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We gratefully acknowledge the support of the sponsors for making this meeting possible.

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Oral presentation Abstracts

The Cambrian Explosion: Animals or Fossils?

Kevin J. Peterson
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Paleontologists have long pondered whether the Cambrian explosion of animal life represents the initial and coeval diversification of animals themselves, or instead simply the first appearances of animal fossils. Molecular clocks fully support an extended, but cryptic, Precambrian history of animals, with their initial diversification taking place in the latter part of the Cryogenian, and much of the bilaterian diversification, including the initial evolution of most phylum-level total-groups, occurring during the Ediacaran; the clock also suggests that the evolution of most phylum-level crown-groups took place during the latest Ediacaran-Cambrian, consistent with the known fossil record. To explore why the fossil record does not record this initial diversification it is necessary to tease apart the relative size and complexity of these Precambrian bilaterians: were they small and simple like a modern acoel flatworm, or were they relatively large and complex like a living enteropneust or polychaete annelid? To distinguish between these two end points, we turned to microRNAs, regulatory RNA genes whose evolution seems to track relative morphological complexity such that complex animals like vertebrates have many more microRNAs than simple animals like sponges. Characterization of the microRNA repertoires of two morphologically simple bilaterians – acoel flatworms and rotifers – strongly suggests that these animals are not primitively simple, but instead are secondarily reduced. The microRNA data further suggests that the last common ancestor of living bilaterians should have been large and complex enough to leave some sort of trace fossil record at some point in the 100 million years leading up to the Cambrian explosion, assuming environmental controls on animal size like relative oxygen content were the same then as today. Given the unlikelihood of that statement being true though might help to elucidate the underlying reasons for the discrepancy between the known geologic and the genetic fossil records.

Speaker Biography

Kevin J. Peterson is a professor of Biological Sciences at Dartmouth College (Hanover, NH). He received his undergraduate training in Biology at Carroll College (Helena, MT), and earned his Ph.D. in Geological Science from the University of California, Los Angeles. His works centers on using molecular tools to address the origin and early evolution of animals.

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Homeobox genes and body patterning at the dawn of Bilateria

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In trying to understand the Cambrian explosion we must not ignore the developmental and genetic changes that happened within animals. Most animal phyla, and especially those that expanded in diversity at the base of the Cambrian, belong to the Bilateria. This is a vast clade of animals sharing (ancestrally) bilateral symmetry, centralised nerve cords, anterior sense organs, a brain, lateral muscle blocks and a through-gut with separate mouth and anus. Together, these features enabled animals to exploit the world in three-dimensions, including burrowing, crawling, swimming, and active hunting or escaping. We argue that there are core sets of developmental control genes involved in building this body plan right across the Bilateria, including three related sets of homeobox genes for patterning the central nervous systems, the mesoderm and the gut. For example, we suggest that the ancestral bilaterian gut was patterned by a ParaHox gene cluster including genes for mouth, midgut and anus. The evolution of these developmental patterning systems was likely to have been pivotal in the emergence of animal diversity.

Speaker biography

Peter Holland is the Linacre Professor of Zoology and Head of the Department of Zoology at the University of Oxford. After a degree in Zoology and a PhD in Genetics, he has spent the past 25 years undertaking research into animal diversity, with a particular focus on the evolution of homeobox genes. He has been awarded the Genetics Society Medal, the De Snoo Prize, the Scientific Medal of the Zoological Society, the Linnean Medal for Zoology and the Kowalevsky Medal, and is a Fellow of the Royal Society. His recent book *The Animal Kingdom: A Very Short Introduction* (OUP) provides an overview of animal evolution for the non-specialist.

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Transient Ocean Chemistry during the Cambrian Explosion

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The Great Unconformity formed during an episode of extensive continental denudation during the Late Neoproterozoic and Early Phanerozoic that affected the interiors of multiple cratons. The stripping and removal of large volumes of preexisting sedimentary rock cover required to form the Great Unconformity resulted in exposure of crystalline basement rocks across an area that is unprecedented in the rock record. Because rates of chemical weathering of continental crust are controlled largely by exposure of silicate basement rocks to the atmosphere, the formation of this surface may have strongly affected the ionic composition of seawater immediately prior to and during the Cambrian period.

