
ABSTRACT VOLUME

INTERNATIONAL CONFERENCE

— ON THE —

CAMBRIAN EXPLOSION

WALCOTT 2009

— EDITORS —

MARTIN R. SMITH

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(Walcott standing in the Phyllopod Bed Quarry, 1911, cover)

FOREWORD

Welcome to the International Conference on the Cambrian Explosion, 2009. This special meeting commemorates the centenary of the discovery of the Burgess Shale by Charles D. Walcott. We are delighted to welcome a broad spectrum of over 135 Cambrian Explosion workers from across the globe, attending this conference to exchange ideas on current research and to visit the famous localities, part of the Canadian Mountain Parks World Heritage Site.

This abstract volume is a compilation of the abstracts for keynote, oral and poster presentations. The suite of abstracts received is a testament to the quality and diversity of current research in this field, one hundred years after the discovery of the first Burgess Shale animals. Presentations topics range from the Neoproterozoic to the Cambro-Ordovician and cover geochemistry to taphonomy, ichnology to phylogeny, and the history of Burgess Shale research to discoveries of new Burgess Shale-type fossils across the globe. New and exciting interpretations of famous (and infamous) Cambrian animals are proposed. We would like to extend our thanks to all of our contributors, and trust that the presentations will stimulate interesting and profitable conversation. We are excited to host eight keynote addresses by many of the largest names in Cambrian palaeontology, and trust that these will fascinate delegates and members of the public alike.

We would like to express our appreciation to all of our sponsors for their kind financial assistance, in particular; Parks Canada; the Canadian National Committee for the International Year of Planet Earth; Devon Energy; the Paleontological Society; the Palaeontological Association; the Paleontology Division of the Geological Association of Canada; the Polk Family Charitable Fund; and the Fritz Fund. The commemoration events are under the patronage of the International Palaeontological Association and the Canadian Commission for UNESCO.

We hope your time here in Banff is both memorable and enjoyable!

Martin Smith, Lorna O'Brien & Jean-Bernard Caron

Abstract Volume, Editors

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SCHEDULE

PDC: Professional Development Centre; MB: Max Bell building; WBB: Wally Burden building

MONDAY AUGUST 3RD

- 06:00 *Collect lunch and breakfast bags – PDC main lobby lounge*
- 06:30 *Field trips depart – front of PDC*
- 19:00 *(approx) - Trilobite beds hike returns to Banff Centre*
- 19:30 *(until 22:00) Icebreaker and registration – Whyte Museum*
- 20:00 *(approx) - Walcott Quarry hike returns to Banff Centre*

TUESDAY AUGUST 4TH

- 07:00 *Breakfast –WBB dining room*
- 08:00 *Install posters – MB 252*
- 08:30 *Introduction / Welcome*
Jean-Bernard Caron
Session Chair: Mr. David Rudkin
- 08:40 *The Discovery of the Burgess Shale Site on Fossil Ridge, British Columbia*
Desmond Collins
- 09:00 *Walcott's Insights on Lower Cambrian Biostratigraphy: Stratigraphy and Palaeontology of the Esmeralda Basin, Nevada and California*
J. Stewart Hollingsworth, Norman S. Brown & William H. Fritz
- 09:20 *The Cambridge–Geological Survey of Canada Excavation of the Walcott Quarry in 1967*
David L. Bruton
- 09:40 *What Counts as a Phylum? Systematics, Evolution, and the Burgess Shale*
Keynyn Brysse
- 10:00 *Coffee and posters – MB central foyer / MB 252*
Session Chair: Dr. Douglas Erwin
- 10:30 *Multiple Lines of Chemical Evidence for Pelagic Neoproterozoic Acritarchs*
Alison Olcott Marshall, Craig P. Marshall, Malgorzata Moczydlowska & Sebastian Willman
- 10:50 *Where's the Glass? Biomarkers, Molecular Clocks and MicroRNAs Suggest a Near 200-Million-Year Missing Precambrian Fossil Record of Demosponges*
Erik A. Sperling, Davide Pisani & Kevin J. Peterson

11:10	Doushantuo Formation Microfossils (~600 Ma): Giant Sulfur Bacteria, Embryos, or Both? Frank A. Corsetti & Jake V. Bailey
11:30	Reconstructing a Lost World: Exceptional Preservation of Ediacaran Rangeomorphs from Spaniard's Bay, Newfoundland Guy M. Narbonne, Marc Laflamme, Lija I. Flude, Carolyn Greentree & Peter Trusler
11:50	Attachment Adaptations of Ediacaran Sedentary Organisms Ekaterina A. Serezhnikova
12:10	Trends and Transitions in Early Animal Evolution: Towards a Palaeogenomic Synthesis David J. Bottjer
12:30	<i>Lunch – WBB dining room</i>
13:30	Keynote address: Walcott, Trilobites, and the Cambrian Radiation Nigel C. Hughes
	<i>Session Chairs: Dr. Jean Vannier and Dr. Maoyan Zhu</i>
14:30	Evolutionary Relationships Within the Avalonian Ediacara Biota: New Insights from Laser Analysis Martin D. Brasier & Jonathan B. Antcliffe
14:50	<i>Coffee and posters – MB central foyer / MB 252</i>
15:30	Possible Ediacaran Ancestry of the Halkieriids Jerzy Dzik
15:50	Taphomorphs Within the Ediacaran Biota of Avalonia: an Explanation of <i>Ivesheadia</i> and Related Forms Alexander G. Liu†, Duncan McIlroy, Jonathan B. Antcliffe & Martin D. Brasier
16:10	Priapulid Origin of Treptichnids: Evidence from Experimental Ichnology Jean Vannier, Ivan Calandra, Christian Gaillard & Anna Żylińska
16:30	Ichnofaunal Variability in an Early Cambrian Sand-Rich Shallow-Marine Complex: The Gog Group of the Southern Canadian Rocky Mountains Patricio R. Desjardins†, M. Gabriela Mángano, Luis A. Buatois & Brian R. Pratt
16:50	Evolutionary and Environmental Controls on Ediacaran-Cambrian Ichnofaunas Luis A. Buatois & Gabriela Mángano
17:10	Episodic Bio-Radiations and Extinctions During the Precambrian-Cambrian Transition: Insight from South China Maoyan Zhu
17:30	Keynote address: When Life got Big: the Ediacara Biota and the Origin of Animals Guy M. Narbonne
18:30	<i>Dinner – WBB dining room</i>
20:00	Special talk: The Panorama Photographs of Charles D. Walcott Sarah Staurderman – <i>Whyte Museum</i>
21:00	<i>Close</i>

WEDNESDAY AUGUST 5TH

07:00 *Breakfast – WBB dining room*

Session Chair: Dr. Jean-Bernard Caron

08:20 The Sirius Passet Lagerstätte (Early Cambrian) of North Greenland
John S. Peel & Jon R. Ineson

08:40 The Emu Bay Shale Revisited: New Discoveries From a Lower Cambrian
Lagerstätte in South Australia

John R. Paterson†, Gregory D. Edgecombe, Diego C. García-Bellido,
James G. Gehling, James B. Jago & Michael S. Y. Lee

09:00 The Preservation of the Cambrian Murero Biota in the Mesones Group,
Cadenas Ibéricas, Spain

José Antonio Gámez Vintaned, Eladio Liñán, Andrey Yu. Zhuravlev,
Blanca Bauluz, Rodolfo Gozalo, Samuel Zamora & Jorge Esteve

09:20 Raman Imaging of Early and Middle Cambrian Soft-Bodied Arthropods from
the Pioche Shale, Nevada, USA

Craig P. Marshall, Alison N. Olcott Marshall & Bruce S. Lieberman

09:40 A New Fossil Lagerstätte from the Stephen Formation, Kootenay National
Park, British Columbia: Broadening the Search for Burgess Shale-Type
Deposits in the Canadian Rockies

Jean-Bernard Caron, Robert R. Gaines, Gabriela Mángano & Michael Streng

10:00 *Coffee and posters – MB central foyer / MB 252*

Session Chair: Dr. Douglas Erwin

10:30 A Phylogenetic Tree Assembled from rRNA Sequences of Almost 200 Taxa
from Across the Metazoan Animals

Jon M. Mallatt, Catherine W. Craig & Matthew J. Yoder

10:50 MicroRNAs Resolve an Apparent Conflict Between Annelid Systematics and
their Fossil Record

Erik A. Sperling, Jakob Vinther, Benjamin M. Wheeler, Derek E. G. Briggs &
Kevin J. Peterson*

11:10 One Hundred Years of Burgess Shale Arthropods
Graham E. Budd

11:30 Cambrian Crustaceans and the Evolution of Arthropod Feeding Complexity
Thomas H. P. Harvey†

11:50 Revision of Aglaspidid Phylogeny: Towards a Better Understanding of
Arachnomorph Relationships

Javier Ortega-Hernandez† & Simon J. Braddy

12:10 Fossil Arthropods, Early Brains: Inferring Cerebral Complexity from
Preserved Sensilla

Nicholas J. Strausfeld

12:30 *Lunch – WBB dining room*

13:30	Keynote address: The Deep Root of Modern Animal Diversity Junyuan Chen
14:30	Keynote address: The Burgess Shale Faunal Complex Desmond Collins
15:30	<i>Coffee and posters – MB central foyer / MB 252</i>
	Session Chairs: Dr. Xinglian Zang & Mr. Martin Smith
15:50	Taking a Bite out of <i>Anomalocaris</i> James W. Hagadorn
16:10	From Limbs to Jaws — the Nature of the Mouthparts of Anomalocaridids Xingliang Zhang
16:30	Anomalocaridid Diversity in the Middle Cambrian Burgess Shale, Canada Allison C. Daley† & Graham E. Budd
16:50	A New Anomalocaridid from the Chengjiang Biota Peiyun Cong† & Xianguang Hou
17:10	At First Sight – Functional Analysis of Lower Cambrian Eye Systems Brigitte Schoenemann, Euan N. K. Clarkson & Zi-Bo Yuan
17:30	Keynote address: The Cambrian Explosion: Developmental Potential and Ecological Opportunity Douglas H. Erwin
18:30	<i>Dinner – WBB dining room</i>
20:00	Keynote address: Micro-Burgess Shales Nicholas J. Butterfield & Thomas H. P. Harvey
21:00	<i>Close</i>

THURSDAY AUGUST 6TH

07:00	<i>Breakfast – WBB dining room</i>
	Session Chair: Ms. Lorna O'Brien
08:20	Morphology of Lower Cambrian Lobopodian Eyes and their Evolutionary Significance Xiaoya Ma†
08:40	Cambrian Lobopods: Comparisons and Evolutionary Significance Jianni Liu†, Degan Shu, Jian Han, Zhifei Zhang & Xingliang Zhang
09:00	Movement Palaeoecology of the Chengjiang Biota Stephen Q. Dornbos, Roy E. Plotnick & Junyuan Chen
09:20	The Origin of the Brachiopod Bodyplan Christian B. Skovsted, Lars E. Holmer & Glenn A. Brock
09:40	Soft-Bodied Gelatinous Fossils (Cnidaria/Ctenophora) from the Lower Cambrian, Chengjiang Biota, Yunnan Province, China George D. Stanley, Steve Haddock, Xianguang Hou & Ailin Chen
10:00	<i>Coffee and posters – MB central foyer / MB 252</i>

Session Chair: Dr. Stephen Dornbos

10:30 Using Decay Experiments to Constrain Interpretations of Soft-Bodied Fossils: Application to the Emergence of the Chordata
Robert S. Sansom†, Sarah Gabbott & Mark A. Purnell

10:50 The Trace Fossil Record of the Burgess Shale
Gabriela Mángano & Jean-Bernard Caron

11:10 Burgess Shale Chancelloriids – A Prickly Problem
Stefan Bengtson & Desmond Collins

11:30 A New Stalked Filter Feeder from the S7 Burgess Shale Community, Mount Stephen
Lorna J. O'Brien & Jean-Bernard Caron

11:50 *Nectocaris*, a Cephalopod-like Animal from the Burgess Shale
Martin R. Smith & Jean-Bernard Caron

12:30 *Lunch – WBB Dining room*

13:30 Keynote address: **Preservation of Burgess Shale Fossils**
Derek E. G. Briggs

Session Chairs: Dr. Robert Gaines & Dr. Paul Johnston

14:30 Evidence for the Mechanism of Burgess Shale-Type Preservation from the Chengjiang Scientific Drilling Project
Robert R. Gaines, Emma Hammarlund, Donald E. Canfield, Xianguang Hou & Sarah E. Gabbott

14:50 Water Column Chemistry at Chengjiang
Emma Hammarlund†, Robert Gaines, Donald E. Canfield, Xianguang Hou & Stefan Bengtson

15:10 *Coffee – MB central foyer*

15:30 *Poster session – MB 252*

16:20 Geology and Palaeoecology of Ancient Seeps at the Mount Stephen Trilobite Beds, Burgess Shale, Yoho National Park, British Columbia
Paul A. Johnston, Kimberley J. Johnston & Stanley B. Keith

16:40 Mud Volcanism and Exhalative Brines, Burgess Shale, Fossil Ridge
Kimberley J. Johnston, Paul A. Johnston & Stanley B. Keith

17:00 Cambrian Tectonic Setting and Fluid Source for the Burgess Shale Seep-related Ecosystem
Stanley B. Keith, Kimberley J. Johnston, Paul A. Johnston & Monte M. Swan

17:20 The Potential for Exceptional Preservation at Brine and Hydrocarbon Seeps Tested *in situ* in the Gulf of Mexico
Karla Parsons-Hubbard, Richard Krause & Bradley Deline

17:40 Environmental Insights into Paleobiological Patterns of the Cambro-Ordovician Port au Port and St. George Groups, Western Newfoundland
Sara Pruss, Matthew Hurtgen & Alexandra Breus

18:00 Keynote address: **Burgess Shale-Type Faunas and the Origin of Animal Bodyplans: Continuing Confusion?**
Simon Conway Morris

19:00 *Banquet – Donald Cameron Hall*

FRIDAY AUGUST 7TH

06:00 *Collect lunch and breakfast bags – PDC main lobby lounge*

06:30 *Field trips depart – front of PDC*

19:30 *(approx) - Trilobite beds hike returns to Banff Centre*

20:00 *(approx) - Walcott Quarry hike returns to Banff Centre*

SATURDAY AUGUST 8TH

06:00 *Collect lunch and breakfast bags – PDC main lobby lounge*

06:30 *Field trip departs – front of PDC*

20:00 *(approx) - Walcott Quarry hike returns to Banff Centre*

The symbol † denotes presentations which are eligible for the prize for students and young scientists under the age of thirty. Asterisks (*) mark the presenting author. Keynote addresses are open to the public.

KEYNOTE PRESENTATIONS

INTERNATIONAL CONFERENCE

— ON THE —

CAMBRIAN EXPLOSION

WALCOTT 2009

PRESERVATION OF BURGESS SHALE FOSSILS

Derek E. G. BRIGGS^{1,2}

¹ Department of Geology and Geophysics, Yale University, New Haven, Connecticut, USA

² Yale Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA

Investigations of the preservation of fossils from Walcott's Burgess Shale and other Burgess Shale-type localities address a variety of questions including: Why and how are soft tissues preserved? What impact have decay and preservation on the morphology that survives, and on the interpretation of these Cambrian animals? Does an understanding of depositional setting and preservation help us to predict where other soft-bodied fossils might be found? Why are occurrences of soft-bodied fossils relatively common in Cambrian rocks compared to younger strata? In researching such questions, the focus of enquiry has ranged from regional to microscopic, from environmental context to chemical composition. Common factors have emerged as work on Cambrian soft-bodied fossils has progressed – the survival of organic material appears to be fundamental, for example. But the concept of 'Burgess Shale-type preservation' has become less useful as additional discoveries have broadened the range of preservational styles known to be involved in the preservation of Cambrian soft-bodied fossils. The preservation of organic materials associated with phosphatic gut traces and clay minerals, formed both early and late, is now known from a range of stratigraphic and environmental settings (some of them post Palaeozoic) in addition to the Burgess Shale. Moreover, Cambrian soft bodied fossils with tissues preserved in calcium phosphate, pyrite and silica have been documented. I will review the range of preservational styles among Cambrian soft-bodied organisms and consider the extent to which the Burgess Shale-type preservational window extends beyond the Middle Cambrian.

