Neoproterozoic carbon-isotope values from carbonates are unusually positive, with typical pre-glacial and inter-glacial values of about +5 to +10‰ [47,52, 53,64,78,111]. Production of these remarkably heavy values requires large relative partitioning of organic carbon into sedimentary reservoirs, assuming volcanic outgassing input of the same order as today.

We suppose that, as today, significant fractions of such organic carbon would be converted to methane by methanogenic Archaea; at appropriate depths and temperatures this gas would be trapped in the form of methane hydrate. Further assuming basic similarity to the Tertiary carbon cycle conditions, since no Tertiary carbon-isotope highstand approaches such heavy values, the Neoproterozoic and Cambrian organic carbon record attests to reservoirs much larger than those present in the Tertiary or on modern Earth.

2.2.2. Accumulation space for methane hydrates

Efficient accumulation of methane hydrate requires burial of organic-rich sediments and bacteriogenic-gas diffusion upward into an area within the clathrate stability field. Organic sediments typically accumulate on shallow tropical shelves which are neither deep nor cold enough to stabilize clathrate; thus conditions today for clathrate accumulation, such as in the modern-day Caribbean, are relatively rare (today, significant Arctic-shelf clathrate reservoirs likely exist but lie inaccessible and undiscovered). Neoproterozoic ocean basins, however, may have been more conducive to clathrate stabilization.

Schrag et al. [95] note that the post ~900 Ma presence of widespread passive margins at low latitude following the Neoproterozoic breakup of the supercontinent Rodinia and the equatorward drift of its fragments [34,57] may suggest enhanced susceptibility to local- or regional-scale anoxia. In this scheme, enhanced weathering of tropical landmasses increases riverine carbon and phosphorus inputs into nutrient-rich waters. Efficient recycling of phosphorus in anoxic basins allows for enhanced productivity and greater relative burial of organic to inorganic carbon [95].

Since, by Latest Vendian time, large areas of these organic-rich Laurentian and West Gondwanan rifted margins had moved (we suggest via true polar wander) from the tropics to high southerly latitudes, their methane-clathrate holding capacity was likely optimized (Figs. 3 and 4). During the ~50 million years separating the termination of the Marinoan glaciation and the base of the Cambrian, large reservoirs of

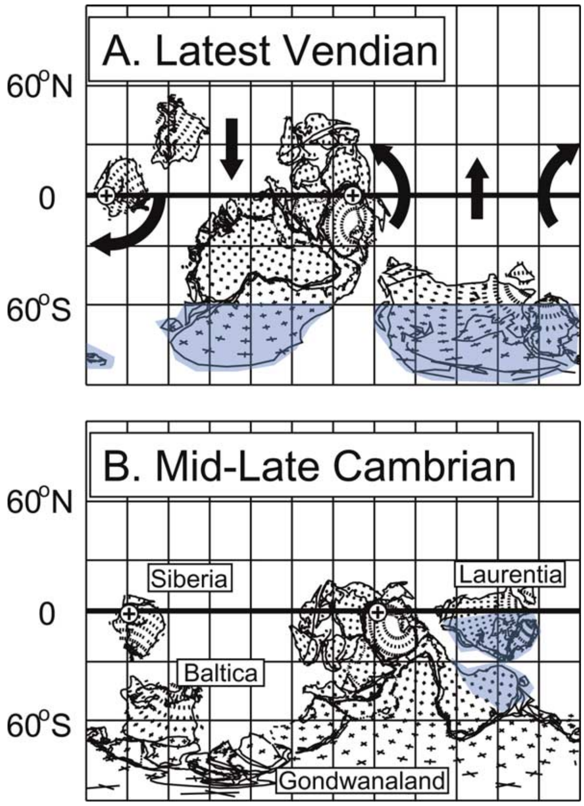

Fig. 3. IITPW reconstructions for Early and Mid/Late Cambrian time, adapted from Kirschvink et al. [62]. The areas located initially at high latitudes (above 60°) are shaded blue on both diagrams. The large ⊕ marks in Antarctica and Siberia are the approximate locations of the axis of the minimum moment of inertia, around which the solid part of the planet spins during the TPW event.

Fig. 3. Reconstitutions d'IITPW pour le Cambrien ancien, moyen et récent à partir des travaux de Kirschvink et al. [62]. Les secteurs situés initialement à des latitudes élevées (au-dessus de 60°) sont ombrés en bleu sur les deux diagrammes. Les grands signes ⊕ sur l'Antarctique et la Sibérie correspondent aux localisations approximatives du moment minimum d'inertie, autour duquel tourne la partie solide de la planète pendant l'événement TPW.

methane hydrate might expectedly accumulate in equilibrium with polar conditions.