Multiple lines of evidence suggest that elevated chemical weathering of continental crust resulted in an enhanced flux of HCO_3^-, Ca^{2+}, Fe^{3+}, $H_3SiO_4^-$, Mg^{2+}, and K^+ to the terminal Neoproterozoic-Cambrian oceans, coincident with the initial acquisition of skeletons by metazoans and the Cambrian explosion. The global curve of $^{87}Sr/^{86}Sr$, which tracks relative contributions from continental crustal weathering (^{87}Sr) vs. volcanic (^{86}Sr) inputs, reaches a ~1 b.y. maximum during the Cambrian period despite evidence for extensive ridge activity Evidence of transient changes in the weathering flux of continental crustal weathering products to the ocean comes from unusual patterns of chemical sedimentation during the Cambrian. The inner detrital belt is marked by a Phanerozoic peak in the abundance of glauconite and non-analogue conditions of glauconite authigenesis, in which precipitation occurred more rapidly and across a broader range of environments than during most times in the Phanerozoic. In addition, abundant sandstone intraclasts, often in association with glauconite, provide evidence of carbonate cementation at or near the seafloor prior to wave disturbance. The carbonate platform belt is marked by Phanerozoic highs in both area and burial flux of shelf carbonate, the majority of which was photosynthetically-derived and grain-poor. Peaks in the abundance of flat-pebble conglomerates and oncolites also reflect the influence of early carbonate precipitation. The mudstone-dominated outer detrital belt is characterized by pervasive carbonate cementation at the seafloor, a factor that was critical in promoting widespread preservation of Burgess Shale-type fossils. Carbonate nodules and concretions bearing seawater $\partial^{13}C$ values are also common.

Continental denudation to exhume igneous and metamorphic rocks formed at crustal depths must have occurred at diachronously across different cratons, resulting in the formation of regolith at and above the Great Unconformity. The chemical weathering potential of regolith is rapidly expended in the absence of physical mobilization and reworking that expose fresh mineral surfaces to atmospheric weathering. Wave action associated with transgression would have provided an effective means of mobilizing continental regolith and increasing reactive surface area. Subsequent regression would have resulted in the exposure of fresh, wave-broken sediments to atmospheric weathering. Terminal Neoproterozoic regression, and the many episodes of regression that occurred during the overall Cambrian transgression, provided a mechanism for synchronous pulses of chemical weathering products to the oceans before, during, and after the Cambrian explosion, prior to the re-covering of large areas of cratonic basement rock beneath early Phanerozoic sediments that remain there to this day.

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Glacio-eustasy during the Cambrian Explosion – a control on macroevolutionary patterns?

Howard A. Armstrong[1] David A. T. Harper[1] João Trabucho-Alexandre[1] M. Paul Smith[2]

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The Cambrian Explosion is widely regarded as occurring during a long interval of greenhouse climate following the intense glaciations of the late Neoproterozoic "Snowball Earth." The notion of a prolonged Early Palaeozoic greenhouse climate has been challenged for the Ordovician when repeated glaciations (ice ages) have been attributed to orbitally induced amalgamation of small – medium-sized ice sheets. The $p\mathrm{CO}_2$ and GCM model for the Mid- and Late Cambrian indicates similar global mean temperature and latitudinal temperature gradients to those of the Ordovician and raises the possibility of Cambrian ice ages. Here we reconstruct the depositional environment and sequence stratigraphy of the distal Buen Formation (Atdbanian-Botomian: *syn.* "Transitional Buen") and associated Sirius Passet Lagerstätte. We report: 1) a storm-dominated shelf environment with background sedimentation controlled by a combination of pelagic and advective processes; 2) 4th order (400 kyr) and 3rd (1.2, 2.4 myr) order eustatic cycles, and 3) coincidence with the onset of the Mingxinsi Carbon Isotope Excursion MICE positive carbon-isotope excursion. Together these indicate the formation spans an icehouse to greenhouse interval that coincides with an increase in ordinal extinctions. This Ice Age terminated the Early Cambrian radiation.

Speaker Biography

Howard's early research concentrated on conodont palaeobiology and the Hirnantian mass extinction. More recently he has been involved in innovative work on: 1) Early Palaeozoic climate change, mapping climate belt shifts during extreme climate change; 2) Understanding the controls on third order eustasy and black shale deposition in shelfal settings; 3) Studies of monsoon dynamics during the Neogene linked to Himalayan and Andean exhumation; 4) the geological evolution of the Eastern Tethys and, 5) geotectonic controls on the initiation of the Antarctic Ice.