MICRO-BURGESS SHALES

Nicholas J. BUTTERFIELD¹ and Thomas H. P. HARVEY²

¹ Department of Earth Sciences, University of Cambridge, England, UK

² Department of Geology, University of Leicester, England, UK

Burgess Shale-type fossils are best known as macroscopic compressions on bedding surfaces, but they can also be extracted by dissolving away the shale matrix with hydrofluoric acid (HF). Most of these isolated organic-walled fossils are microscopic, but readily identifiable as the disarticulated remains of larger organisms – both animals and "plants". Some of these can be associated with known macrofossils and shed important new light on their (micro) constructional anatomy and phylogenetic relationships (e.g., *Wiwaxia*, hyolithids, chancelloriids). Others have yet to reveal their overall form, but can be classified on the basis of diagnostic characters, including the oldest documented occurrences of sophisticated crustacean and molluscan feeding apparatuses. Still others remain entirely problematic, but promise a substantially improved account of Early-Middle Cambrian palaeobiology. Perhaps most significantly, these microscopic biotas are proving to be far more widespread than their elusive macroscopic counterparts, with a potential for greatly increasing the stratigraphic and palaeogeographic resolution of

Burgess Shale-type fossils. In this presentation, we will report on material recovered from the Mahto Fm. (Early Cambrian, Alberta), Forteau Fm. (Early Cambrian, Newfoundland), Mount Cap Fm. (Early-Middle Cambrian, NWT), Burgess Shale Fm. (Middle Cambrian, British Columbia), Kaili Fm. (Middle Cambrian, South China), Pika Fm. (late Middle Cambrian, Alberta) and Earlie Fm. (Middle-?Late Cambrian, Saskatchewan).

THE DEEP ROOT OF MODERN ANIMAL DIVERSITY

Junyuan CHEN

Institute of Geology & Palaeontology, Nanjing, China

Beautifully preserved organisms from the Lower Cambrian Maotianshan Shale in central Yunnan, southern China, document the sudden appearance of diverse metazoan body plans at phylum or subphylum levels, which were either short-lived or have continued to the present day. These 530-million-year-old fossil representatives of living animal groups provide us with unique insight into the foundations of living animal groups at their evolutionary roots. Among these diverse animal groups, many – including ctenophores, priapulids, sipunculans, arrow worms, tunicates, and linguloids – are conservative, changing very little since the Early Cambrian. Others, especially the Panarthropoda superphylum, evolved rapidly, with origination of novel body plans representing different evolutionary stages, one after another, in a very short geological period of Early Cambrian time. These nested body plans portray a novel ‘big picture’ of panarthropod evolution as a progression of step-wise changes both in the head and the appendages. During the evolution of the panarthropods, the head/trunk boundary progressively shifted to the posterior, and the simple annulated soft uniramous appendages progressively changed into stalked eyes in the first head appendages; into whip-like sensorial and grasping organs in the second appendage; and into jointed and biramous bipartite limbs in the post-antennal appendages. The two-segment head in the original arthropod body plan may be related to the *otd/ems-Hox* boundary, which would explain why this boundary is buried within the head. It also challenges the deeply-rooted hypothesis of the tripartite-brain. *Haikouella* is one of most remarkable fossils representing the origin body plan of Crustozoa, or “crest animals” (procraniates+craniates). The anatomy of Early Cambrian crest animals, including *Haikouella* and *Yunnanozoon*, contributes to new understanding and discussion of the origins of the vertebrate brain, neural crest cells, branchial system, and vertebrae. Lophophore-bearing organisms include a group of sessile, stalked organisms known as *Phlogites* (= *Chenungkongella*) and a group of medusoid organisms (including *Eldonia* and *Rotadiscus*), which have been interpreted as tunicate and problematic, respectively. Restudy of their body plans reveal that they are likely the fossil representatives of extinct basal deuterostomes, in a close affinity with echinoderms. Vetulicolians remain one of the Cambrian’s biggest controversies, being recently interpreted as a basal deuterostome group. Restudy of their body plan suggests that they were a distinct panarthropod group.

THE BURGESS SHALE FAUNAL COMPLEX

Desmond COLLINS

501-437 Roncesvalles Avenue, Toronto, Ontario, Canada

Beginning in 1975 with a season of talus picking below the Walcott and Raymond quarries on Fossil Ridge, field parties from the Royal Ontario Museum devoted 5 seasons of reconnaissance and 12 seasons of excavation to the discovery and collection of the Burgess Shale faunal complex on Fossil Ridge and Mount Stephen. Further fossil localities were examined on Mount Odaray and Mount Bosworth in Yoho National Park, and near Stanley Glacier and in Monarch Cirque in Kootenay National Park, 60 km to the southeast.

By 2000, two new faunas low in the formation (Collins quarry; S7) had been discovered on Mount Stephen, to add to the Trilobite Beds there; one new fauna (Collins UE/EZ quarry) had also been found above the other two quarries on Fossil Ridge. The Raymond Quarry was greatly enlarged, yielding new species, and another 5 metres of fossil-bearing shale was excavated below the Walcott/Geological Survey of Canada Quarry. During these excursions, the stratigraphy was also mapped – leading to the formal description of the Burgess Shale Formation and its ten constituent members in the basin, and differentiating it from the Stephen Formation up on the Cathedral platform. The positions of the various faunas in the formation were then established on both sides of the Kicking Horse Valley.

This work has furthered our understanding of both the complex structure and biological diversity of the Burgess Shale Formation.

BURGESS SHALE-TYPE FAUNAS AND THE ORIGIN OF ANIMAL BODYPLANS: CONTINUING CONFUSION?

Simon CONWAY MORRIS

Department of Earth Sciences, University of Cambridge, England, UK

If the Burgess Shale and similar Fossil-lagerstätten (notably Chengjiang and Sirius Passet) are famous for anything other than their spectacular preservation, it is the remarkable diversity of forms, amongst which some look “very strange”. Or so they did, because whilst a number remain in phylogenetic limbo (for example *Dinomischus*), in many other cases it is now apparent that, despite their bizarre appearances, the various fossil taxa are of unique importance in documenting how various body-plans are assembled. The importance of this scarcely needs emphasis. First, even though Darwin spelt out the solution fifty years before Charles Walcott “stumbled” on the Burgess Shale, half the biological community seems to persist in thinking that common ancestors are some vague set of chimaeras, conveniently simplified and carrying a burden of characters they might just need in the next hundred million years or so. The reality is very different: ancestors are complex and to the first approximation look very different from what some workers think they “ought” to look like and more importantly from their descendant “phyla”. Second, these transitions are achieved in an unremarkable, microevolutionary fashion: no

sudden jumps, no sudden noises. Third, groups we now identify at the highest taxonomic level were, in the Cambrian, arising from closely related taxa, separated by both trivial genetic and morphological differences. Here I will outline, in collaboration with my co-workers Jean-Bernard Caron (Toronto), John Peel (Uppsala), and Degan Shu (Xi'an), how we can document some of the key steps in the evolution of the deuterostomes (notably vetulicolians and yunnanozoans), lophotrochozoans (notably halkieriids), and ecdysozoans (notably the palaeoscolecids).

THE CAMBRIAN EXPLOSION: DEVELOPMENTAL POTENTIAL AND ECOLOGICAL OPPORTUNITY

Douglas H. ERWIN^{1,2}

¹ Department of Paleobiology, Smithsonian Institution, Washington, District of Columbia, USA

² Santa Fe Institute, Santa Fe, New Mexico, USA

The Ediacaran-Cambrian diversification of animal life, like most major evolutionary transitions, involved interplay between environmental possibility, ecological opportunity and developmental potential. Understanding these events requires consideration of the role of each element this macroevolutionary triad and their interactions. Here I focus on the role of developmental and ecological innovations.

The discovery that the basic developmental toolkit is highly conserved across all animals, including sponges and cnidarians, and that bilaterians include expanded repertoires of many elements of this toolkit, including many gene families of transcription factors and microRNAs, provides a new perspective on the early history of animal development. It is now clear, for example, that the burst of morphologic complexity was not accompanied by an increase in the number of genes, but rather in the degree of regulatory control, allowing more precise formation of spatial and temporal patterning within the developing animal embryo. One implication of the early appearance of the metazoan developmental toolkit is that almost all of the Ediacaran organisms could represent cnidarian-grade organisms. Recent studies of developmental gene regulatory networks also demonstrate how the locus of selection changed during the Ediacaran-Cambrian. The construction of tightly linked regulatory feedback loops (kernels) shifted selection from individual genes to gene networks. Such non-uniformitarian developmental changes challenge traditional (if implicit) uniformitarian assumptions of both microevolution and macroevolution.

Much of this developmental potential originated by 575 Ma, and the full bilaterian toolkit probably by 555 Ma. Taking full advantage of this developmental potential, however, was dependent upon the construction of progressively more connected ecological networks. Palaeontologists have often invoked 'open ecospace' or logistic growth models as explanations for such diversifications, but they miss the critical point, which is one of network dynamics: how to construct webs of trophic interactions. The most important interactions in building such networks are those that involve positive spillover effects, where ecosystem engineering effectively bootstraps greater biodiversity. During the Cambrian the initial positive spillover effect was likely provided by increased oxygen levels, and then further enhanced by bioturbation, which changed substrate redox

gradients and triggered blooms of microbes. The adaptations of Cambrian organisms can be roughly classified in terms of their potential feedback effects.

WALCOTT, TRILOBITES, AND THE CAMBRIAN RADIATION

Nigel C. HUGHES

Department of Earth Sciences, University of California, Riverside, California, USA

Charles Walcott's early interest in palaeontology was fuelled through extensive fossil collection in his native New York State, where he developed a particular fascination with trilobites. Both these attributes were critical to his later successes as a professional palaeontologist, including his work on the Burgess Shale fauna. Walcott's talents as a collector were honed as his private collection grew in both scientific and monetary value and, as with many early "amateur" palaeontologists, served as a key to his later appointment as a professional scientist. Walcott understood the value of specific items within his collection. Although trilobites had been described scientifically for over an hundred years, their possession of limbs during life remained a matter of active debate as late as 1876. In that year Walcott published his second paper, which was an account of limbs in *Ceraurus pleurexanthemus*. That work demonstrated not only the careful observation of those who first recognized the limbs, but also Walcott's technical ability in devising how to analyze and present his results. As early as 1878, Walcott also published the first ontogenetic sequence for a North American trilobite that included multiple developmental stages, and went on to describe scores of new trilobite taxa and the rocks that contain them. Throughout his career he maintained his active interest in trilobite soft tissues and his conclusions on the form of the "spiral" trilobite limb, which were first presented in his earliest investigations. He published a seminal review paper on trilobite appendages in 1918, and a long description of *Olenoides serratus* from the Burgess Shale in 1924.

Walcott's views on the unique structure of the trilobite limb stand in contrast to his interpretations of other arthropods in the Burgess Shale fauna. A recent view holds that although trilobites had a series of unique defining characteristics that distinguish them from other living or fossil arthropod groups, their extensive history may in some ways be representative of the evolutionary history of "trilobitomorph" arthropods as a whole. This is important because the trilobite fossil record is far richer in terms of taxonomic, ecological, and temporal diversity, and in ontogenetic coverage, than that of non-biomineralized fossil arthropods. The trilobites and their allies appear to be quite phylogenetically basal within the Euarthropoda, the group to which all familiar living arthropods belong. If so, trilobites may throw light on the developmental and body patterning condition of early euarthropods, and the record of their evolution might serve as a proxy for early euarthropod evolution. Studies of trilobite and other early arthropod development hint that early euarthropods developed through a prolonged series of moult stages, each accompanied by relatively modest morphological change. As expected, there appear to have been limits to the amount of size change possible per moult. During the Cambrian, early members of the group displayed wide variety in the number, size, and pattern of articulation of individual segments in the trunk. Later evolutionary radiations commonly focused on the morphological differentiation of numerically standardized sets

of segments. With respect to segmentation, we see contrasting sets of morphological character evolution, with different patterns of character variability represented at different times in phyletic history – just as Darwin predicted.

WHEN LIFE GOT BIG: THE EDIACARA BIOTA AND THE ORIGIN OF ANIMALS

Guy M. NARBONNE

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The Ediacara biota (578–543 Ma) represents a fundamental watershed in the history of life on Earth – the appearance of abundant large eukaryotes after 3 billion years of mostly microbial evolution. The biota comprises cm- to m-scale, soft-bodied organisms preserved as impressions under rapidly deposited beds of sandstone or volcanic ash. Ediacara-type fossils are known from about 40 localities worldwide, and immediately preceded the shelly fossils of the Cambrian.

Early Ediacaran fossils (578–558 Ma) are known exclusively from deep-water deposits in Newfoundland, England, and NW Canada, implying that large and complex eukaryotes evolved in this environment. The oldest-known Ediacaran megafossils, metre-long fronds and other fossils from deep-water turbidites in Newfoundland, immediately followed the final Neoproterozoic ice age (Gaskiers glaciation; 580 Ma) during a period of massive oxygenation of the deep sea. Most early Ediacarans are rangeomorphs, an extinct clade (“failed experiment”) utilizing self-similar branching elements that were used as modules to construct an array of taxa with highly divergent shapes (e.g. *Fractofusus*, *Bradgatia*, *Pectinifrons*). Rangeomorph communities were similar to those of modern suspension-feeding animals, implying that rangeomorphs may have been stem-group animals, but there is no evidence for guts, brains, or mobility among any taxa.

Younger assemblages of Ediacara-type fossils (558–543 Ma) are known mainly from shallow-water settings, including the Flinders Ranges in Australia, the White Sea and Ukraine in Europe, and Namibia in southern Africa, with a few deeper-water occurrences in Siberia and western Canada. Rangeomorphs are present but much reduced in importance and mostly found in deeper-water environments. Shallow-water assemblages are dominated by petalonamids, an extinct clade that utilized straw-like elements as modules to build a variety of growth forms. Possible sponges have been reported but, despite early reconstructions that showed the Ediacara biota dominated by jellyfish and soft corals, no unequivocal cnidarians have been described. Abundant peristaltic burrows attest to the presence of bilaterians and some intriguing taxa such as *Kimberella* and *Spriggina* may represent bilaterian body fossils. Calcareous shells of *Cloudina* and *Namacalathus* represent the oldest evidence of skeletonization. Other ecological innovations included mobile grazing on the microbial mats that covered much of the sea floor, but there is no evidence of macrophagous predation or scavenging among any of the soft-bodied organisms of the Ediacara biota.

The youngest-known Ediacaran megafossils are 543 Ma petalonamids (*Pteridinium* and *Swartpuntia*) immediately below the base of the Cambrian in Namibia. A few possible Ediacaran survivors have been reported from the Cambrian but are controversial. Earlier attempts to explain the disappearance of the Ediacara biota as reflecting a taphonomic loss are seemingly contradicted by their apparent absence from Cambrian lagerstätten such as the Burgess Shale. Latest Neoproterozoic anoxia and/or predation and competition from newly evolving Cambrian animals represent more likely explanations for the abrupt demise of the Ediacara biota, an early experiment in the evolution of large eukaryotes.

KEYNOTE

TALKS

POSTERS

ORAL PRESENTATIONS

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CAMBRIAN EXPLOSION

WALCOTT 2009

BURGESS SHALE CHANCELLORIIDS – A PRICKLY PROBLEM

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Chancelloriids were discovered by Walcott and described in his 1920 monograph on Burgess Shale sponges. The cactus-like organisms, with their characteristic bundles of sharp protruding spines, were likely candidates for a sponge affinity, but later research showed that the spines themselves were formed as dermal sclerites, rather than as spicules by enveloping sclerocytes. This important homology with sponges thus appears to be lacking. Currently there is no consensus on the affinity of chancelloriids – the “sponge school” views them as calcareous sponges, in which the spines may possibly be homologous to sponge spicules, while the “coeloscleritophoran school” suggests that the sclerites represent a metazoan plesiomorphy also found in bilaterally-symmetrical early animals, such as halkieriids.