2.2.3. Sedimentary burial and overpressurization

At typical sedimentation rates along passive continental margins of approximately ten meters per million years, we expect ~500 m of sediment to accumulate in a 50-million-year interval. At this depth, the geothermal gradient brings a sedimentary package out of its clathrate stability field. Notably, at the start of the

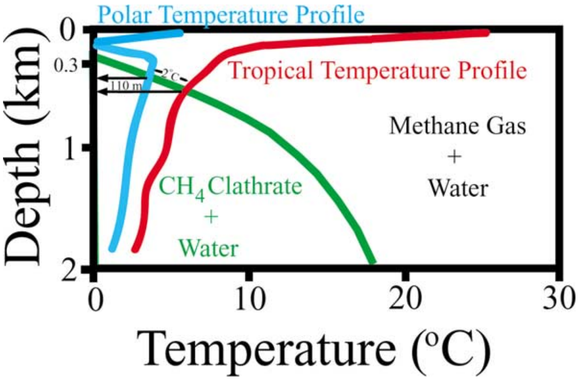

Fig. 4. Conservative, schematic tropical and polar water temperature profiles superimposed on the methane clathrate stability field. Note that in modest shelf-and-slope facies, the clathrate-free gas phase boundary shows relative sensitivity to changes in pressure over changes in temperature. An IITPW-induced non-eustatic sea-level rise of ∼110 m during Cambrian pole-to-equator transit (see [80]) would destabilize clathrates because of even moderately higher water temperature, depending on depth. Figure is modified from http://woodshole.er.usgs.gov/project-pages/hydrates/what.html and from http://www.msc.ucla.edu/oceanglobe/pdf/thermo_plot_lab.pdf.

Fig. 4. Profils schématiques conservatifs de température de l'eau tropicale et polaire, superposés au champ de stabilité du clathrate de méthane. À noter que, dans les faciès de talus et de pente modestes, la limite de la phase dépourvue de clathrate est relativement plus sensible aux variations de pression que de température. Une élévation non eustatique d'environ 110 m du niveau de la mer, induite par l'IITPW, pendant le transit pôle–équateur du Cambrien (voir [80]), déstabiliserait les clathrates, en raison d'une augmentation, même modérée, de la température de l'eau, en relation avec la profondeur. Figure d'après http://woodshole.er.usgs.gov/project-pages/hydrates/what.html et http://www.msc.ucla.edu/oceanglobe/pdf/thermo_plot_lab.pdf, modifiée.

Cambrian IITPW event large areas of Laurentia and Gondwanaland would be subjected to additional sedimentation as they slid from the pole toward the equator and into the carbonate belt. These areas would also experience an IITPW-induced non-eustatic sea level rise [62].

2.2.4. *Episodic release*

The epistatic nature of global circulation patterns coupled with pressure changes induced by sea level variations could subject broad regions to geologically sudden warming events, inducing sediment failure during rapid bursts of clathrate destabilization and methane emission. In scenarios involving multiple, rapid IITPW events or a prolonged IITPW event in which different continental margins experience climatic transition at different times, some or all of the extreme Cambrian carbon cycles could be accounted for by methane release.

3. Elaboration of the IITPW–methane hypothesis

3.1. *Perturbations to the carbon cycle*

Clathrate destabilization might account for portions of Cambrian carbon cycles either directly, by liberating isotopically light carbon into the global carbon cycle, or indirectly, by inducing second-order effects such as differential weathering and climate change, whose consequences (including changing riverine carbon-fluxes to ocean basins) could perturb the carbon cycle as well.

Furthermore, IITPW events might reasonably be expected to produce these sorts of consequences independently of methane-release, simply by altering paleogeographic positions relative to the Earth's spin axis on a quick and global scale. Thus synergistic factors may lead or lag actual clathrate destabilization and methane 'bursts'. Future carbon-budget models calculating conceivable methane-release volumes corresponding to the measured Cambrian carbon cycle values must thus be considered as upper-limits only, with all assumptions taken in perspective. Depending upon the mass and extent of the terrestrial biosphere, large methane clathrate deposits could also build up in permafrost layers on land.

At the initiation of a Cambrian inertial interchange event, these portions would move into lower latitudes and experience the start of major sea-level transgression for Laurentia, noted earlier. Both the warming local climate and the incursion of warmer (though still cold) seawater could destabilize permafrost-bound clathrate deposits [67]. Permafrost destabilization might in particular be responsible for the ∼five million year isotopic low observed during the first half of the Nemakit–Daldyn zone at the base of the Cambrian (Fig. 1).

3.2. *Clathrate-destabilizing mechanisms*

Methane clathrate deposits clearly should respond (stabilizing in some regions, destabilizing in others) to non-eustatic IITPW-induced sea-level change, but other physical 'triggers' lie in wait as well. IITPW events should alter ocean-scale thermohaline circulation by changing loci of bottom-water formation and patterns of global heat advection. Any duration of time many millions of years long will experience normal tectonic disruptions in some seafloor settings as well. Even regional-scale eddies – semi-chaotic and unpredictable in nature – can easily drive epistatic changes in, and evolution of, sediment-wave packages. Altogether, methane release by sedimentation regime change must be considered on equal footing with more-straightforward methane release by relative sea-level change in a fair and encompassing hypothesis.