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Recent advances in understanding Cambrian Lagerstätten - the Emu Bay Shale

Gregory D. Edgecombe, James G. Gehling, James B. Jago, Diego C. García-Bellido, Michael S. Y. Lee, Allison C. Daley, and John R. Paterson
Natural History Museum, London

The early Cambrian (Series 2, Stage 4) Emu Bay Shale is the most diverse Cambrian Konservat-Lagerstätte known from Australia and provides a unique source of data on the composition of animal communities from the main window of the Cambrian explosion in East Gondwana. The Emu Bay Shale occurs within a clastic-rich shelf succession dominated by conglomerate and sandstone. Non-biomineralised fossils were first found alongside trilobites at Big Gully on the north coast of Kangaroo Island, South Australia, in the early 1950s, and the first formal descriptions in 1979 documented a palaeoscolecid, bivalved arthropods (*Isoxys* and *Tuzoia*), and vermiform problematica. Subsequent descriptions in the 1990s added *Anomalocaris*, revised *Myoscolex* as an opabiniid, and revised the more common trilobites. Biannual excavations since 2007 in a quarry 500 m inland of the original coastal sites have increased the number of species to a total of over 50, among them various animal groups not previously known from Australia. The basal 10 m of the Emu Bay Shale containing the Konservat-Lagerstätte is composed of dark grey to black laminated micaceous mudstones interpreted as having been deposited in isolated, stagnant, anoxic to oxic depressions on the sea floor. The water column was normally oxic, with a sharp redox boundary at the sediment-water interface. About 75% of the species are non-biomineralised, though trilobites (especially *Estanigia* and *Redlichia*) are numerically the most abundant fossils. About half the species are arthropods, including new genera related to taxa already known from Burgess Shale-type (BST) deposits on other palaeocontinents, such as a new group of nektaspids (two genera classified as the family Emucarididae), a helmetiid (*Australimicola*), and a leanchoiliid (*Oestokerkus*). Some arthropod genera, such as *Squamacula* and *Kangacaris*, are shared only with the Chengjiang biota, as expected from the relative palaeogeographic proximity of South China and East Gondwana. Other elements in the biota include sponges, a vetulicolian, brachiopods, hyoliths, an *Odontogriphus*-like mollusc, a polychaete, and an armoured lobopodian. Recent studies have revised the two species of *Anomalocaris*, revealing internal structures in the body flaps not known from species in other BSTs, and revised the palaeoscolecids as two species of *Wronascolex*. Although the constituent taxa represent a typical Burgess Shale-type fauna, Emu Bay Shale fossils commonly display a range of taphonomic modes that otherwise rarely occur in most other BST deposits, particularly phosphatisation and pyritisation. This allows such structures as midgut glands, muscle and the visual surfaces of eyes to be preserved. In particular, complex compound eyes of arthropods (including those of *Anomalocaris* with the visual surface well preserved) show that acute vision had evolved by the early Cambrian.

Speaker Biography

Greg Edgecombe has been a Research Leader at the Natural History Museum in London since 2007. He worked as a researcher at the Australian Museum for 14 years. His research involves the relationships between major arthropod groups based on morphology (including fossils) and molecular sequence data, and the systematics of centipedes.

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Recent developments in understanding Cambrian Lagerstätten – Sirius Passet

David A. T. Harper[1], M. Paul Smith[2], Emma U. Hammarlund[3], Martin Stein[4] and Jakob Vinther[5]

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Sirius Passet, located in Nansen Land on the northern edge of Greenland, is the most remote and arguably poorest known of all three key Cambrian Lagerstätten. Recent expeditions in 2009 and 2011 measured and sampled, bed-by-bed, the critical exposure of the Transitional Buen Formation (lower Cambrian) at the classic locality southwest of the Sirius Pass. Field counts and identifications of thousands of *in situ* fossils through almost 13 m of exposed strata have precisely delimited the context and extent of the Lagerstätte horizons and charted in outline, for the first time, faunal dynamics through the section. These data have helped develop new insights into the environmental setting of one of the first animal-dominated ecosystems. Firstly, the new collections contain at least ten new taxa and rarefaction curves for many horizons suggest there are still more awaiting discovery. Secondly, the distributions of some 50 species, dominated numerically by the abundant trilobite *Buenellus* and the bivalved *Isoxys* have been related to substrate type, geochemical proxies and the presence of microbial mats and trace fossils. The abundance data, displayed as spindle diagrams, through the middle part of the succession maps out a range of biofacies characterized by varying proportions of annelids, arthropods and lobopods amongst many others. Thirdly, specific associations have been identified, for example the marked correlation between the occurrence of large soft-bodied arthropods, microbial mats together with sub and under-mat miners. Fourthly detailed sedimentology and the geological setting confirm the deep-water setting of the Sirius Passet faunas, predominantly composed of near autochthonous faunas with some allochthonous elements, transgressing an older carbonate platform. Finally a number of taphonomic pathways, including the mouldic preservation and silicified gut contents, supplement the widespread Burgess Shale Type of preservation.