Our restudy of Walcott’s material and of substantial new collections of Burgess Shale chancelloriids shows that three genera, *Chancelloria*, *Allonnia* and *Archiasterella*, are present among the material originally described by Walcott as a single species, *Chancelloria eros*. Walcott interpreted the varying ray arrangements of the sclerites as a taphonomic artefact, caused by different degrees of burial within a three-layered body wall. However, this interpretation is flawed – as shown by numerous sclerites, both isolated and in position in the body. *Chancelloria* has the highest variability of sclerites, whereas the sclerites of *Allonnia* and *Archiasterella* typically vary only in size, not in basic morphology. An apical tuft of slender spines is present in all taxa. It is particularly conspicuous in *Allonnia*, where the spines form a palisade around the central opening. No other openings in the body wall have been observed; the integument between the sclerites has a rhombic texture of imbricating scales, recurring at 60–100 µm intervals. No internal organs have been observed. The presence of circular contractile tissue is indicated by an infrequent body contraction, which appears to have had the function of emptying the internal cavity. The chancelloriid body was basally anchored to other organisms, usually sponges or other chancelloriids, or to shell debris in the soft sediment. We explore alternative interpretations of chancelloriid biology and affinities, from stem-group metazoans to bilaterians.

TRENDS AND TRANSITIONS IN EARLY ANIMAL EVOLUTION: TOWARDS A PALAEOGENOMIC SYNTHESIS

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The early history of animals on Earth is characterized by geologically long intervals with similar biotic trends punctuated by geologically short transitions to the next interval.

Recent biomarker data places the origin of sponges in the Cryogenian before the end of the Marinoan glacial event (635 Ma). Microscopic fossils of metazoan affinity in the Doushantuo biota (580–600 Ma), and the lack of macroscopic animal fossils before the onset of the Ediacara biota, indicate that this first interval – which trends through the initial part of the Ediacaran – is one of microscopic animals, characterized by abundant sponges as well as the likely presence of animals with cnidarian and bilaterian affinities. The transition to the Ediacara biota, which first appeared 575 Ma, marks the first evolution of macroscopic animals. This interval, characterized by many intriguing and large soft-bodied animals such as the extinct rangeomorphs, also includes the first macroscopic bilaterians, such as *Kimberella*. The transition at the end of the Ediacaran into the Cambrian marks the initiation of the third interval, where the fossil record shows the appearance of biomineralized animals and a proliferation of crown group bilaterians. Indeed, this interval should more properly be called the “Cambrian crown group explosion”.

These patterns of trend and transition from the fossil record of early animals are best understood within the context of changing environments, taphonomy and evolution. Evolutionary processes determining size increase, and the proliferation of crown group bilaterians, each mark a major transition. Their relative contributions need to be assessed against a backdrop where the various superclades into which modern metazoa fall were likely extant through much of the Ediacaran. Ultimately, the combination of data from the fossil and stratigraphic record with modern studies in molecular biology will provide the paleogenomic synthesis necessary to most fully understand early animal evolution.

EVOLUTIONARY RELATIONSHIPS WITHIN THE AVALONIAN EDIACARA BIOTA: NEW INSIGHTS FROM LASER ANALYSIS

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This talk will focus on new high resolution scanning of the type material for the earliest, complex Ediacaran genera *Charnia*, *Charniodiscus*, *Bradgatia* and *Ivesheadia* from Charnwood, UK, and compare these with the recently described *Beothukis mistakensis*, *Charnia wardi*, *C. antecedens* and *Fractofusus* spp. from broadly coeval strata in Newfoundland. We use laser and other techniques to both map and discuss the similarities and differences in morphology between these Ediacaran forms. Key features can now be seen to include the number of growth axes, the number and placement of growth tips, the presence of radiating or sub-parallel axes for the first and smaller order branches; the extent of displayed or undisplayed leaf-like architecture; and the extent of furling of the margins of these leaf-like elements. We use these origami-like features to suggest homologies between the major taxa, leading to a preliminary phylogenetic hypothesis for the evolution of the Avalonian Ediacara biota.

THE CAMBRIDGE–GEOLOGICAL SURVEY OF CANADA EXCAVATION OF THE WALCOTT QUARRY IN 1967

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In 1966, a preliminary opening of the Walcott quarry was undertaken by the Geological Survey of Canada, organized by Jim Aitken and led by Harry B. Whittington. The following year, during a month's work, more than 350 cubic metres of rock was removed with the help of limited blasting aided by a petrol driven rock drill. Blocks were then split with chisels and hammers and fossils collected, marked as to their position in the quarry, wrapped, and carried down to the camp at the end of each day. Specimens were then trimmed using a rock saw and packed in wooden boxes made on site. The group consisted of seventeen in all: three geologists with wives, four children, a cook, a blaster, four student assistants and the author. All lived and ate well, and food was delivered by pack horse every Friday. Water was a problem, as the party relied on melting snow, which did not last long in the record warm July–August weather of that year. The talk will include photographs of life in camp, and the planning which led to the description of the collected fossils.

WHAT COUNTS AS A PHYLUM? SYSTEMATICS, EVOLUTION, AND THE BURGESS SHALE

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Stephen Jay Gould argued that the Burgess Shale fossils, remnants of the Cambrian explosion, represent previously unknown (and now extinct) body plans, of equivalent morphological disparity and taxonomic rank to modern animal phyla. He contrasted his own interpretation with that of Charles Walcott, discoverer of the Burgess Shale, who (Gould said) had “shoehorned” the Burgess fossils into modern animal phyla and classes.

For much of the twentieth century, these two choices seemed to be the only ones available to palaeontologists: either the Burgess fossils were members of the known animal phyla, or they must be classified in new phyla of their own. However, a third option became available in the late 1980s, when other palaeontologists, including Derek Briggs and Graham Budd, began to recast Burgess and other Cambrian forms as stem-group species. On this new understanding, the former “weird wonders” of the Burgess Shale were given a new place in the tree of life, ancestral to (but not themselves members of) the modern crown groups. The debate continues, not only about how to classify the Burgess creatures specifically, but how to incorporate both extinct and extant animal groups in a coherent system of biological classification.

A closer examination of this disagreement reveals it is not merely a dispute over taxonomic ranking, but opens a window onto scientists' understanding of the fundamental workings of evolution. I will discuss how the debate over the interpretation

of these Cambrian fossils draws on and illuminates larger debates over the tempo and mode of evolution, and the relative roles in evolution of contingency versus convergence, and adaptationism versus structuralism, as well as systematic methodology and the pattern of the history of life. Another Burgess Shale palaeontologist, Simon Conway Morris, has played a crucial role in these debates. Decisions about how to classify Burgess Shale organisms are not mere disputes over stamp collecting, but instead reflect such critical biological issues as how to define a phylum, and whether all animal species belong in this most fundamental of taxonomic groups.

EVOLUTIONARY AND ENVIRONMENTAL CONTROLS ON EDIACARAN–CAMBRIAN ICHNOFAUNAS

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A compilation of Ediacaran–Cambrian ichnofaunas allows analysis of the role of evolutionary and environmental controls. Re-evaluation of Ediacaran ichnofaunas indicates very limited diversity and complexity levels, because almost all the ichnogenera that were considered exclusive to the Ediacaran (e.g. *Yelovichnus*, *Palaeopascichnus*) are no longer regarded as trace fossils. However, resting traces of *Dickinsonia* and *Yorgia*, and scratch marks of *Kimberella*, represent recently documented additions to Ediacaran global ichnodiversity. An increase in complexity is revealed by the terminal Ediacaran with the appearance of branched burrow systems (Treptinids) in shallow-marine deposits. Ichnological evidence (e.g. the *Helminthopsis* ichnoguild) supports the notion that benthic communities developed in association with widespread microbial matgrounds. Ediacaran deep-marine ichnofaunas are even less diverse than their shallow-marine counterparts, and essentially consist of nonspecialized grazing trails (e.g. *Helminthoidichnites*), indicating exploitation of microbial mats.

Ichnodiversity levels had changed dramatically by the earliest Cambrian, with the appearance of much more diverse assemblages - particularly in shallow-marine environments. Relatively diverse ichnofaunas dominated by arthropod trackways (e.g. *Diplichnites*, *Dimorphichnus*) and resting traces (*Rusophycus*), and moderate to large shallow grazing, locomotion and feeding trace fossils (e.g. *Psammichnites*, *Didymaulichnus*) of deposit feeders are known worldwide. This increase in diversity is paralleled by an increase in complexity, with the appearance of more sophisticated feeding strategies as revealed by patterned fodinichnial structures (e.g. *Treptichnus pedum*, *Psammichnites saltensis*). The highest ichnodiversity occurred in upper-offshore to shelf environments, ranging from the fair-weather wave base to slightly below storm wave base, revealing the onset of an archetypal *Cruziana* ichnofacies. Colonization of high-energy areas, such as subtidal sandbodies and foreshore-shoreface complexes, was slightly delayed until the establishment of vertical dwelling structures (*Skolithos*, *Diplocraterion*, *Arenicolites*) of suspension feeders and passive predators, reflecting the appearance of the *Skolithos* ichnofacies. The J-shaped spreite trace fossil *Syringomorpha* is also present in high-energy shallow-marine deposits, apparently restricted to the early–middle Cambrian. Integrated ichnological and sedimentological

data suggest that colonization was not restricted to fully marine environments, but instead that some arthropods were able to foray into brackish-water embayments.

Ediacaran-style ecosystems persisted in the deep sea during the Cambrian, with benthic styles essentially linked to the widespread occurrence of matgrounds. However, *Oldhamia* flourished in early Cambrian deep-marine environments, experiencing a remarkable behavioural diversification and revealing increased levels of complexity in feeding strategies. Also, arthropod trackways are relatively common in deep-marine deposits. The face of the deep started to change significantly during the early Ordovician, with the establishment of complex graphoglyptids and grazing trails leading to the ultimate demise of matground-dominated ecosystems and signalling the arrival of the agronomic revolution to the deep sea.

ONE HUNDRED YEARS OF BURGESS SHALE ARTHROPODS

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Burgess Shale arthropods have played a pivotal role in our understanding of the Cambrian explosion over the last hundred years, sometimes even being taken as a proxy for the explosion as a whole. However, their interpretation has changed dramatically over this period of time, with Walcott's alleged shoehorning developing to modern cladistic classifications. Complementary discoveries from China, Greenland and Sweden have illuminated the importance of the arthropods, but Burgess Shale arthropods remain central to any attempt to reconstruct early arthropod evolution. Here I review progress in understanding these famous fossils, and show that a new degree of consensus has begun to emerge about their placement on the arthropod tree. Nevertheless, reconstruction of the euarthropod crown group remains problematic, especially at its base; it seems that considerably more work will be required before the transition from stem group to crown group is fully understood.

A NEW FOSSIL LAGERSTÄTTE FROM THE STEPHEN FORMATION, KOOTENAY NATIONAL PARK, BRITISH COLUMBIA: BROADENING THE SEARCH FOR BURGESS SHALE-TYPE DEPOSITS IN THE CANADIAN ROCKIES

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The Burgess Shale-type (BST) deposits of the Canadian Rocky Mountains, including the classic localities on Fossil Ridge, occur along the basinal edge of the Cathedral Escarpment. This geological feature has traditionally been considered important in the

preservation and spatial distribution of the Burgess Shale biota. Above the escarpment, the “platformal” or “thin” Stephen Formation is widespread and well-exposed regionally. BST fossils collected from talus material in 1996 from the Stanley Glacier area, Kootenay National Park (British Columbia) were thought to belong to this formation. However, the exact stratigraphic origin of the fossils remained unknown. In 2008, a Royal Ontario Museum party conducted detailed geological studies in this area. Fossils were excavated from a three-meter thick interval including non-biomineralized animals within mm-thick mudstone beds with diagenetic carbonate cement. This interval occurs a few meters below the contact with the overlying Eldon Formation in the upper part of the Waputik Member, an upward shallowing succession comprised of six shale–wackestone parasequences. This succession lies within the *Ehmaniella* zone and fills an important temporal gap between two of the principal BST biotas, the Burgess Shale and the Wheeler Formations.

Sedimentological attributes, trace fossils and species composition indicate consistent environmental conditions throughout the section sampled and suggest the recurrence of a single community type. The epibenthic hyolithid *Haplophrentis* and the brachiopod *Lingulella* are numerically dominant, followed by nekto-benthic or pelagic raptorial arthropods, *Sidneyia*, *Tuzoia*, *Hurdia*, and a new *Hurdia*-like organism. *Chancelloria*, the hexactinellid sponge *Diagonella*, the alga *Margaretia* and *Anomalocaris* are also present. Many of these species are particularly abundant in some basinal localities (e.g., Raymond Quarry) suggesting environmental and/or ecological similarities. One arthropod and several species of worms represent new species possibly endemic to this environment. A specimen of *Tuzoia* with preservation of frontal appendages, which suggest a potential predatory habit, is recorded for the first time in a BST deposit. Evidence of *in situ* burial includes an indeterminate worm preserved in its burrow; complex rhabdoglephid structures; dwelling burrows of endobenthic predators; small traces associated with non-biomineralized carapaces; clusters of articulated *Haplophrentis* with specimens of various sizes; and putative moult assemblages of *Sidneyia* and *Hurdia*.

The presence of diminutive trace fossils directly associated with non-biomineralized animals suggests that carcasses or moults remained near the water-sediment interface during short-lived episodes of dysoxic bottom water conditions. However, time of residence and decay prior to burial was limited; disarticulation of the carcasses was minimal, suggesting a low-energy environment affected by frequent events of rapid sedimentation. This conclusion is corroborated by the presence of complete specimens of the delicate sponge *Diagonella*. The presence of this sponge further indicates a low sedimentation rate and a relatively deep water environment. The palaeoenvironment was a muddy ramp that lay below storm wave base. This depositional setting is distinct from the setting of the Burgess Shale localities on Fossil Ridge, but is similar to that of other BST deposits worldwide. It is likely that BST preservation is regionally widespread in the Waputik Member, compared to the patchy distributions of the classic basinal deposits.

THE DISCOVERY OF THE BURGESS SHALE SITE ON FOSSIL RIDGE, BRITISH COLUMBIA

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Cambrian fossils were first discovered in the Kicking Horse Valley by geologists dropped off at the CPR railhead at the top of Kicking Horse Pass in 1884. Two years later, a carpenter working on the construction of Mount Stephen House in Field was prospecting for minerals on his day off, when he found rock “bugs” on the slope of Mount Stephen overlooking Field. He showed them to Otto Klotz, an Ontario surveyor working along the railway line, who, in turn told a GSC geologist, Richard G. McConnell, about them. On the 13th of September 1886, McConnell found the site, now called the Mount Stephen Trilobite Beds, and made a collection of fossils, including *Anomalocaris* claws. This was the first Burgess Shale site discovered.

Klotz sent his assistant to collect from the beds, and sent the fossils to a family friend, Dr. Carl Rominger – the recently retired State Geologist for Michigan – who described the fossils in 1887. This set in motion a series of rather controversial events involving, among others, Charles Walcott, then a palaeontologist at the U.S. Geological Survey; Byron Walker, a bank manager on the 1897 BAAS excursion; George Matthew, a New Brunswick Customs official; Edward Whymper, the first man to climb the Matterhorn; and Henry Woodward, Keeper of Geology at the British Museum (Natural History) in London. These events eventually cumulated in Walcott and his family’s famous ride along Fossil Ridge in late August, 1909, where the Walcott Quarry was discovered.

To a great degree, Charles Walcott was pointed to the discovery of what he thought was the geographic extension of the Mount Stephen Trilobite Beds on Fossil Ridge, which he soon called the Burgess Shale.