3.3. Temporal independence and long-term susceptibility to methane release

Any IITPW event, regardless of duration, can leave a legacy of eddy instability patterns and sedimentation/erosion changes that are different from one geographic area to the next. Shifting eddies might be ephemeral or they might persist. A particular methane clathrate reserve might lie, untouched, as its sedimentation rate remains constant for some time during or after IITPW only to receive an independent or chain-effect perturbation to sedimentation/erosion further down the road [48].

3.4. Spatial independence and widespread susceptibility to methane release

Finally, during Inertial-Interchange True Polar Wander, continental margins located near the Earth's minimum inertial axis should rotate up to 90°, remaining upon the equator but switching their orientation. Even these shelf-and-slope regions, which move neither pole-to-equator nor equator-to-pole and which experience constant non-eustatic sea level, should experience fluctuating sedimentation and erosion rates due to thermohaline circulation changes.

4. Discussion

4.1. Predictions

Although some previous authors suggest that many of the sharp variations in carbon isotopes observed in the geological record may be related to methane release (e.g., [5,29,43,44,46,66,73,77,83,85,86]), to our knowledge no one has suggested a plausible scenario in which enormous quantities of methane could be stored and released on a timescale and in a repeated way capable of accounting for the Cambrian carbon cycles. The IITPW–carbon hypothesis outlined above may do this. This hypothesis also leads to some testable predictions: (**a**) barring tectonic overprinting or geodynamic recycling, there should be evidence of sedimentary disruptions in deeper-water facies associated with methane release; (**b**) there should be significant thermal perturbations associated with the faster carbon oscillations; and (**c**) if related and not merely coincident with biological diversification during the Cambrian Explosion, there should be a genetic link between these geophysical and geochemical events and natural selection pressures that drive evolution. We consider each in turn (§3.1.1–3.1.3).

4.2. Sedimentary disruptions

Cambrian time is, in fact, littered with examples of sedimentary slumping and intraformational breccias, flat-pebble conglomerates, etc. Some of these sedimentary structures occur on a massive scale, ranging from disrupted bedding horizons in Sardinia [15] and Colorado [81] to the collapse of a ∼60-km length of carbonate platform preserved in present-day British Columbia [102]. To our knowledge, these have not been examined systematically such that they can test the hypothesis suggested here that they might relate to sudden methane escape. Previous interpretations have mainly invoked biological processes (e.g., [99]).

4.3. Temperature fluctuations

By analogy with the LPTM event outlined above, the addition of carbon from methane in quantities large enough to perturb inorganic carbon-isotope ratios (e.g., [28]) ought to produce a measurable temperature increase through simple greenhouse warming – both due to potent atmospheric methane during the volume-dependent but brief period of time immediately following a clathrate destabilization event and during the prolonged, exponential decay of its oxidized CO_2 decay-product. Shifts in the carbonate oxygen-isotope record would best test for such an effect. Unfortunately the oxygen signature for most ancient carbonates has been altered by subsequent diagenesis and is only rarely preserved.

4.4. The IITPW–carbon hypothesis as a mechanism for the Cambrian Explosion

In response to the LPTM 'methane shotgun' warming pulse, the terrestrial biosphere underwent a massive burst of speciation (e.g., [14]). In effect, the Eocene mammalian radiation is analogous to the Cambrian Explosion except that it consists of one short evolutionary burst rather than a series of repeated bursts.

In the modern world, temperature is the physical parameter that displays the strongest correlation with biological diversity [22]. Biochemical metabolism kinetics are faster at higher temperatures and thus decrease a species' generation time while supporting a robust population more likely to survive sudden or extreme selection pressures. Therefore, in one possible explanation for the Cambrian Explosion, repeated IITPW-induced, methane-release thermal-cycling events incrementally inflate biological diversity, filling and refilling niches with increasingly optimized communities of species. This hypothesis is broadly supported by quantitative models consistent with expansive modern datasets [1] and with paleontological databases [93]. Indeed, as noted previously, many major excursions in Early Cambrian carbon cycles are followed by a clear evolutionary burst in one or more phyletic groups.

In summary, we suggest that the rapid diversification of species and innovation of bodyplans in the Early Cambrian could have been driven by extreme environmental conditions forced by methane clathrate decomposition, induced by an inertial interchange true polar wander event and recorded in the unique sequence of Cambrian carbon cycles.

Acknowledgements

The authors acknowledge Paul Hoffman and an anonymous reviewer; Eiichi Tajika, Ryuji Tata, Keiko Matsuoka, and Tatsuo Oji; Rob Ripperdan, Jess Adkins, David Evans, Adam Maloof, Bob Berner, Mark Pagani, Jim Kasting, Ellis Yochelson, and Osvaldo Ulloa gave helpful and probing comments. This work was supported by the NASA Astrobiology Institute, by NSF-EAR 98-14608 to JLK and by an NSF Graduate Fellowship to TDR.

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