Speaker Biography

David Harper is a leading expert on major events in the history of life and numerical methods in palaeontology. He is Professor of Palaeontology in the Department of Earth Sciences, Principal of Van Mildert College and Deputy Head of Colleges (Research and Scholarly Activities). He was previously Professor of Palaeontology and Head of Geology in the Natural History Museum of Denmark, University of Copenhagen. He is a Foreign Member of the Royal Danish Academy of Sciences and Letters, an Einstein Professor in the Chinese Academy of Sciences and a past President of the International Palaeontological Association. He has published over 10 books and monographs, including a couple of influential textbooks, as well as over 250 scientific articles and, together with Øyvind Hammer, the widely-used software package PAST. His research is mainly field-based and he has led expeditions to many parts of the world including central Australia, Chile, Greenland and Tibet.

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The hard parts of the Cambrian explosion - multiple origins of animal skeletal biomineralization

Duncan Murdock
University of Bristol/University of Bath

The origin of mineralized skeletons is integral to the controversy around the nature of the Cambrian explosion, confounding the 'animals or fossils' debate; the advent of hard tissues fundamentally changed both the ecology and preservation potential of many Cambrian animals. The fossil record alone has failed to resolve this. It is not clear whether the abundant skeletal remains of the Lower Cambrian represent the simultaneous acquisition of novel structures, or the explosive diversification of an existing ancestral skeleton. Traditional methods of unravelling this history, from the neontological record, have aimed to derive a theory of the development of biomineralization through evolution by the comparison of mineralized systems in model organisms. This has led to the recognition of the 'biomineralization toolkit' and raised the question of the homology of mineralized tissues versus convergent or parallel evolution. The 'new animal phylogeny' reveals that many of the groups known to biomineralize sit among close relatives that do not, and it favors an interpretation of convergent or parallel evolution for biomineralization in animals. By combining recent analyses of divergence time estimates for deep branches of the animal tree with first appearance data, interpretations of biological affinity and ecology of the small shelly faunas it is possible to demonstrate that the fossil record of the earliest mineralized skeletons presents a rapid proliferation of biomineralization across a range of animal phyla with fossil representatives of many modern biomineralizing phyla. In addition, a growing consensus around the importance of developmental drivers of the Cambrian explosion supports the convergent or parallel evolution of biomineralization in animals at the phylum level. The fossil record of the Cambrian explosion, therefore, not only provides vital evidence for the evolution of animal mineralized tissues but also suggests a mechanism for its rapid and synchronous convergent origin.

Speaker Biography

Duncan Murdock is a post-doctoral researcher at the University of Bristol (currently a temporary teaching fellow at the University of Bath). His doctoral research focussed around developing and applying micro-tomography and computational functional analysis to unravel the mode of growth, affinity and ecology of some of the earliest biomineralizing animals. His subsequent research has led to the application of the same techniques to the remains of some of the earliest terrestrial plants, contributing to our understanding of the acquisition of characters that allowed plants to colonise the land. Other research interests include: the relationship between taphonomy and phylogeny, having conducted decay experiments on velvet worms to better place controversial lobopodian taxa on the panarthropod stem; and the early evolution of the oldest biomineralizing vertebrates, the conodonts.

NOTES

Animal-substrate interactions and the Cambrian explosion

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The Cambrian explosion has been essentially analysed based on three different datasets: the traditional body-fossil record, molecular clocks, and the trace-fossil record. The trace-fossil record has three advantages with respect to the body-fossil record: (1) it provides evidence of soft-bodied organisms, (2) it is by far the most continuous record through the Ediacaran-Cambrian boundary, and (3) it represents direct evidence of behaviour, recording the multiple ways in which organisms interact with the substrate. This makes them an excellent proxy to decipher breakthroughs in marine ecology at a macroevolutionary scale.

A systematic analysis of the ichnologic record of the Ediacaran-Cambrian transition, based on a database comprising 369 stratigraphic units, strongly supports the Cambrian explosion, and provides further detail into the timing of different events. By the Fortunian, the diversification event evidenced by the appearance of complex architectural designs reflecting behavioral innovations was well underway. The high ichnodiversity and ichnodisparity clearly indicate that a major phase of the evolutionary radiation occurred earlier than suggested according to the classic Cambrian explosion scenario.

In addition, the ichnological record of the Ediacaran-Cambrian transition indicates that body-plan diversification and ecological structuring were decoupled. The appearance of a wide repertoire of behavioural strategies and body plans occurred by the Fortunian. However, a major shift in benthic ecologic structure, recording the establishment of a suspension-feeder infauna, increased complexity of the trophic web, coupling of benthos and plankton, and re-organization of the infaunal ecospace took place during Cambrian Stage 2. Both phases were accompanied by different styles of ecosystem engineering, but only the second one resulted in the establishment of the modern mixground ecology. In turn, the suspension-feeding infauna may have been the ecologic drivers of a further diversification of deposit-feeding strategies by Cambrian Stage 3.