A NEW ANOMALOCARIDID FROM THE CHENGJIANG BIOTA

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The spinose great appendages of anomalocaridids are usually preserved in isolation, and it is therefore postulated that they were composed of more skeletonized cuticle, in comparison to the rest of the body, making the spines harder and more suitable for predation. Functionally, the spine patterns of anomalocaridid great appendages can be grouped into two types. The first is that of *Anomalocaris*, *Amplectobelua* and *Parapeytoia*, with rigid spines which might have functioned to impale, subdue and immobilize their prey. When curved, the appendage would have squeezed and torn the prey. The second type is comb-like spine pattern, such as those of *Laggia* and *Cassubia*. Their auxiliary spines (AS) are also comb-like. This type of appendage probably functioned to sieve water and sediment in search of food, rather than attacking prey directly.

Here we report another unique type of great appendage belonging to a new anomalocaridid from the Chengjiang Biota. This type of appendage is characterized by a reduction in the number of spines (and possibly the number of appendage segments) and differentiation of proximal and distal spines. There are eight pairs of spines of this new type. The three most proximal pairs are very stout and almost equally wide from proximal to distal ends, along which at least six pairs of AS are present. The proximal AS are short and slender, while the two most distal pairs are relatively longer and stronger. The other five pairs of spines are very simple and have no AS.

This unique spine pattern shows that the proximal spines of the new anomalocaridid are greatly specialized, and the distal ones are relatively simplified (compared to the normal spine structure which usually has AS). The differentiation of spines indicates that the new animal must have a feeding habit that differs from other anomalocaridids. The edge between the two kinds of spines is greatly curved, which indicates that the new animal might only use the distal five simple spines for predation, with the prey being transferred to the three pairs of proximal spines for tearing. After tearing, the prey would be carried to the mouth by the spines, because they show some kind of flexibility, e.g. curving at varying degree. Together with the four genera (five species) previously described, the new anomalocaridid from Chengjiang Biota reveals the morphological diversity and disparity of the anomalocaridid feeding apparatus, the great appendage, and indicates the diversification of predation strategy in the Early Cambrian.

DOUSHANTUO FORMATION MICROFOSSILS (~600 MA): GIANT SULFUR BACTERIA, EMBRYOS, OR BOTH?

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Certain microfossils of the Neoproterozoic Doushantuo Formation (c. 600 Ma), including structures interpreted as the oldest known metazoan eggs and embryos, display features similar to giant vacuolate sulfur bacteria. Colourless sulfur bacteria of the genus *Thiomargarita* have sizes and morphologies similar to many Doushantuo Formation globular microfossils, including symmetrical cell clusters that result from multiple stages of reductive division in three planes; a multilayered cell ultrastructure; and associations with complex epibiont communities. The bacterial hypothesis does not invalidate the possibility that some Doushantuo Formation globular microfossils are indeed animal eggs and embryos, because the two hypotheses are not mutually exclusive. Indeed, recently collected samples from the oxygen minimum zone along the Costa Rica Margin contain benthic accumulations of *Thiomargarita* mixed with spiny globular protists and invertebrate eggs, providing an interesting analogue for Doushantuo Formation biostratinomy.

One of the most unusual attributes of the Doushantuo Formation assemblage is the phosphatization of the microfossils. As an important and commonly limiting nutrient, large accumulations of phosphorous are somewhat unusual in the geologic record—why did the phosphorite form at this particular time? *Thiomargarita* is known to mediate

phosphate accumulation in modern sediments, and we have found sulfur bacteria fossils related to *Thiomargarita* (putative *Beggiatoa* and *Thioploca*) in younger phosphorites. The interpretation of certain Doushantuo microfossils as *Thiomargarita*-like bacteria provides an explanation for the phosphorite precipitation that preserved the fossils. Furthermore, *Thiomargarita* lives at the interface between oxic conditions above and sulfidic conditions below. It may not be coincidence that *Thiomargarita*-like fossils accompanied by phosphatization appear in the rock record nearly coincident with proposed benthic oxygenation in Neoproterozoic time.

ANOMALOCARIDID DIVERSITY IN THE MIDDLE CAMBRIAN BURGESS SHALE, CANADA

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The anomalocaridids are one of the most recognizable organisms of the Burgess Shale, owing to their large size, complex morphology, inferred predatory lifestyle and controversial phylogenetic affinity. The complex history of discovery of these animals can be partly attributed to the variable preservation potential of different parts of the anomalocaridid body. Frontal appendages and mouthparts preserve much more readily than whole-body assemblages, so the earliest work on these animals examined these structures in isolation. It was only relatively recently that the three Burgess Shale genera, *Anomalocaris*, *Laggania* and *Hurdia*, were described in full.

New isolated frontal appendage material of three Burgess Shale taxa shows that the diversity of anomalocaridids in this formation is higher than previously thought. New specimens housed at the Royal Ontario Museum, Toronto, include (1) the first known occurrence of *Amplectobelua* outside of China; (2) a new morph of the *Hurdia* appendage exhibiting high morphological variability; and (3) a completely new anomalocaridid appendage, which is similar to the *Anomalocaris* appendage but has a straighter outline and a different arrangement of spines. This new anomalocaridid material was contemporaneous with the previously described taxa *Hurdia*, *Laggania*, and *Anomalocaris*, and differences in frontal appendage morphology of all these taxa are thought to reflect different feeding strategies employed in order to alleviate competition for prey items. The stratigraphically oldest quarry, S7 on Mount Stephen, yields appendages from all the anomalocaridid taxa, but assemblages found in younger quarries on Mount Field are dominated by *Anomalocaris* and *Hurdia* only, which may indicate a decrease in anomalocaridid diversity with time.

ICHTHOFAUNAL VARIABILITY IN AN EARLY CAMBRIAN SAND-RICH SHALLOW-MARINE COMPLEX: THE GOG GROUP OF THE SOUTHERN CANADIAN ROCKY MOUNTAINS

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The trace fossils of the Gog Group record animal-sediment interactions on a broad continental shelf of early Cambrian age. This poorly fossiliferous unit has been largely overlooked from an evolutionary standpoint, despite the insights it provides to the understanding of early Phanerozoic ecosystems. Our study focuses on the lower portion of the Gog Group, which reaches some 320 m in thickness. It integrates sedimentological and ichnological datasets with the main objective of characterizing the palaeoecological factors controlling the distribution of trace fossils.

Five facies associations with distinctive assemblages are recognized: (1) Non-bioturbated tabular bodies of planar and trough cross-stratified sandstone, comprising the Fort Mountain Formation. (2) Packages of sandstone interbedded with shale and wavy-and lenticular-bedded sandstone. This facies characterizes the Lake Louise Formation which contains the highest ichnodiversity (*Arthropycus*, *Conostichus*, *Cruziana*, *Diplichnites*, *Diplocraterion*, *Halopoa*, *Monomorphichnus*, *Palaeophycus*, *Phycodes*, *Planolites*, *Rhizocorallium*, *Rosselia*, *Rusophycus*, *Skolithos*, *Teichichnus*, *Treptichnus*). (3) Tabular to lenticular bodies of cross-stratified and parallel-laminated sandstone intercalated with wavy to lenticular thin-bedded sandstone, which are included in the lower St. Piran Formation. Robust pipe rock ichnofabrics occur within the sandy packages, while *Planolites* and *Teichichnus* are associated with the thinly bedded heterolithic intervals. (4) Compound cross-stratified sandstone packages locally bioturbated with *Skolithos* and *Rosselia*. (5) Unconformably overlying the latter facies, the lowermost deposits of the upper St. Piran Formation are dominated by heterolithic intervals showing wavy, lenticular and flaser bedding containing an impoverished trace-fossil assemblage composed of *Diplichnites*, *Helminthopsis*, *Helminthoidichnites*, *Monomorphichnus*, *Planolites*, *Rusophycus* and *Skolithos*.

Facies associations 1 and 4 reflect strong unidirectional currents and a rapidly shifting substrate in a shallow subtidal environment. The *Skolithos*-bearing intervals reflect the activity of suspension-feeders that colonized stable dunes. By contrast, the highly-bioturbated facies association 2 records the benthic activity of mainly deposit-feeding faunas in muddy areas of the shelf characterized by low-energy conditions and discontinuous sand sedimentation. Prograding over this unit, facies association 3 records the growth of a sand-sheet complex. Pipe rocks dominated by dwelling trace fossils of suspension-feeders occur at the margins and fronts of individual components of the complex, reflecting a moderate-energy environment, discontinuous sand sedimentation, and little or no mud deposition. Finally, facies association 5 reflects deposition on a marginal-marine setting in which progradation of a tidal-flat complex over the shallow shelf is demonstrated by an impoverished suite dominated by grazers and shallow-tier trace fossils of detritus-feeders.

Overall, the ichnofauna of the Gog Group provides a remarkably actualistic picture of Lower Cambrian shallow-marine benthic communities. Tiering and intense bioturbation (mostly by suspension-feeders), record the establishment of a mixground ecology early in the Phanerozoic.

MOVEMENT PALAEOECOLOGY OF THE CHENGJIANG BIOTA

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Nathan *et al.* (2008, PNAS) have called for a new “movement ecology paradigm for unifying organismal movement research.” This approach views movement as resulting from the interactions of the organism’s internal state (“why move?”), its biomechanical ability to move (“how to move?”), and its navigation capacity (“where to move?”), with each other and with the external environment. Exceptionally preserved body fossils provide direct information regarding the latter two factors through the preservation of limbs and sensory organs, making the study of “movement palaeoecology” possible. One way to examine this during the Cambrian radiation is through study of the Early Cambrian Chengjiang biota of southwest China. The Cambrian radiation is characterized by the profound environmental and biological changes associated with the bilaterian radiation. These include the advent of macroscopic predation, an increase in the size and energy content of organisms, and the transition in seafloors from laminated matgrounds to mixgrounds. The overall effect of these transitions was to markedly increase the spatial complexity of the marine environment. This increased spatial complexity likely drove the evolution of macroscopic sense organs in mobile bilaterians, leading to their first appearance during the Cambrian. The morphology and distribution of these sense organs should therefore reflect the life habits of the animals that possessed them.

Presence/absence data of macroscopic sensory organs (eyes and antennae) were collected from 5,597 specimens of 31 genera from the Chengjiang biota, and mapped onto the relative abundance and life mode data. The results reveal an interesting difference between the sensory organ distribution of mobile epifaunal and nektonic forms. While the presence of antennae is ubiquitous in both mobile epifaunal and nektonic genera (98% of mobile epifaunal and 94% of nektonic specimens have antennae), only nektonic genera are overwhelmingly dominated by forms with eyes (95%). In contrast, only 63% of mobile epifaunal specimens possess eyes. There is a statistically significant ($p < 0.0001$) difference between epifaunal and nektonic eye distribution. This difference may be attributable to the need of nektonic organisms to visually detect flow direction in order to navigate toward the source of an odour plume. Epifaunal organisms can achieve similar results through mechanosensory. These preliminary results support two general hypotheses: that essentially modern sensory systems evolved very early in animal evolution; and that sensory systems differed between epifaunal and nektonic forms. Even by the Early Cambrian, there does appear to be a difference in the selective pressure to develop certain sensory organs based on the local environment of an organism and its life mode.

POSSIBLE EDIACARAN ANCESTRY OF THE HALKIERIIDS

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About sixty million years separate the early Cambrian Meishucun-type deposits from the preceding, taphonomically similar Doushantuo phosphorites, with no comparable taphonomic windows in between. The lineages of modern animals can be traced back to near the base of the Cambrian, but not into the Ediacaran. However, body plans of the Spiralia, and other main animal phyla, undoubtedly originated in the Ediacaran without leaving a convincing fossil record. The Ediacaran biotas, although both taphonomically and ecologically rather bizarre, remain virtually the only source of fossil evidence on these events. Unfortunately, metazoan affinities of the Ediacarans are still weakly supported. Trace fossils are the oldest evidence of the Ecdysozoa, and indirectly imply that the priapulid body plan emerged near the end of the Ediacaran. The possible relationship between the Ediacaran petalonamean 'sea pens' and the ctenophores is consistent with molecular expectations, but awaits convincing connecting links before it can be accepted. Some putative anatomical homologies between the dickinsoniid dipleurozoans and chordates (Deuterostomia) were also suggested. *Kimberella* is believed to represent an Ediacaran proto-mollusc, even though it does not closely resemble Cambrian molluscs. This introduces some uncertainty regarding affinities of this widely accepted pre-Cambrian member of the Spiralia. It is suggested here that the gap in the stratigraphic succession may be filled with the Namibian *Ausia*. The distribution of proposed dorsal cuticular protuberances in an undescribed *Ausia* specimen resembles the distribution in the halkieriids. Although limited, the new evidence also suggests a close relationship between the halkieriids and cancelloriids, supporting the concept of the Coeloscleritophora. The affinity of halkieriids to the molluscs is another question. Their jaw apparatuses rather remotely resemble the molluscan radula, but also show some similarity to underived polychaete jaws, e.g., of the Ordovician *Archaeoprion*.

EVIDENCE FOR THE MECHANISM OF BURGESS SHALE-TYPE PRESERVATION FROM THE CHENGJIANG SCIENTIFIC DRILLING PROJECT

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Cambrian Burgess Shale-type (BST) deposits occur worldwide, and provide the most important record of the initial Phanerozoic radiation of the Metazoa. It has recently been

demonstrated that the fossilization of BST biotas worldwide followed a single major taphonomic pathway by which primary organic remains of fossil taxa were conserved as carbonaceous compressions. The preservation of BST biotas must have involved taphonomic conditions which differ from those present in modern marine environments. The specific conditions that produced BST preservation have been the subject of debate. Here, we present data from a core drilled through the Chengjiang deposit near Haikou, Yunnan, China. The sediment fabric and $\delta^{34}\text{S}$ data indicate the suppression of microbial activity within the sediment, via oxidant restriction. This provides a possible mechanism of BST preservation in the Chengjiang.

In the Chengjiang, BST fossils occur in 1–5 cm-thick gray claystones, which were deposited in discrete depositional events, and are separated by intervals of black claystone that represent slower, pelagic sediment accumulation between depositional events. The event beds and intervening “background” beds were systematically sampled downcore. Event beds are characterized by heavy $\delta^{34}\text{S}$ values that range from +46.1 to –10.1 ‰, (average $+7.1 \pm 3.0$ ‰), whereas background beds exhibit lighter values and a narrower range of +6.3 to –12.3 ‰ (average -6.0 ± 0.6 ‰). Heavy $\delta^{34}\text{S}$ values in the event beds indicate sulfate-restricted, “closed system” conditions during early diagenesis, relative to the lighter values of background beds that exhibit normal fractionation from seawater. We interpret this as evidence that microbial sulfate reduction was suppressed by oxidant deprivation shortly after burial. Sulfate deprivation may have resulted from a combination of influences which included: (1) low SO_4^- concentrations in the global ocean; (2) the influence of turbidite deposition on SO_4^- diffusion; and (3) pervasive early carbonate cements at bed tops which may have acted to suppress diffusion. Samples of other BST deposits are characterized by similarly heavy $\delta^{34}\text{S}$ values. $\delta^{34}\text{S}$ evidence, in combination with fine scale sedimentological data from the Chengjiang, Burgess, and other principal BST deposits, suggests that Burgess Shale-type preservation worldwide occurred as a result of early closure of the diagenetic system.

THE PRESERVATION OF THE CAMBRIAN MURERO BIOTA IN THE MESONES GROUP, CADENAS IBÉRICAS, SPAIN

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The upper-Lower–mid-Middle Cambrian Mesones Group of the Cadenas Ibéricas (NE Spain) yields diverse exceptionally-preserved fossils, including algae, intact sponges, palaeoscolecoid and other cephalorhynch worms, xenusians, trilobites and other arthropods, cancelloriid scleritomes, pedunculate linguliformeans, and very diverse fully-articulated echinoderms (the Murero biota). It includes a significant part of the entire Cambrian soft-bodied taphonomic window of about 10 Ma. Of those fossils, seventeen species representing eight phyla were analyzed with dispersive x-ray spectrometry, allowing semi-quantitative chemical detection, and some were studied under a petrographic microscope. The integuments, skeletons, and soft tissues of the

Murero fossils are replicated in chlorite, illite, and some accessory minerals. This raises the question of whether these minerals formed: (1) as death masks; (2) during early diagenesis, after some mineral precursors; or (3) by replacement of former organic and mineral fabrics during metamorphic alteration. At first glance, the third possibility seems most plausible because the entire Mesones Group underwent anchimetamorphism. However, the chlorite that replicated the skeletons and cuticles, irrespective of their pristine composition (carbon, calcite, apatite), contains high Mg and Fe, and low Al, Si, and K, relative to the detrital chlorite and illite in the surrounding rock matrix. When present, Ca is confined to replicating euhedral chlorite and fibrous illite, but only in the fossils. Both chlorite and illite selectively replaced the primary microstructures. These features, as well as the aggregation of chlorite flakes as tangentially oriented euhedral and subhedral blades, and high Fe/(Fe+Mg) and Al/Fe ratios in the mineral composition, are indicative of secondary formation of chlorite and illite after a Fe- and Mg-rich verdine-type clay. In modern marine environments within a temperature range of 20–40 °C, the authigenic verdine-type clay can be transformed into either euhedral chlorite or fibrous illite crystals via the catalytic actions of bacteria. In some cases, if organic shell compounds are acidic enough, as in a linguliformean shell, they mediate the growth of clay minerals by themselves.

In general, the Cambrian soft-bodied taphonomic window was open for a large variety of mineralogies preserving exceptional fossils (carbonaceous, phosphatic, pyritic, and even quartzose replicas are well known). This window coincided with the mass appearance in the fossil record of diverse ecdysozoans (arthropods, xenusians, and cephalorhynchs), which compose the bulk biovolume and species diversity of any Cambrian lagerstätte. The closure of this window occurred during the late Middle Cambrian. This interval is signified by several important events pointing to the end of an icehouse epoch and the beginning of a greenhouse epoch.

TAKING A BITE OUT OF ANOMALOCARIS

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Anomalocaridids are hypothesized to have consumed trilobites. Other than their large size, their midgut glands, and malformed trilobites, there is little direct evidence that they did so. New taphonomic, compositional, and modelling evidence suggests that anomalocaridid mouths were soft, could not close completely or chew, had biting kinematics incompatible with many trilobite malformations, and were well suited to manipulate or suck soft prey.

Anomalocaridid mouth plates and their tips are never broken, nor are tips worn. If plates were hard, and were used to manipulate, puncture, crush, or masticate biomineralized prey, they would be expected to show evidence of abrasion or breakage. Absence of this evidence is striking given the frequency (0.01-1%) of healed malformations in extant marine arthropods, most of which are due to prey manipulation or feeding. Moreover, anomalocaridid plates and their biting tips are commonly wrinkled, exhibit preburial shearing and tearing, and mantle or are deformed by biomineralized fossils such as

brachiopods, trilobites, and *Scenella*. Plates are preserved as organic carbon and exhibit fracture patterns typical of desiccating arthropod cuticle. Thus anomalocaridid plates, including their tips, were unmineralized and pliable in life.

Computer aided design modelling of the kinematics of mouth opening and closure, together with comparison with muscle movements used by modern circular-mouthed organisms, suggests several plausible models for anomalocaridid mouth movement. These include sphincter-like constricting closure of the circllet of plates, and full- or half-eversion or inversion of the circllet; the latter two movements generate sufficient subambient pressure for suction feeding. In all closure modes, laterally-adjacent opposing plates intersect one another when the mouth closes, which prevents the circllet from closing more than half-way. Orientations of plate tips are consistent with a partial mouth closure model; if full closure was possible, opposing plate tips would not articulate or interlock with one another, as is expected from teeth optimized to masticate or puncture, or teeth which intersect at tooth tips to crush, puncture, or break.

Although bilaterally-oriented trilobite malformations can plausibly be explained by a closure of a circular mouth, most trilobite malformations are arc- or U-shaped. Suction-, eversion-, and sphincter-movement of anomalocaridid jaws cannot produce U-shaped bite marks; these are better explained by predators who had opposable jaws or claws. Finite Element Analysis, and modelling of anomalocaridid plates using cuticle yield strengths from modern shrimp (*Pandalus*) and lobster (*Homarus*), illustrate that plates could withstand maximum forces of up to 6.2 and 13.0 N, should they have bitten into the thoracic segments of a trilobite. The most commonly malformed Cambrian trilobites had maximum skeletal yield strengths ranging from 3.7–37.1 N, suggesting that only weakly mineralized taxa, such as *Elrathia kingii*, could have been broken by an anomalocaridid bite.

Anomalocaridids may have bitten some soft trilobites, but it is more likely that they were suctorial feeders, perhaps using their preoral appendages to comb soft-bodied invertebrates from the benthos. This feeding strategy makes sense given the recent discovery of multiple rows of inwardly pointing serrated plates inside some anomalocaridids' oral cavity; these may have prevented prey from exiting the mouth, or may have been part of a buccal cavity or eversible grasping organ.

WATER COLUMN CHEMISTRY AT CHENGJIANG

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The Chengjiang lagerstätte preserves a record of ocean chemistry during a time of rapid metazoan diversification on Earth. A core drilled near Haikou, Kunming in Yunnan, China, penetrated the Helinpu Formation, which is comprised of the Yu'an-shan Shale and the

underlying Shiyantou Siltstone. The Yu'an-shan Shale contains the Chengjiang biota, which occurs stratigraphically 30 m above the base of the first occurrence of trilobites in the lowest part of the Yu'an-shan Member. Geochemical data from this core reveal dynamic changes in the paleoenvironment before and during the interval bearing exceptionally preserved fossils. Iron speciation results from the interval containing Chengjiang biota are inconclusive (FeHR/FeT 0.26 ± 0.08), but indications of anoxia occur in the base of this interval, and decrease upcore. Non-mineralized fossils of the Chengjiang biota appear to have been deposited below an increasingly oxic water column. Bioturbation is completely absent from this interval of the core, however, and evidence favours fluctuating water column redox conditions, and possibly bottom-water anoxia. The latter would account for the lack of bioturbation in this interval and is consistent with models for Burgess Shale-type preservation. In the lower part of the Chengjiang interval, pyrite is the dominant iron phase (FePY/FeHR 0.65 ± 0.13 when $\text{FeHR}/\text{FeT} > 0.30$) and the isotopic composition of the pyrite shows a consistent fractionation of about 40‰, indicative of active sulfate reduction.

Below the Chengjiang interval, iron extraction results indicate either one or two euxinic events, which occurred during the transgression that characterizes the lowermost Yu'an-shan. Our results seem to indicate a stratified water column with an oxic upper layer, a ferruginous middle zone and euxinic deep water. The water column overlying the Yu'an-shan Shale may have gone through all three states in a couple of million years.

In a portion of the lowermost Shiyantou, during a sea level highstand, iron enrichment is absent (FeHR/FeT 0.22 ± 0.09), and iron oxides occur as a dominant iron phase. This is interpreted as an early pulse of oxic ventilation of the deeper water column. Moderate bioturbation (ichnofabric index 3) occurs throughout the Shiyantou, but body fossils are not preserved. The $\delta^{34}\text{S}$ values become increasingly heavy upcore within the Shiyantou siltstone ($7.4 \pm 11.2\text{‰}$), a trend that is stronger than the assumed shifts in oceanic sulfate composition. Oxidative respiration in the uppermost sediments might have pushed the zone of sulfate reduction deeper into the sediment, with slow diffusion driving these values heavy, but this trend is also clear in anoxic intervals of the Shiyantou. We speculate that sufficient background sedimentation rates, low oceanic sulfate concentrations, and carbonate precipitation in pore spaces have all influenced the geochemical signals present in this core.

CAMBRIAN CRUSTACEANS AND THE EVOLUTION OF ARTHROPOD FEEDING COMPLEXITY

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In the modern world, crustaceans are taxonomically and ecologically dominant among aquatic arthropods, while their terrestrial descendants, the insects, account for the vast majority of animal diversity. Insights into the origins of this success are provided by the opening of a new window onto early crustacean evolution. An exceptionally preserved assemblage of organic-walled arthropod cuticle from the early Cambrian Mount Cap Formation (Northwest Territories, Canada) contains a diversity of sophisticated feeding

devices, including mandibular grinding surfaces, co-planar filter plates, and several styles of substrate-scraping machinery. Equivalent structures are known from various extant crustaceans and other mandibulate arthropods, where they represent adaptations for the precise handling of fine particulate food. However, comparable structures are apparently absent from the millimetre-scale individuals preserved in Orsten-type assemblages, which have previously provided the only reliable record of crustaceans in the Cambrian. I compare the appendage characters preserved among the Mount Cap and Orsten-type fossils in terms of morphology and functional significance, and discuss to what extent the differences are influenced by phylogeny, ontogeny, ecology, and taphonomy. The implications for arthropod relationships and feeding complexity evolution are considered in the context of longer term patterns in the arthropod fossil record.

WALCOTT'S INSIGHTS ON LOWER CAMBRIAN BIOSTRATIGRAPHY: STRATIGRAPHY AND PALAEOLOGY OF THE ESMERALDA BASIN, NEVADA AND CALIFORNIA

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Charles Doolittle Walcott was certainly the premier Cambrian stratigrapher and paleontologist in North America during his 50-year career, which ended in 1927. One notable and oft-neglected accomplishment was his recognition of early lower Cambrian faunas in thick sequences of lower Cambrian rocks in the White-Inyo Mountains of eastern California and the adjacent areas of Esmeralda County in western Nevada. Walcott's field investigations in this area were limited to brief periods in 1894, 1896 and 1897. He collected fossils and measured a nearly complete Lower Cambrian section at Waucoba Springs. In 1899 he sent an assistant to the area to measure the Barrel Springs section and to collect more fossils. Unfortunately, Walcott never returned to this area. In 1910 he published descriptions of the trilobites and suggested a zonation beginning with *Nevadina*, *Elliptocephala*, and *Callavia* Zones and ending with the *Olenellus* Zone at the top of the Lower Cambrian. The recognition that *Nevadina* was the oldest was significant, but these observations were completely neglected by B. F. Howell and the Cambrian subcommittee in their correlation chart published in 1944.

Mapping in the region by C. A. Nelson began around 1960. He recognized the *Fallotaspis* assemblage as even older than the *Nevadina* fauna. In 1972, W. H. Fritz proposed a lower Cambrian trilobite zonation consisting of *Fallotaspis*, *Nevadella* and *Bonnina-Olenellus* zones based largely on his work in northwestern Canada. This zonal scheme has been widely accepted for North America. Recent work in the Esmeralda Basin has led to the designation of an even older trilobite interval, the *Fritzaspis* Zone, beginning with the oldest trilobites in Laurentia; and to a possible five-zone breakdown of the *Nevadella* Zone. Meanwhile the internationally accepted base of the Cambrian was moved downward to include the small shelly faunas and placed at the first appearance of the trace fossil *Treptichnus pedum* in Newfoundland.

Walcott had an amazing ability to find trilobites and it is surprising that he travelled within a hundred yards of *Fallotaspis*-bearing rocks on Westgard Pass, California, and that his assistant collected an abundant fauna of younger trilobites within yards of a second *Fallotaspis* occurrence, without ever finding this important fauna. The Barrel Springs section measured by Weeks, rather than by Walcott, was confused by faulting and intrusive rocks – so much so that the collections were out of sequence and this section has not yet been convincingly relocated. Perhaps another field session by Walcott would have solved these problems, but even with limited data, he reached the important conclusion that this area had the oldest Laurentian trilobites in thick, complete lower Cambrian sections.

GEOLOGY AND PALAEOECOLOGY OF ANCIENT SEEPS AT THE MOUNT STEPHEN TRILOBITE BEDS, BURGESS SHALE, YOHO NATIONAL PARK, BRITISH COLUMBIA

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The Mount Stephen Trilobite Beds occur within the Campsite Cliff Shale Member of the Burgess Shale, which overlies the Yoho River Limestone Member. The topographically uppermost reaches of the beds are the Upper Trilobite Beds (UTBs). These are remarkable for their density of fossils, mostly trilobites, which occur in an 80 m wide, 8 m thick, diamond-shaped lithosome visible from the Kicking Horse Valley. Lateral to this lithosome, fossil abundance wanes dramatically and lithological character changes. About 100 m upslope, the Burgess Shale terminates against the Cathedral Escarpment. The UTBs occur near a change in direction of the Escarpment from SW to SE. This 'corner' marks the intersection of two faults that controlled the shape of the Escarpment surface locally, and focused brines and clinochlore mud that were expelled onto the seafloor. A 2.5 m-wide vertical mud/brine conduit is exposed above the UTBs. H₂S in the brines promoted microbial activity, with an attendant increase in the abundance of animals compared to background faunal density, as occurs around modern marine brine seeps.

A newly discovered section at the UTBs reveals stacked facies which, in ascending order, are: (1) a thin facies of mostly non-fossiliferous, black clinochlore; (2) a thin, densely fossiliferous (nearly exclusively *Ogygopsis*), low-diversity, black-weathering facies; (3) a thin, red-weathering, high-diversity, less densely fossiliferous facies; and (4) a thick, green-weathering, high-diversity, even less densely fossiliferous facies. Facies 1, only a few centimetres thick below the UTBs, thickens to about 2 m adjacent to the Escarpment. Here, the lowest beds contain euhedral dolomite rhombs floating in clinochlore matrix. Facies 2, 3 and 4 are interpreted as successively distal facies from the fluid source. The Lower Trilobite Beds are mostly grey- to tan-weathering, more fissile than the UTBs, and represent a more distal facies relative to the brine source. Major-element analyses show anomalous seep-related MgO concentrations of up to 27.0 wt% in the clinochlore compared to typically < 2.0 wt% in the more peripheral beds.

The underlying Yoho River Limestone also exhibits seep-related structures including: carbonate mud mounds and 0.5 m-wide, vertical, calcite pipes. Bedding plane exposures of the uppermost beds show extensive orthogonal sets of dilational cracks. Vast bedding surfaces are covered with 'ripple' marks of varying wavelength (20–24 cm; 2–3 cm amplitude). These are unlikely to be a result of contour currents or shallowing because none shows cross-bedding. We suggest these may instead represent surficial wrinkling resulting from flowing mud.

The brines and clinochlore were likely derived from serpentinization of mantle-derived lherzolitic peridotite source materials above subducting ocean floor off the north (now west) coast of Laurentia. Mud volcano-dominated seafloor environments of the eastern Mediterranean and Mariana forearc are suitable modern analogues for the Trilobite Beds on Mount Stephen.

MUD VOLCANISM AND EXHALATIVE BRINES, BURGESS SHALE, FOSSIL RIDGE

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Exhalative deposits and associated putative chemosynthesis-based communities have been described from several localities in the Burgess Shale, but not from the classic outcrops on Fossil Ridge. We report the discovery of a 30 m thick sequence of dolostones interbedded with a dark green to black weathering, non-fossiliferous lithofacies that resembles the brine seep lithosomes on Mount Stephen and The Monarch. The study interval occurs within the Odaray Shale Member above the Upper Ehmaniella Quarry. The dark lithofacies returned MgO values >30 wt% and, based on x-ray diffraction, is mineralogically nearly pure clinochlore. One distinctive bed is *c.* 1 m thick and can be traced laterally for at least 100 m.

Three clinochlore-bearing conduits cross-cut dolostones of the Cathedral Formation near its contact with the Burgess Shale. The largest conduit, with a diameter of *c.* 0.5 m and an exposed length of 10 m, is roughly lateral to the Walcott Quarry. The conduit is filled with a pebble breccia of laminated clinochlore clasts and trends towards an embayment in the platform before disappearing into the outcrop 15 m from the "Escarpment" face. Two narrower and shorter vein-like conduits angle upwards to flat-bottomed embayments roughly lateral to the Raymond Quarry and Upper Ehmaniella Quarry, respectively. Clinochlore is a Mg-rich product from hydrothermal alteration of mafic minerals and its occurrence here cannot be explained by regional low-grade metamorphism of basinal mudstones. Likewise, late-stage diagenetic emplacement of clinochlore bodies is improbable because there is syndepositional slumping in some clinochlore beds as well as reworked rounded clinochlore pebbles in some clastic beds.