The discovery of trace fossils in lower to middle Cambrian Burgess Shale (BS)-type deposits provided uncontroversial evidence of an *in situ* benthic community in environments that were previously regarded as anoxic. However, if these ichnofaunas are compared with those typical of sub-wave base coeval environments, BS-type ichnofaunas show very limited colonization of the infaunal ecospace, suggesting stressed conditions for an epibenthic and shallow burrowing biota. In particular, the small size and the negligible penetration depth of biogenic structures indicate that the redox discontinuity surface was close to the sediment-water interface, whereas the fine preservation of morphologic details suggests firm substrates. In addition, preservation of surficial and shallow-tier BS-type trace fossils reflects an evolutionary signal. The deep-tier *Chondrites-Zoophycos* ichnoguild, formed by permanent structures of deposit feeders and chemosymbionts in dysoxic settings, does not occur in BS-type Cambrian deposits, representing a later evolutionary innovation. The absence of deep-tier colonization in Cambrian dysoxic settings and of a well-developed mixed layer opened a taphonomic window for the exceptional preservation of diminutive, delicate surficial and shallow-tier trace fossils.

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Did bioturbating 'ecosystem engineers' fuel the Cambrian explosion?

Duncan McIlroy
Memorial University of Newfoundland

Since the definition of the Precambrian-Cambrian boundary at the base of the *Treptichnus (Phycodes) pedum* ichnozone—at the type section in southeastern Newfoundland—ichnological research has been a key part of the evidence for the early evolution of complex animal life. Study of the most complete stratigraphic successions worldwide has largely vindicated the usefulness of the boundary decision. That the base of the Phanerozoic can be defined on ichnological grounds also supports the inference that the advent of burrowing is in some way tied to the evolution of early animal life.

This talk explores from a conceptual perspective the first order biogeochemical challenges that the earliest (Ediacaran) benthic macro-organisms would have experienced.

1) Why did macro-organisms first locomote?
2) Why did they first burrow?
3) What drove the adaptive (behavioural) evolution of burrowing styles?

The biological controls on the evolution of the benthos are explored through consideration of the Precambrian to Cambrian transition in Newfoundland, Canada. Recent work has uncovered the earliest trace fossils (surface trails) from the Mistaken Point Formation of southeastern Newfoundland, and the trace fossil rich strata of the type sections of the Precambrian-Cambrian boundary allow us to track the evolution of complex burrowing strategies through the Fortunian stage of the Lower Cambrian. The complete spectrum of fundamental behavioural styles that characterize the rest of the Phanerozoic are inferred to have been present at around the base of Cambrian Stage 2.

Earlier work has suggested that the evolution of bioturbation was likely to have increased the microbial biomass of marine sediments, creating a positive feedback loop that is hypothesized to have fuelled the Cambrian Explosion of complex animal life. With the advent of pervasive bioturbation there is an increased supply of bio-limiting nutrients to the microbiota of the sediment, which in turn constitutes the food resource to sustain larger more efficient bioturbators.

Modern understanding of the linkages between bioturbation and nutrient cycling allows refinement of this model. The first burrowing organisms are here considered to be ecosystem engineers- organisms that modify their environment through their life actions. The evolution of burrowing organisms was transformational in creating dynamic, strongly three dimensional (Phanerozoic-type) benthic environments from the pre-existing—essentially two dimensional—Precambrian seafloor. This is considered to be ecosystem engineering on the grandest scale.

Speaker Biography

Professor Duncan McIlroy is Canada Research Chair in petroleum Geoscience at Memorial University of Newfoundland, Canada. The evolution of early animal life, has been a focus of Duncan's research since starting his Ph.D. at Oxford University with Martin Brasier. Duncan has published widely on the subject of ichnology as it relates both to the early evolution of complex animals and to petroleum geology. The ichnology research group at Memorial is a thriving centre for ichnological research, currently with a team of 14 graduate students and one technician (www.ichnology.ca).

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The invention of Phanerozoic food webs

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Food webs are patterns of who eats whom, and the associated cycling of nutrients and biomass. At the base of all food webs are primary producers, which are consumed and redistributed through a variety of heterotrophic organisms, often arranged sequentially via trophic tiering. The local expression of any particular food web is determined by the interplay of 'bottom-up' resources (competition) and 'top-down' consumers (predation). On a larger scale, however, they are dependent on the overall diversity, body sizes and connectivity of the constituent nodes, which in turn controls ecosystem function, biogeochemical feedbacks and evolutionary potential.