The substantial volume of clinochlore evulsed onto the seafloor at Fossil Ridge is consistent with serpentinite-sourced mud volcanism. Large, circular, slump features may

represent post-eruption depressurization and collapse of the mud volcano caldera. Modern submarine mud volcanoes are typically associated with brine seeps, brine pools and chemosynthetic communities. In our fieldwork experience, clinochlore deposits in the Burgess Shale occur at or near the contact of platform and basin and are fringed by concentrations of animal fossils. At Fossil Ridge, the slope of the modern mountainside exposes the clinochlore-rich interval close to the NNW–SSE trending segment of the Cathedral fault, which lies within, and is parallel to, the ridge. The lower quarries are successively further away from the buried “Escarpment”, so any clinochlore lithosomes associated with these fossils remain unexposed.

The discovery of exhalative clinochlore on Fossil Ridge indicates that the seep model provides a general palaeoenvironmental explanation for the distribution and composition of fossil assemblages within the Burgess Shale.

CAMBRIAN TECTONIC SETTING AND FLUID SOURCE FOR THE BURGESS SHALE SEEP-RELATED ECOSYSTEM

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Palaeogeographic reconstructions of the Middle Cambrian tectonic plates show an extensive subduction zone that consumed thousands of kilometres of oceanic crust as Laurentia moved northward throughout the Paleozoic. While the Middle Cambrian margin is commonly described as “passive”, new evidence shows early north-south (shortening-axis) compressive deformation of Middle Cambrian age overprinted by NE-SW (shortening-axis) Laramide-age compressive fabrics. Structural evidence includes zebra-spar dolomite filled tensile fabrics within southerly-directed bedding parallel thrusts (Eldon Formation, Mount Wapta) that are cross-cut by NE-directed calcite-filled reverse fault fractures. Within early-dolomitized Eldon Formation laminites from Fossil Ridge scree, reverse faults are filled with coarse ferroan dolomite. At the renowned Walcott Quarry, southerly-directed reverse faults, consistent with Middle Cambrian kinematics, cut the phyllopod beds. Cross-cutting NE-striking tensile faults and NW-striking low-angle normal faults can be interpreted as macro normal-slip C-planes, accommodating Laramide NE-directed simple-shear strain.

At the topographic level of the Walcott Quarry, an excavation named the Adkins Quarry revealed the ‘Escarpment’ contact, where the Burgess Shale is deformed – it is dragged vertically against the Cathedral Formation. This “smearing” is related to syn-sedimentary faulting (basin downthrown) at the contact of the Cathedral and Burgess Shale formations; there is no offset upsection. Normal south-directed slip in this zone contains Reidel-tensile gashes filled by coarse hydrothermal dolomite. Immediately north of the Cathedral fault at the Walcott Quarry, NW-striking, high-angle faults contain hydrothermal Mg-chlorite (clinochlore)-filled shear fabrics and northerly-striking clinochlore filled gash fractures, which indicate synhydrothermal right-slip on NW-

striking fault elements. The NW-striking faults project NE toward NW-striking faults along the access trail which contain strike-slip shear fabric. The NNW strike of the Monarch and Kicking Horse hydrothermal dolomite-hosted Zn-Pb deposits, also fits the right-slip model for the Cathedral fault system.

We propose that the Cathedral 'Escarpment' is a non-erosional fault, probably related to a deep-seated right-slip wrenching that was active during N-S far-field compression above the subducting oceanic plate. Dehydration in this subduction zone triggered deep melting of alkaline lherzolitic peridotite mantle sources and some of these melts may have been serpentinitized by metagenic water in the mid-crust. Large volumes of magnesium-charged brine then utilized the deep-seated Cathedral fault pathway to migrate to the sediment-water interface within the Burgess Shale basin. Serpentinization can be held responsible for bulk volumes of serpentinite mud (much of the Burgess Shale Formation) which also utilized the Cathedral conduit system.

TAPHOMORPHS WITHIN THE EDIACARAN BIOTA OF AVALONIA: AN EXPLANATION OF IVESHEADIA AND RELATED FORMS

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One of the most problematic factors in interpreting the Ediacara biota is that of recognising the influence of preservational styles and post-mortem changes upon the morphology and taxonomy of these organisms. We have observed bedding planes in both the Charnwood and Newfoundland regions of Avalonia that we consider to contain several taphomorphs of a single taxon on the same surface. We consider that these taphomorphs demonstrate a taphonomic spectrum, ranging from finely preserved specimens of organisms such as *Fractofusus* and *Charnia*, through progressively more decayed stages, to effaced taphomorphs such as *Ivesheadia*.

This research explores the hypothesis that saprophytic microbial degradation of Ediacaran organisms on the palaeo-seafloor prior to burial by event beds can explain both this taphonomic spectrum, and the 'effaced' appearance of several key Avalonian taxa, such as *Ivesheadia*, *Shepshedia* and *Blackbrookia*. We argue that these important fossils may merely represent taphomorphs of other, more widespread Ediacaran taxa. This suggestion, if accepted, would have significant implications for the palaeoecology of the earliest macrobiotic ecosystems, and for the proposed diversity of the Ediacaran biota.

CAMBRIAN LOBOPODS: COMPARISONS AND EVOLUTIONARY SIGNIFICANCE

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Knowledge of Cambrian lobopods has increased dramatically since the description of *Aysheaia pedunculata* from the Burgess Shale in the last century, and sixteen genera (twenty-one species) of lobopods displaying diverse morphologies are currently recognized from Early and Middle Cambrian lagerstätte deposits. Lobopods are now considered to be possible ancestors to the arthropods. Intermediate forms, such as *Miraluolishania*, possess a mosaic of both lobopod and arthropod characters, lending support to this hypothesis. The lobopod features of *Miraluolishania* are its worm-like body design, dorsal spines, and non-segmented limbs or lobe-like legs; arthropod features include primary cephalization with paired eyes, paired antennae, and incipient tagmosis. *Jianshanopodia*, a large form with complex branched appendages, may throw new light on the origin of biramous limbs. *Megadictyon* cf. *haikouensis* had a head bearing caecae-like structures resembling those of the arthropod *Naraoia* and some chelicerates, and bore 'Peytoia'-like mouthparts and frontal appendages. The latter features are similar to those of the AOPK (*Anomalocaris-Opabinia-Pambdelurion-Kerygmachela*) group. Thus, Cambrian lobopods exhibit a much wider morphological diversity than extant onychophorans, and present evidence suggests that frontal appendages are homologous features that appear deep in the lobopod-arthropod phylogeny.

As members of the Ecdysozoa, lobopods are also regarded as having affinities with priapulids. Dzik and Krumbiegel hypothesize an origin from priapulid-palaeoscolecoid-like worms through the development of segments and limbs. In lobopod evolution, whatever the origin, the mode of life changed from priapulid burrowing to lobopod-style crawling. Complete specimens of *Facivermis yunnanicus*, showing both priapulid and arthropod characters, provide strong support for this proposed affinity.

MORPHOLOGY OF LOWER CAMBRIAN LOBOPODIAN EYES AND THEIR EVOLUTIONARY SIGNIFICANCE

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Evidence of fossil visual systems is crucial for understanding the origin and evolution of eyes. This study investigated the rare visual organs of Cambrian lobopodians from the Chengjiang lagerstätte, Kunming, China, using a new technique, Infinite Focus Microscopy, which can reproduce 3D topographic information. The eyes of *Hallucigenia fortis* and *Cardiodictyon catenulum* are reported for the first time, and the morphological details of the eye of *Luolishania longicruris* are revised. The eyes of *H. fortis* and *L. longicruris* are composed of three visual units, each of which has a pigment cup and a 'lens'. The eye of

C. catenulum only has a single visual unit with a deeply sunken ‘lens’. Cladistic analysis among Cambrian lobopodians suggests that their visual systems may have evolved from an eyeless condition to a single-unit eye and then to a tri-unit eye. The eyes of *H. fortis* and *L. longicruris* are not similar to the simple eyes (ocelli) of tardigrades and onychophorans, but resemble arthropod lateral visual organs, especially the stemmata of myriapods. They appear to represent the ancestral visual systems of arthropods and perhaps gave rise to the two major types of arthropod lateral eyes (lateral compound eyes and lateral simple eyes). Calculation of their focal distance suggests that the eyes of *L. longicruris* and *H. fortis* were capable of forming an image.

A PHYLOGENETIC TREE ASSEMBLED FROM rRNA SEQUENCES OF ALMOST 200 TAXA FROM ACROSS THE METAZOAN ANIMALS

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We use nearly-complete large-subunit and small-subunit rRNA gene sequences to assemble a phylogenetic tree of animals. This work studies the relations among the many animal phyla that originated during or before the early Cambrian, many of which are represented as fossils in the Burgess Shale.

We calculated our tree using statistical likelihood methods after improving the gene-alignment technique to better reflect the secondary structure of rRNA, and by using an advanced tree-building method that treated each paired site in the rRNA as an evolving character. These methodological innovations, however, did not improve tree resolution, so the main benefit of our study is the incorporation of so many taxa (197) from across the Metazoa.

In general, the findings matched those of past studies that used smaller subgroups of metazoans, recovering clades of the “new animal phylogeny” such as Ecdysozoa (the molting animals), Lophotrochozoa (annelids, molluscs, brachiopods, platyhelminths, etc.), Ambulacraria (hemichordates with echinoderms), and Pancrustacea (insects among the crustaceans). Most of these clades, however, could only be recovered after eliminating some highly divergent, rapidly evolving rRNA sequences that otherwise disrupted the tree and went in unlikely positions: those of cephalopod molluscs, chaetognath arrowworms, of symphylan and pauropod myriapods, and tunicates. Fortunately, these “rogue” sequences comprised only 5% of the 197 sequences. Like other rRNA-based studies, we obtained evidence that the acoelomorph worms are not platyhelminths, as was traditionally believed, but instead diverged from the base of the bilaterian animals. We also document the conserved nature of the rRNA genes of cnidarians (jellyfish, hydras, sea anemones, etc.), supporting cnidarians as the immediate sister group of Bilateria. A new finding is that the extremely simple Placozoa joined with Cnidaria.

Overall, our rRNA-based results agree with recent animal phylogenies that were calculated from multiple protein-coding genes and were likewise taken from a broad range of taxa across the Metazoa. In conclusion, after the rogue sequences are removed,

both rRNA- and protein-based phylogenies are now converging to support the same basic clades of the new animal phylogeny.

THE TRACE FOSSIL RECORD OF THE BURGESS SHALE

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The Burgess Shale is well known for its soft-bodied animals, but its ichnofossils have received scant attention. Often considered to be rare, their relevance to environmental and palaeoecological interpretation has been questioned. While macrofaunal vertical ichnofabrics seem to be restricted to localized bedding surfaces, such as in the Raymond Quarry Member, horizontal trace fossils display a wide variety of morphologies and are more widely represented than previously realized. Several horizons preserve non-biomineralized organisms alongside biogenic structures.

Our census of ichnofossils from several Burgess Shale localities in Yoho and Kootenay National Parks, British Columbia, unravelled a wide range of morphologies recording the activities of both macrofaunal and meiofaunal benthic components. The macrofaunal component is represented by several morphological groups: trackways, cruzianids, U-shaped and simple vertical structures, rosary-like structures, rosette structures, branching networks, pellet-infilled tubes, and a variety of simple, horizontal vermiform structures. The low diversity of trace-fossil assemblages, which are often monospecific to paucispecific, suggests the absence of a mature endobenthic community. For the most part, trace fossils are small, suggesting prevailing dysoxic bottom waters. Most trace-fossil assemblages penetrate no more than 3 mm into the compacted sediment, and well-developed endobenthic ichnofabrics are strikingly absent. This suggests a redox boundary almost coincident with the sediment water interface, which would produce anoxic pore-waters. However, exceptional trace-fossil assemblages, such as the *Diplocraterion* assemblage in the Raymond Quarry, delineate distinctive stratigraphic surfaces in which the prevailing redox conditions were drastically altered. *Diplocraterion*-like structures are incompatible with permanently anoxic pore waters, and indicate brief oxygenation events probably related to exhumation and erosion (i.e. *Glossifungites* ichnofacies). The meiofaunal benthic component is represented by minute biogenic structures which are particularly abundant in the Raymond Quarry and from Stanley Glacier, but absent in the Walcott Quarry. Diminutive vermiform trails are common within or just below cuticular elements of *Banffia*, *Hurdia*, *Odaraia*, *Sidneyia* and *Tuzoia*, suggesting grazing behaviour on microbe-enriched detritus. These trace fossils rarely extend into the surrounding sediment. This micro-scale concentration of biogenic structures may be explained by the mediation of thin, flexible cuticles that provided optimum conditions for differential preservation buffering compaction effects. In this sense, body fossils provided a unique taphonomic window for preserving meibenthic trace fossils.

Trace fossils are instrumental to further expanding our understanding of the Burgess Shale palaeoecology and depositional environment. Ichnological data provide robust

evidence of the indigenous benthic community, revealing the presence of a hidden diversity and trophic level of trace-making organisms. Trace fossil evidence also supports

RAMAN IMAGING OF EARLY AND MIDDLE CAMBRIAN SOFT-BODIED ARTHROPODS FROM THE PIOCHE SHALE, NEVADA, USA

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The post-burial processes which preserved Burgess Shale organisms are controversial. Typically, fossils consist of collapsed carbonaceous sheets, coated by diagenetic aluminosilicate films. These highly compressed, layered fossils are typically just micrometres thick. Models of the preservational process focus on either the carbonaceous compressions or aluminosilicate films as the main preservational agent. The composition of aluminosilicates associated with Burgess Shale-type fossils differs from aluminosilicates in the surrounding matrix, which implies that the aluminosilicate films are diagenetic, not sedimentary, in origin. The aluminosilicates cannot have been derived from the surrounding sediment, either by forcible injection into the body cavity during burial, or by leaking into decay-generated voids in organisms. A number of scenarios have been postulated to account for these aluminosilicates.

Over the past decade, elemental mapping has emerged as a useful chemical tool to determine the composition of fossil material. However, energy dispersive X-ray spectroscopy (EDS) cannot identify mineral phases as a standalone technique. Raman micro-spectroscopy, another non-destructive technique, is capable of complementing elemental data with more informative molecular structural information. Raman micro-spectroscopy is based on the fundamental vibrational motions of molecules, molecular ions, and crystals; this allows it to elucidate the mineralogy and carbonaceous composition of Burgess Shale-type fossils. Raman imaging simultaneously collects spectra from individual areas of the sample, so the distribution of each material present can be visualized. We used Raman imaging to identify the distribution and mineralogy/carbonaceous composition in various Cambrian species, including *Tuzoia* and *Anomalocaris*, as preserved within the Burgess Shale-like Pioche Shale. The imaging analysis produced various 2D and 3D images showing the spatial arrangement between carbonaceous materials and hematite throughout the fossil. Significantly, in agreement with recent studies, the fossil mineralogy is different from the host rock. This gives us a better understanding of preservational modes in Cambrian lagerstätten.

RECONSTRUCTING A LOST WORLD: EXCEPTIONAL PRESERVATION OF EDIACARAN RANGEOMORPHS FROM SPANIARD'S BAY, NEWFOUNDLAND

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Ediacaran fronds at Spaniard's Bay on the Avalon Peninsula of Newfoundland are among the best preserved Ediacara-type fossils, with exquisite, three-dimensional preservation of morphological features less than 0.05 mm in width visible on the best preserved specimens. All of the nearly 100 specimens are members of the rangeomorph clade, an Ediacaran group which dominated the early evolution of complex multicellular life. Five fossil taxa are present (four of them recognizable worldwide), and the predominance of mainly juvenile forms at Spaniard's Bay provides important information about the growth of these previously enigmatic organisms.

Spaniard's Bay rangeomorphs are characterized by centimetre-scale architectural elements exhibiting self-similar branching over several fractal scales. Larger structures were constructed by using these elements as 'modules'. Small leek-shaped fossils appear to represent current-aligned, juvenile specimens of the characteristic Avalonian fossil *Bradgatia*. Complete ontogenetic studies of more than 200 juvenile and adult specimens of *Bradgatia* from the Avalon Peninsula of Newfoundland allows for the interpretation of the growth of this taxon as being entirely inflationary or fractal over more than an order of magnitude of growth.

Four genera of rangeomorph fronds exhibit a bifoliate array of primary rangeomorph branches that pass off a central stalk. These taxa form a series, ranging from symmetric rangeomorph branches that were unconstrained except at their attachment to the central stalk, and thus free to rotate and pivot relative to neighbouring branches; through "single-sided" (developmentally overfolded) branches whose movement was increasingly constrained; to single-sided branches that were fixed relative to each other. This series provides a developmental linkage between *Rangaea*-type and *Charnia*-type rangeomorphs. It is marked by a shift from mainly inflationary growth to growth mainly by branch addition at the apex of the frond. The combination of architectural and ontogenetic characters represents a fundamental shift in Ediacaran taxonomy; it forms scaffolding from which a higher-level classification of these enigmatic organisms may be supported.

A NEW STALKED FILTER FEEDER FROM THE S7 BURGESS SHALE COMMUNITY, MOUNT STEPHEN

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The S7 locality on Mount Stephen (Campsite Cliff Member of the Burgess Shale Formation) was discovered by the Royal Ontario Museum in the early 1980s and is currently thought to be comparable in age to the Trilobite Beds. The S7 community is dominated by an undescribed, gregarious, stalked, epibenthic organism nicknamed the "Tulip animal". The name refers to its shape; a large cup-shaped calyx connects to a long, narrow stem. This study is the first detailed description of this new organism. It is based on observations of over 700 specimens, mostly laterally preserved, found both as isolated individuals and as large clusters (65+) on single slabs. The abundance of specimens on single surfaces, and the absence of extensive evidence of decay, suggest preservation by the smothering of live communities with little transportation.

Specimens range in length from 50 to 250 mm (including the stem) and 16 to 59 mm in width (at the calyx). Internally, the calyx contains a sac-like stomach, followed by an intestinal tract that extends to the top of the calyx, terminating in a central opening interpreted to represent the anus. The stomach is arranged over a rigid conical structure, which gives a triangular shape to the base of the calyx in lateral specimens. Surrounding the stomach are six radially symmetrical comb-like elements, each consisting of a central spine, from which two rows of tooth-like projections extend towards the centre of the calyx. These comb-like elements extend away and taper towards the top of the calyx. They are interpreted to represent a filter feeding apparatus, which captured food particles and moved them downwards into the stomach, presumably via a central mouth. The calyx is enclosed by a flexible outer sheath which folds in around the comb-like elements. The stem has a uniform width and is generally preserved straight. The stem is composed of two layers: an inner rigid core surrounded by a soft deformable outer sheath. The stem terminates in a small holdfast, which varies in shape from a flattened disc to a bulb; it often has granular elements at its base.

This animal occupies one of the highest epibenthic tiers of all Burgess Shale-type deposits and provides evidence of a complex tiering structure in the S7 community. The biological affinities of the "Tulip animal" remain unclear. Due to the morphological limitations imposed by their mode of life, convergence in form is common among sessile filter feeders (e.g., Cnidaria, Entoprocta, Ectoprocta). The body of the "Tulip animal" does not compare well with extant stalked organisms. The stalk and calyx is reminiscent of *Dinomischus*, a small, solitary species known from several Burgess Shale-type localities in Canada, including S7, as well as China; but the internal morphology is not comparable, and these animals are probably not directly related. A comparison with stalked Ediacaran organisms is worth considering, despite inherent difficulties in interpreting morphologies preserved in two different taphonomic modes.

MULTIPLE LINES OF CHEMICAL EVIDENCE FOR PELAGIC NEOPROTEROZOIC ACRITARCHS

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For over 1300 million years, acritarch diversity (organic-walled microfossils of unknown origin) was dominated by non-ornamented leiospherid forms. In the late Neoproterozoic, a morphological radiation produced large spiny forms, the acanthomorphs. As both Proterozoic leiospheres and acanthomorphs were orders of magnitude larger than their Paleozoic counterparts, it has been suggested that these forms represent benthic, not pelagic, algae. The Early Cambrian radiation of small rapidly diversifying acanthomorphic acritarchs is thought in turn to represent the advent of true plankton in the ocean. Some have even speculated that this ecological shift from the benthic to the pelagic helped spur the Cambrian Explosion.

However, with the exception of acritarchs found attached directly to sediment surfaces, determining the habitat of these enigmatic fossils is difficult. Today, both pelagic and benthic algae eventually settle on the sea floor, and while size can be an indicator of buoyancy, algae are known to precipitate CaSO₄ or BaSO₄ in their vesicles to make themselves more or less buoyant. While morphology is not sufficient to determine the palaeoecology of acritarchs, their chemical makeup can provide clues to their habitat. Here we infer their palaeoecology based on multiple lines of chemical evidence, including the carbon isotopic fractionation preserved within individual acritarchs; their biopolymer composition; and their bioinorganic minerals. While these techniques all examine different chemical features, the resulting data all indicate that leiospherid acritarchs were likely to have been benthic organisms, but the acanthomorphic acritarchs that radiated in the late Neoproterozoic were likely to have been pelagic, despite their large size.

REVISION OF AGLASPIDID PHYLOGENY: TOWARDS A BETTER UNDERSTANDING OF ARACHNOMORPH RELATIONSHIPS

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Aglaspidids are a group of poorly-understood Lower Palaeozoic arachnomorph arthropods that remain phylogenetically problematic, despite previous efforts to resolve their affinities as either chelicerates, stem-chelicerates, sister taxa to cheloniellids, or triobite-allied arachnomorphs. Consequently, they are regarded as a “bucket taxon” in which numerous taxa have been included based only on a general resemblance. They are usually characterized by a semicircular and convex cephalon, devoid of facial sutures; a faint glabellar region; and a pair of anteriorly oriented oval eyes. Despite the recognition of a labrum in Cambrian representatives and a hypostome in some Ordovician forms, no formal account of all aglaspidids and aglaspidid like arthropods has been undertaken.

This study presents an extensive re-evaluation of aglaspimid taxonomy and phylogenetic affinities. Re-study of alleged aglaspimid-like arthropods from the Upper Ordovician Letná Formation (Czech Republic) allows their reinterpretation as representatives of the Trilobita and Xiphosura. We also describe a new genus of aglaspimid arthropod from the Upper Cambrian of Tasmania. A phylogenetic analysis indicates that Aglaspimida *sensu stricto* forms a clade, which includes the Tasmanian aglaspimid, and which is a sister-group to the trilobitomorpha. Aglaspimid-like arthropods comprise a polyphyletic aggregation of taxa that are usually poorly preserved, and whose morphology is only superficially similar.

THE POTENTIAL FOR EXCEPTIONAL PRESERVATION AT BRINE AND HYDROCARBON SEEPS TESTED IN SITU IN THE GULF OF MEXICO

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Exceptional preservation requires conditions that fall outside those of the typical oxygenated sea floor, such as anoxia, low energy, and/or rapid burial. In addition to these scenarios, lagerstätten may be the result of unusual geochemical processes ranging from those in highly acidic bog deposits and brines, to early diagenetic processes such as replication of soft tissues (by clays or pyrite). Active seeps provide an opportunity to study decay processes in unusual geochemical environments. This study is the result of *in situ* experiments on the longevity of crabs (*Calinectes sapidus*) and urchins (*Echinometra* sp. and *Heterocentrotus* sp.) at two hydrocarbon seeps and a brine seep in the Gulf of Mexico (USA). Crab and urchin carcasses were put in mesh bags and placed on the sediment surface in 1993 with soft parts intact (frozen until deployment), and were observed after 2, 8, and 13 yrs.

The two active hydrocarbon seep localities (GB425 at 570 m and GC234 at 550 m) support chemosynthetic communities of clams and tubeworms (at GC234 only), with associated arthropods, echinoderms, and grazing gastropods, as well as exhibiting abundant microbial mat development. Fine siliciclastic mud at these sites is strongly bioturbated, except immediately beneath patches of microbial mat. Beneath each mat is a black anoxic zone that extends several centimeters into the sediment. Could these local anoxic zones beneath mats serve to enhance preservation of soft tissue and/or articulation? Our results indicate that this is not the case. Crabs and urchins collected at GB425 and GC234 were as degraded as, or more degraded than, samples collected at five non-seep localities. Claws were usually all that remained of the *Calinectes* samples, and urchins had lost spines and either remained articulated tests or had disarticulated to single plates. The anoxic zone below patches of bacterial mat is neither pervasive enough nor continuous enough to promote exceptional preservation. At the anoxic brine (200 ppt) seep, *Calinectes* carcasses remained articulated, with muscle tissue present and carapace softened, yet intact, and exhibiting original colour, even after 8 years. The

microenvironments bordering the brine pool, possibly corresponding to the exaerobic zone of Savrda and Bottjer (1987), produced either the most efficient destruction (in the brine stream associated with the production of sulfuric acid) or the most exquisite preservation of the entire Gulf of Mexico experiment. One urchin, from a site tens of meters away from the brine pool that supported thin bacterial mats on very coarse carbonate sand, was collected with spines attached, and tendons replicated by a mineral crust. It is clear from our results that taphonomic signatures vary widely even within a single zone of active seepage, from accelerated loss of skeletal material to outstanding preservation.

THE EMU BAY SHALE REVISITED: NEW DISCOVERIES FROM A LOWER CAMBRIAN LAGERSTÄTTE IN SOUTH AUSTRALIA

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The Lower Cambrian (Series 2) Emu Bay Shale lagerstätte on the north-east coast of Kangaroo Island, South Australia, first discovered in the 1950s, remains Australia's most informative Burgess Shale-type locality. Previous research on the Emu Bay Shale lagerstätte has focused on collections sourced from the cliff and wave-cut platform exposures outcropping on the shoreline immediately east of the mouth of Big Gully, approximately 3 km east of Emu Bay. Recent excavations at a new locality situated further inland (Buck Quarry) have revealed a far greater diversity of organisms than previously recognized from the lagerstätte, including taxa known from other Cambrian lagerstätten. Better-preserved soft-bodied structures of several previously-known taxa were also recovered.

The Buck Quarry biota is dominated by arthropods in terms of abundance and diversity. Trilobites are the most common fossils, particularly *Estaingia bilobata* and *Redlichia takooensis*; antennae and thoracic appendages are sometimes preserved in *R. takooensis*. The most abundant non-mineralized arthropods are bivalved taxa, including *Isoxys communis* and *Tuzoia australis*, alongside new species of these genera; specimens of these taxa commonly preserve eyes, cephalic and trunk appendages, and midgut glands. Putative stem-group arthropods are relatively rare at Buck Quarry. Representative specimens include frontal appendages and lateral flaps of *Anomalocaris*, as well as the enigmatic *Myoscolex ateles*; the rare occurrence of the latter at Buck Quarry contrasts with it being the most common non-mineralized taxon from the shoreline outcrop. Other new arthropod taxa include a possible xandarellid, a megacheiran with affinities to genera such as *Alalcomenaeus*, *Leancoilia* and *Utahcaris*, in addition to a new family within the

Nektaspida (including two new monotypic genera) that represents a sister group to Naraoiidae + Liwiidae.

The other members of the biota represented at Buck Quarry comprise leptomitid demosponges; palaeoscolecids (including *Palaeoscolex antiquus*); hyoliths; cancelloriids; linguliformean brachiopods; a banffozoan; an *Odontogriphus*-like taxon; and a variety of other problematic forms.

THE SIRIUS PASSET LAGERSTÄTTE (EARLY CAMBRIAN) OF NORTH GREENLAND

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The Sirius Passet biota is the oldest major Cambrian lagerstätte in Laurentia. Trilobite occurrence places it in the *Nevadella* Zone (Montezuman Stage of the Waucoban Series) of the North American standard, equivalent to series 2, stage 3 of the developing chronostratigraphic scale for the Cambrian. The locality on the northern coast of Greenland (82°47.6' N, 42°13.7' W) preserves an assemblage of about 40 species, dominated by weakly sclerotized arthropods, including *Buenaspis*, *Kleptothule*, *Pauliterminus* and *Isoxys*; the lobopodians *Kerygmachela*, *Pambdelurion* and *Hadranax*; and a number of species under publication or awaiting description. Worms include the annelid *Phragmochaeta* and palaeoscolecids. *Buenellus*, *Halkieria evangelista* and rare hyolithids and archeocyathids are the only calcareous forms. With the exception of large *Choia*, the sponge fauna is undescribed; brachiopods are rare.

Fine details of soft tissues such as mineralized digestive glands and muscle fibres, gut traces and limbs are often visible. Their preservation is variable within specimens, and within and between taxa, reflecting the different life styles and taphonomic histories of the various faunal elements.

The Sirius Passet locality lies at the transition between the southern shelf and the northern deep water trough of the trans-arctic Franklinian Basin. The depositional setting of the lagerstätte is reminiscent of the younger Burgess Shale: the fossiliferous fine-grained, siliciclastic sediments of the Buen Formation accumulated in close proximity to the degraded, abrupt, scarp of an extensive aggradational carbonate platform (the Portfjeld Formation). Following exposure and karstification, with shedding of extensive sheets of debris and olistoliths into the trough, the carbonate platform was transgressed in the early Cambrian, with the fine-grained Sirius Passet sediments accumulating in an oxygen-deficient, sheltered pocket in the upper slope coarse-sediment bypass zone. As the basin expanded, continued subsidence and accompanying eustatic sea-level rise caused the siliciclastic Buen Formation to drape the platform.

The northern deep water trough of the Franklinian Basin forms the locus of Ellesmerian deformation with the Sirius Passet locality lying within a zone of southerly directed

thrusts and folds; as suggested for the Burgess Shale, proximity to the carbonate platform probably shielded the Sirius Passet lagerstätte from pervasive deformation. Chloritoid porphyroblasts indicate temperatures in excess of 300°C.

ENVIRONMENTAL INSIGHTS INTO PALEOBIOLOGICAL PATTERNS OF THE CAMBRO-ORDOVICIAN PORT AU PORT AND ST. GEORGE GROUPS, WESTERN NEWFOUNDLAND

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Marine ecosystems experienced significant changes during the Cambro-Ordovician interval. The Cambrian Explosion established new ecosystem complexity and an increase in marine invertebrate diversity, yet the Middle Cambrian–Lower Ordovician interval is characterized by low abundance of skeletal organisms, such as reef builders. Recent work on the carbonate-clastic strata of the Cambro-Ordovician Port au Port and St. George Groups, western Newfoundland, has focused on quantifying skeletal abundances and analyzing geochemical proxies as a way to provide the environmental framework for the observed biological pattern. Measurements of $\delta^{13}\text{C}_{\text{carbonate}}$ and $\delta^{34}\text{S}_{\text{(sulfate and pyrite)}}$ reveal a possible link between environmental fluctuations and the abundance of skeletal organisms. The geochemical data from Middle-Upper Cambrian strata show systematic shifts in $\delta^{34}\text{S}_{\text{sulfate}}$ of $>15\text{‰}$ over relatively short stratigraphic distances (10 m, likely <1 Ma), low average $\delta^{34}\text{S}_{\text{sulfate-pyrite}}$ (ca. 23‰) and a general positive coupling between $\delta^{13}\text{C}_{\text{carbonate}}$ and $\delta^{34}\text{S}_{\text{sulfate}}$. In combination, these results indicate that Middle to Late Cambrian sulfate concentrations were low and that the sulfate reservoir was more sensitive to isotopic variability than it was in either terminal Neoproterozoic or Cenozoic oceans.

The skeletal abundances from the same Cambro-Ordovician sections were examined alongside the geochemical data. Carbonate facies were analyzed in thin section to determine the proportion of carbonate that was skeletal. In general, skeletal abundance is low during the Middle and Late Cambrian and shows a small increase in the Early Ordovician. The major radiation of carbonate skeletal organisms occurs in the second half of the Early Ordovician and Middle Ordovician in western Newfoundland, indicating that environmental conditions were favourable for diversification of skeleton-secreters. Future work on Lower and Middle Ordovician strata exposed in western Newfoundland will determine if the radiation of skeletal organisms occurs concurrently with stabilization of the carbon and sulfur cycles and/or the disappearance of anoxia.