Prior to the rise of ingestive multicellular heterotrophs (animals), food-webs were presumably limited to few tiers and microscopic size, comparable to the bacteria-flagellate-ciliate microbial loop that dominates modern oligotrophic oceans. The small size and billion-year stasis exhibited by pre-Cryogenian fossil assemblages attests to the absence of animal-based ecology and limited trophic innovation.

The early Cryogenian appearance of sponge-grade multicellularity allowed flagellate organisms to overcome the tyranny of viscous flow, introducing a fundamentally new process to food-web dynamics. Macroscopic, turbulent-flow suspension feeding would have had major effects on water column ventilation and nutrient cycling in shallow shelf settings. Even so, the limited ability of sponges to consume larger particles or to move, combined with their inherent unpalatablity, suggests that they contributed relatively little to the expansion of trophic diversity.

The early Ediacaran appearance of cnidarian-grade multicellularity (eumetazoans) introduced both muscular motility and a potential for macrophagous ingestion into the trophic mix. Like sponges, however, jellies are largely a trophic dead-end, and their blind gut and limited brain-power would have had only modest, primarily indirect, effects on early food-web dynamics.

By contrast, the (?)mid-late Ediacaran evolution of cephalized bilaterians with a through gut revolutionized the structure, function and evolutionary potential of food webs. Bilaterians readily eat other bilaterians, and have the neural, locomotory and developmental capacity to derive sequentially higher-order trophic tiers, opening up fundamentally new regions of ecospace based on large body size and complex multi-trophic intercations. Compounding counter-responses in underlying tiers further multiplied diversity and ecological repertoires, including escape into sediments and escape into the plankton. These in turn had profound feedback effects on ecosystem function and evolutionary dynamics, ultimately giving rise to the conventions of the Phanerozoic biosphere. The early exponential phase of this planetary regime change is known as the Cambrian explosion.

Butterfield, N.J. 2011. Animals and the invention of the Phanerozoic Earth system. *Trends in Ecology & Evolution* **26**, 81–87.

NOTES

The Cambrian explosion: towards a synthesis?

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Ever since the writings of Charles Darwin in 1859, there have been three competing kinds of explanation for the missing record of animals. The first of these, here called *Lyell's Hunch*, was the line followed by Darwin himself – that Precambrian rocks are too poorly preserved to reveal the presence of animal ancestors extending far back in time. This hunch still remains popular with biologists, including some respectable researchers into phylogenomics and molecular clocks. But versions of Lyell's Hunch which place the origins of metazoans far back in time are now problematic because: 1, Proterozoic fossils mostly lack characters suitable for calibration of their rates of evolution; 2, rates of gene substitution were arguably higher during conditions of the Ediacaran-Cambrian transition; 3, the quality of fossilization arguably gets better not worse as one travels back into the Proterozoic, not least because soft tissue mineralization could take place very rapidly without the destructive effects of burrowing, grazing and scavenging. Given that micrometre scale preservation of organic matter by phosphate, silicate or sulfide was taking place in deep time, then the absence of metazoan skeletons, body plans or burrows seems deeply paradoxical.

A second class of explanation, here called *Daly's Ploy*, was explored by Canadian geologist R.A. Daly in 1907. These typically seek extrinsic (especially chemical) forcings on the Cambrian explosion. Daly's own hypothesis was that the Precambrian ocean was low in calcium and bicarbonate ions ('limeless'), hence the lack of carbonate shells at that time. But the long history of Archaean to Proterozoic carbonates reveals this reasoning to be flawed. Biomineralized protists are known from c. 750 Ma, while *Cloudina* shells were rock-forming at c. 550 Ma. More recent versions of Daly's Ploy have explored the controlling influence of sea level rise, sea-level fall (the Great Unconformity), nutrient level rise (phosphate), Snowball glaciation and deglaciation, and an increase in oxygen levels. But problems also emerge with such reasoning: 1, such changes were not unique to the Ediacaran-Cambrian transition, and many can now be traced far below; 2, such changes were usually oscillatory, whereas the biosphere changes appear linear.

A third class of explanation, here called *Sollas's Gambit*, was put forward by William Sollas in c. 1905. He invoked intrinsic, evolutionary changes as a driver: 'that the organisms of that time had not passed beyond the stage now represented by the larvae of existing invertebrate, and consequently were… unprovided with skeletons..' Modern versions of this typically invoke the stem vs. crown group concept, the importance of feedbacks, and the self-organizing behaviour of complex systems. It is this class of explanation that I plan to explore here.

To comprehend the nature of the Cambrian Explosion, we need to appreciate that rules for functional biology in the preceding Ediacaran were potentially very different. In a world without bioturbation, then organic matter, anoxia and sulfide sat close to the sediment-water interface. In a world without bilaterian burrowers and poriferan-cleaners, sponge colonies may have been organized differently from now. In an ecosystem without more advanced animals to prey upon, cnidarians may have fed in rather unexpected ways. In multicellular communities without mouths, guts or burrowing capacity, like *Charnia*, then symbioses with prokaryotes and protists may have been rife.

Simpler crawling traces, arguably consistent with radialian body plans, can be seen in Avalonia at c. 565 Ma, while vertical meniscate traces may have appeared by 555 or even 560 Ma. Cnidarian body plans (*Vendoconularia*) may be present in the fossil record of Russia from c. 555Ma, and in Brazil from c. 545 Ma (*Corumbella*). Deep, potentially faecal-filled, burrows of bilaterian type, becomes conspicuous around the globe from c. 544-543 Ma, broadly coincident with a transformation that avalanched down the evolutionary tree: first jaw apparatus (*Protohertzina*)¸ first biomineralized 'cnidarian' skeletons (phosphatic *Carinachites,* calcitic *Anabarites*), first hexactinellid sponges ('*Protospongia*'), alongside the conspicuous demise of large, protist-like *Palaeopascichnus*. By the start of Stage 2 (c. 530 Ma), all forms of animal activity were present, and by the Chengjiang biota of Stage 3 (<520Ma), modern ecosystems were essentially present. Modelling of complex systems now allows us to envisage this transformation from stem to crown group animals as an evolutionary avalanche.

The biological and biogeochemical consequences of the Cambrian Explosion on the Earth System were both large and long term. They involved a stepwise increase in the fractal dimension of the whole biosphere. This increase in surface roughness is currently being modelled and tested against a global petrographic and geochemical database. But this fractal revolution conceivably resulted in the following measurable feedbacks: 1, greater and more rapid capture, and oxidation, of labile organic matter above the sediment-water surface; 2, a lesser rate of burial loss of labile organic matter into sediment; 3, major changes in the patterns of phosphate entrapment; 4, major changes in sulfide entrapment. These changes can, in turn, be regarded as having major consequences for primary productivity, carbon burial, climate and oxygen. After this unique expansion of the biosphere, carbon isotopic extremes became smaller and less long-lived. The carbon, nutrient and sulfur cycles were 'tamed'. Snowball glacial conditions never returned. Animals saved the planet.

NOTES

Burlington House
Fire Safety Information

If you hear the Alarm

Alarm Bells are situated throughout the building and will ring continuously for an evacuation. Do not stop to collect your personal belongings.

Leave the building via the nearest and safest exit or the exit that you are advised to by the Fire Marshall on that floor.

Fire Exits from the Geological Society Conference Rooms

Lower Library:
Exit via main reception onto Piccadilly, or via staff entrance onto the courtyard.
Lecture Theatre
Exit at front of theatre (by screen) onto Courtyard or via side door out to Piccadilly entrance or via the doors that link to the Lower Library and to the staff entrance.
Main Piccadilly Entrance
Straight out door and walk around to the Courtyard.

Close the doors when leaving a room. **DO NOT SWITCH OFF THE LIGHTS**.

Assemble in the Courtyard in front of the Royal Academy, outside the Royal Astronomical Society.

Please do not re-enter the building except when you are advised that it is safe to do so by the Fire Brigade.

First Aid

All accidents should be reported to Reception and First Aid assistance will be provided if necessary.

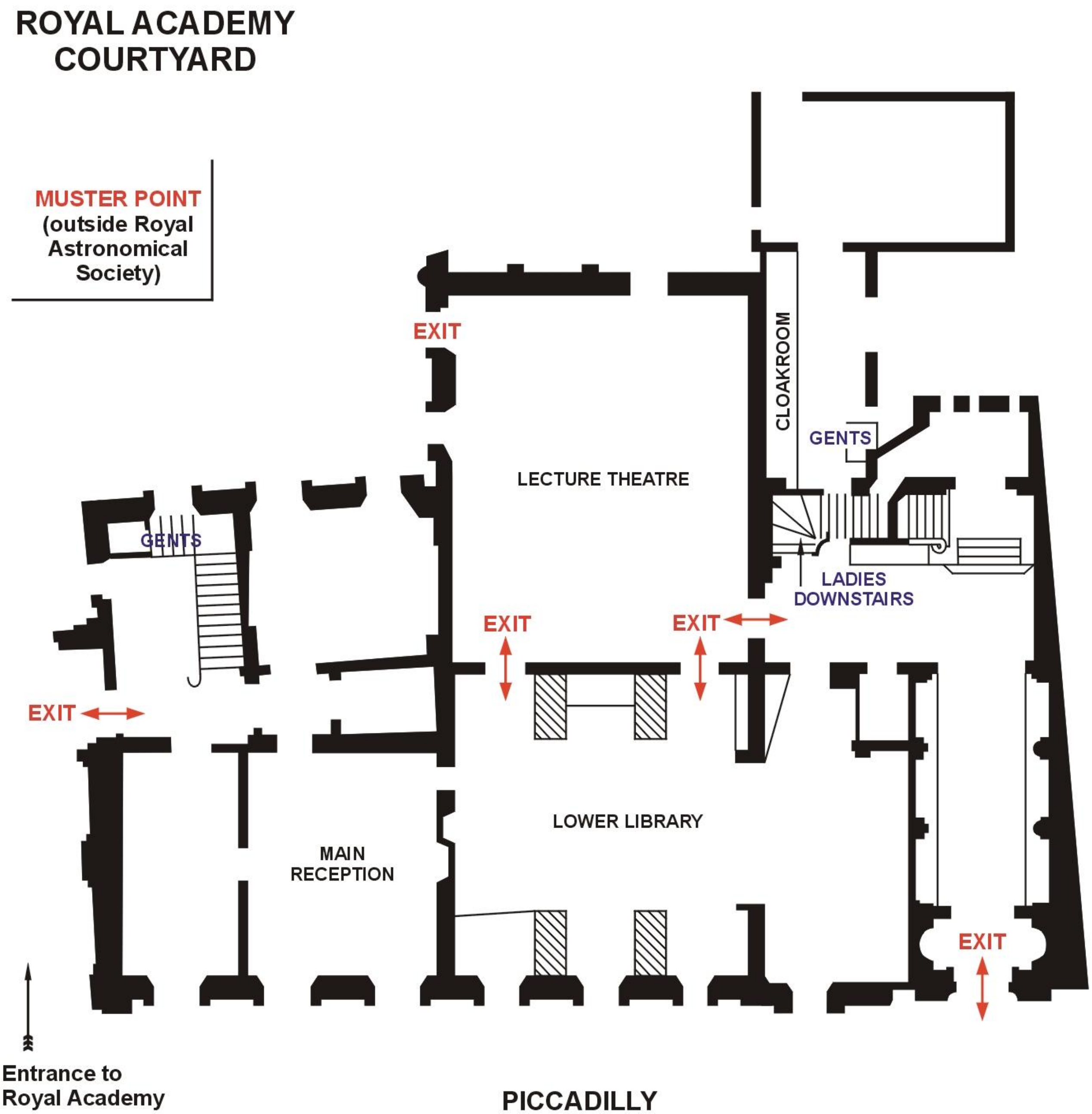
Facilities

The ladies toilets are situated in the basement at the bottom of the staircase outside the Lecture Theatre.

The Gents toilets are situated on the ground floor in the corridor leading to the Arthur Holmes Room.

The cloakroom is located along the corridor to the Arthur Holmes Room.

Ground Floor Plan of the Geological Society, Burlington House, Piccadilly



2013 Geological Society Conferences

27 March	Shell London Lecture – Exceptionally preserved fossils: Windows on the evolution of life	Burlington House
4-5 April	Holocene Climate Change	Burlington House
17 April	Shell London Lecture – Rivers under the sea	Burlington House
29 May	Shell London Lecture – Latest Developments in Carbon Capture and Storage	Burlington House
27 May – 1 June	GSA 125th Anniversary Field Trip: The Great British Tertiary Volcanoes	Field Trip, Scotland
1 – 7 June	GSA 125th Anniversary Field Trip: Structure and tectonics of the NW Highlands of Scotland	Field Trip, Scotland
19-20 June	Microbial Carbonates in Space and Time	Burlington House
25-27 June	William Smith Meeting 2013	Burlington House
3 July	Shell London Lecture – New discoveries of life at deep-sea hydrothermal vents	Burlington House
11 September	Shell London Lecture – Dwarfism in animals on islands	Burlington House
23 – 24 September	100 Years and Beyond	Imperial College, London
9 October	Shell London Lecture – TBC	Burlington House
21-22 October	Exploration, Resource and Mining Geology	Cardiff, Wales
13 November	Founders Day Lecture and Dinner	Burlington House
20 November	Shell London Lecture – TBC	Burlington House
20 November	Geological Society Careers Day	BGS, Keyworth
20 November	Careers Day	Our Dynamic Earth, Edinburgh
18 December	Shell London Lecture – Lakes beneath the Ice	Burlington House