USING DECAY EXPERIMENTS TO CONSTRAIN INTERPRETATIONS OF SOFT-BODIED FOSSILS: APPLICATION TO THE EMERGENCE OF THE CHORDATA

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Many of the early and important episodes of metazoan evolution occur prior to the advent of biomineralization. Consequently, our knowledge of these crucial stages in novel body plan origins is limited to the narrow windows provided by soft-tissue preservation. Often rare, collapsed and partially decomposed, soft-bodied fossils are difficult to interpret unequivocally, principally because of a lack of understanding of the sequence of loss and transformation of key anatomical characters during decay. Nowhere is this more true than the Cambrian fossil record, especially that of chordates. In order to provide rigorous taphonomic constraints upon the interpretation of putative soft-bodied chordate fossils, we undertook laboratory experiments to investigate the decay of chordate characters, using adult *Branchiostoma* (Amphioxus) and larval *Lampetra* (ammocoete) as extant proxies.

Key characters undergo morphological change, and eventually loss, in a non-random sequence. A marked correlation was observed between the relative order of loss of characters, and the phylogenetic level at which characters are informative (e.g. Deuterostoma, Chordata, Cephalochordata or Vertebrata). Different classes of characters thus have different preservation potentials which, if not taken into account, will lead to a systematic bias in the identification of fossil chordates. Recognition of this potential bias, in light of the new taphonomic data, sheds new light upon interpretation of the anatomy and affinity of purported Cambrian chordates from the Burgess Shale and Chengjiang biota such as *Metaspriggina*, *Pikaia*, *Cathaymyrus* and *Haikouichthys*. Exposing the biases due to decay will enable reevaluation of the emergence of the phylum Chordata, and bring to light the potential role of preservation bias in our understanding of other evolutionary episodes.

AT FIRST SIGHT – FUNCTIONAL ANALYSIS OF LOWER CAMBRIAN EYE SYSTEMS

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Over the last 35 years, more than 200 species have been described from the Lower Cambrian Chengjiang lagerstätte. The body plans typical of that time may continue an evolutionary sequence with hidden Precambrian origins; many related forms are still represented in the Middle Cambrian, in the Burgess Shale.

Although the Chengjiang fossils are flattened, their exquisite preservation allows the detailed analysis of features such as cuticular structures, and especially the morphology of eyes. Many of the different eye systems known in recent animals are already present in the Chengjiang fauna. The arthropods that bore these eyes were all adapted to particular life habitats, while the design of visual systems is conditioned by the availability of light and the need for acute vision. All visual systems have to obey the same physical rules in the same way, and an analysis of the structure of fossilized eyes, in comparison to those of marine arthropods living today may reveal how, and under which conditions the now fossilized visual organs may have worked. The result of the investigations presented here is that some of the Lower Cambrian arthropods of the Chengjiang Fauna show “experimental” designs, some of which failed and are no longer present, while others are still represented today. These arthropods may be confidently assigned to a life habitat at a water depth of *c.* 120 m, which is consistent with the geological interpretation of the Kunming area during the early Cambrian.

The analysis of the stalked eyes of *Leanchoilia*, which was thought for a long time to be blind, has shown that the acuity of the eye is far too low to support the idea that this animal was an active free-swimming predator, locating its prey with its eyes. Such optical tracking of prey, however, was possible for the greatest predator of the Cambrian – *Anomalocaris*. It swam with its bulbous eyes extended laterally. The majority of its lenses pointed downwards, and were adapted to vision under dim light conditions as to faster velocities. They were able to scan the world below until they detected a moving target – potential prey. The lateral-most/outermost tip of the eye has smaller lenses but a lower acuity, and is to be interpreted as a zone of growth. A functional analysis of other Chengjiang arthropods is also presented, with a discussion of the relevance of these functions to ecology.

ATTACHMENT ADAPTATIONS OF EDIACARAN SEDENTARY ORGANISMS

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Fixation to the substrate is thought to be an important aspect of the biology and ecology of benthic organisms. However, Ediacaran attachment structures were not considered as a significant object for investigation, due to organism’s disjunction during the fossilization process. Nevertheless, the analysis of attachment patterns makes it possible to recognize some morphological peculiarities of organisms which do not appear to have evident modern analogues. The attachment structures, being preserved *in situ*, serve as unambiguous ecological markers, enabling reliable comparisons between Phanerozoic and Ediacaran communities.

There are seven basic strategies of attachment employed by Phanerozoic organisms. Some were typical for Phanerozoic-style soft substrates with separate hard ground environments; others for rather firm Proterozoic- and Early-Middle Cambrian-style substrates. Based on a taphonomic analysis of representative samples of specimens collected from a single fossiliferous layer, some Ediacaran attachment adaptations were

recognized: (1) fixation on the substrate surface by organic gluing (*Fedomia*); (2) attachment to the substrate with a sucker-like structures (*Vaveliksia*) and peculiar incrustations (*Palaeophragmodictya*); (3) fixation with pointed basal parts inserting into the microbially bound sediment (tubiform *Cloudina* and conical *Thectardis*); (4) anchoring into the sediment by discoidal (*Ediacaria*) and rhizoid-like (*Hiemalora*) holdfasts; (5) partial submergence into the sediment (*Nemiana*) and infaunal life habit (*Petalonama* – *Pteridinium*, *Namalia*, *Ernietta*, *Swartpuntia*, *Rangea*).

Taking into account the adaptations listed above, one can suppose that both Proterozoic-style fixation (1-3) and Phanerozoic-style ones (4-5) were widespread in the Ediacaran communities. If the data on taphonomy and morphology of Ediacaran sedentary organisms are interpreted correctly, we can conclude that most attachment adaptations to the soft and hard substrates had already emerged before the Cambrian.

The observations of Ediacaran community succession suggest that a significant change of attachment strategies took place. For example, Avalon sequences are characterized by minor variants of attachments at the beginning, reaching maximum diversity before a reduction of the variants at the terminal part of the sequence. A similar trend seems to be observed during the existence of the Ediacara biota, although the ambiguity of the interpretation of cyclic fossils makes this scheme less reliable. Such a trend can be explained by intrinsic causes of features' evolution as well as global environmental changes which have been occurred at the beginning of Cambrian.

THE ORIGIN OF THE BRACHIOPOD BODYPLAN

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Brachiopods are bivalved, marine suspension feeders that dominated benthic communities in the Palaeozoic, and have remained moderately diverse into the present. The Brachiopoda are the oldest of all modern phyla; their bivalved body plan evolved in the earliest Cambrian, and the brachiopod crown group was established, at the latest, in the second stage of the period (Atdabanian). The origin and early evolution of the phylum have long been shrouded in mystery. The most popular theory, the 'Brachiopod Fold Hypothesis', contends that the bivalved condition arose through ventral folding of an elongated animal with two dorsal shells. This hypothesis gained support with the description of *Halkieria evangelista*, which exhibits two brachiopod-like shells in addition to numerous spine-like calcareous sclerites. However, new fossil discoveries have recently demonstrated that the bivalved condition of brachiopods evolved through a stepwise reduction of a multi-component tubular skeleton.

The likely ancestors of brachiopods, tommotiids, are one of the most conspicuous organophosphatic components of the Cambrian 'small shelly fossils'. Their small cone or cap-shaped sclerites are among the first skeletal fossils to appear in the lowermost Cambrian. Until recently, tommotiids have only been known from disarticulated material and the gross morphology of the animal; the structure of the skeleton and the

phylogenetic position has been subject to speculation. Tommotiids were usually reconstructed as slug-like animals with a dorsal cover of imbricated sclerites. The first articulated tommotiids, recently found in South Australia, exhibit a radically different body plan.

The scleritome of *Eccentrotheca* is a slowly expanding cone with circular cross section, composed of a multitude of irregular cap shaped sclerites arranged in vertically stacked rings. The tubiform skeleton displays wide variation in form, but was attached to hard substrates via organic structures at the perforated apex. The animal was likely a sessile filter feeder. A second tommotiid scleritome, *Paterimitra*, exhibit a modified version of the tubular model, with a multitude of *Eccentrotheca*-like sclerites surrounding two unequal, bilaterally symmetrical sclerites which define a tubular 'pedicle' opening.

The proposed link between brachiopods and tommotiids was originally based on similarities in shell composition and microstructure, in particular the shared presence of shell penetrating setae in the Cambrian brachiopod *Mickwitzia* and the tommotiid *Micrina*. We now also know that tommotiids, like most brachiopods, were sessile filter feeders, and that they attached to the substrate via a pedicle-like organic structure. We can identify how the two opposing shells of brachiopods evolved from cap-shaped sclerites through a series of intermediate steps. The irregular basal sclerites of *Eccentrotheca* gave rise to the symmetrical sclerites of *Paterimitra* through numerical reduction and specialisation of function of sclerites in the basal sclerite ring. Reduction in tube height through loss of sclerite rings led to a simplified scleritome with 3 or 4 sclerites (*Tannuolina*) and paired fusion of the remaining sclerites resulted in an effectively bivalved scleritome (*Micrina*).

NECTOCARIS, A CEPHALOPOD-LIKE ANIMAL FROM THE BURGESS SHALE

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Nectocaris pteryx was originally described with arthropod-like and chordate-like characters, on the basis of one obliquely preserved specimen from the Walcott Quarry. 91 new specimens from the Burgess Shale permit a re-interpretation of this enigmatic creature.

The predatory animal had a cephalic "nozzle" connected to a large body cavity. Upon entering this cavity through two anterior openings, water was passed through a pair of internal gills into a central canal; it was subsequently exhaled through the flexible nozzle. This exhalent flow would have resulted in a jet of water which could be used in propulsion. This system of organs is strongly reminiscent of the modern cephalopods, and *Nectocaris* shares further characters with this group: it possesses the earliest known camera-type eyes, and a pair of long, flexible tentacles (which were probably used to manipulate prey). The extent of its unmineralized dorsal integument resembles the span of the shell in early larval stages of modern *Nautilus*.

The currently accepted theory of cephalopod evolution suggests that they originated from a benthic chambered monoplacophoran-like ancestor, which became buoyant and then nektonic. *Nectocaris*, which extends the record of cephalopod-like organisms from the Late to Middle Cambrian, is strongly dissimilar from the ancestral cephalopod which such a model would predict.

WHERE'S THE GLASS? BIOMARKERS, MOLECULAR CLOCKS AND MICRORNAS SUGGEST A NEAR 200-MILLION-YEAR MISSING PRECAMBRIAN FOSSIL RECORD OF DEMOSPONGES

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The earliest evidence for animal life comes from the fossil record of 24-isopropylcholestane, a sterane found in Cryogenian deposits, and whose precursors are found in modern demosponges, but not choanoflagellates, calcisponges, hexactinellids or eumetazoans. However, many modern demosponges are also characterized by the presence of siliceous spicules, and there are no convincing fossil spicules until the Lower Cambrian. This temporal disparity highlights a problem with our understanding of the Precambrian fossil record – either these supposed demosponge-specific biomarkers were derived from the sterols of some other organism and are simply retained in modern demosponges, or there is a significant gap in the demosponge spicule fossil record. To resolve this issue, we must establish the phylogenetic placement of another sponge group, the hexactinellids, whose spicules are thought to be homologous to the spicules of demosponges, and who also make their first appearance near the Precambrian/Cambrian boundary. Using two independent data sets – traditional molecular phylogenetic analyses and the presence or absence of specific microRNA genes – we show that demosponges are monophyletic, and that hexactinellids are the sister group of demosponges. Thus, spicules must have evolved before the last common ancestor of all living demosponges. A molecular divergence estimate places the origin of this last common ancestor well within the Cryogenian, consistent with the biomarker record, and strongly suggests that there was a massive failure to preserve siliceous spicules during the Precambrian.

MICRORNAS RESOLVE AN APPARENT CONFLICT BETWEEN ANnelid SYSTEMATICS AND THEIR FOSSIL RECORD

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Both the monophyly and interrelationships of the major annelid groups have remained intractable, despite intensive efforts by both morphologists and molecular phylogeneticists. Morphological cladistic analyses indicate that Annelida is monophyletic and consists of two major monophyletic groups, the clitellates and polychaetes, whereas molecular phylogenetic analyses suggest that polychaetes are paraphyletic and that sipunculids are crown-group annelids. Both of these hypotheses are in conflict with the annelid fossil record – the former because Cambrian taxa are similar to modern polychaetes in possessing biramous parapodia, suggesting that clitellates are derived from polychaetes; the latter because although fossil sipunculids are known from the Lower Cambrian, crown-group annelids do not appear until the uppermost Cambrian. New data – the presence and absence of specific microRNAs – show that both hypotheses are incorrect: annelids are monophyletic with respect to sipunculids, and polychaetes are paraphyletic with respect to the clitellate *Lumbricus*, as suggested by the fossil record. Further, our data resolve sipunculids as the sister group of the annelids, rooting the annelid tree, and hence revealing the polarity of morphological change within this diverse lineage of animals.

SOFT-BODIED GELATINOUS FOSSILS (CNIDARIA/CTENOPHORA) FROM THE LOWER CAMBRIAN, CHENGJIANG BIOTA, YUNNAN PROVINCE, CHINA

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The Early Cambrian Chengjiang biota of southwestern China has yielded exquisite examples of soft-bodied preservation. Previously reported among these were jellyfish, sea anemones, and ctenophores. These fossils provide unparalleled insights into the early evolution of these groups at an important point in the Cambrian explosion of metazoan life. Here, we report new fossils from the celebrated Chengjiang biota, interpreted as extremely fragile gelatinous taxa belonging to Ctenophora, as well as possible siphonophores and hydroids.

The significance of ctenophores has been highlighted in recent molecular studies which place them as a sister group to all metazoans. The presence in the new fossils of eight sets of delicate comb rows, comb plates, a gut, and possible tentacular sheaths; and other features of the anatomy; are all remarkably consistent with some modern ctenophores. However, we apply caution to interpretations of some other fossils (from the Chengjiang biota and the Burgess Shale) with reputed comb rows as they may represent unrelated features.

We report possible hydroids and a siphonophore for the first time. The hydroids are fragmental, and preserved as rows of polyps on individual branches. A single specimen of a jellyfish-like siphonophore possesses elongate tentacles and possible gonozooids.

Details revealed by these remarkable fossils indicate close phylogenetic connections between the 515-million-year-old Chengjiang cnidarians and ctenophores, and their living relatives. These fossils are of great significance to the phylogenies of their respective groups and suggest possible ancestors much deeper in Neoproterozoic time.

FOSSIL ARTHROPODS, EARLY BRAINS: INFERRING CEREBRAL COMPLEXITY FROM PRESERVED SENSILLA

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Apart from a few remarkable fossils from Chengjiang and the Burgess Shale, no others suggest early organization of ganglia and nerve cords. However, knowledge about the degree to which Lower Cambrian arthropods were equipped with brains is crucial to the recent field of neurophylogenetics, which uses a palette of neuronal characters for reconstructing arthropod relationships.

The use of brain structures for inferring affinities within the Arthropoda has an honourable history. Originally employed by Nils Holmgren in 1916, it was the first analysis of its kind to insist on a sister group relationship between the malacostracan crustaceans and insects. A more refined approach, using parsimony analysis of some hundred or so brain characters from species representing all major arthropod groups, supports Holmgren's original contention. However, a malacostracan-like ancestor to the Insecta is strongly disputed by molecular phylogenetics, which proposes an entomostracan-like ancestry.

Observations of traces of cerebral ganglia in the Burgess Shale taxon *Waptia fieldensis* suggest a substantial brain supplied by short-stalked compound eyes and by paired uniramous head appendages equipped with two kinds of sensilla: short brush like extensions, reminiscent of aesthetascs, and longer setae, reminiscent of either mechanosensory structures or mixed mechano- and chemosensory sensilla found on present-day malacostracan antennules. It is of considerable interest whether the crustaceomorph fauna show a loss or reduction of the second pair of head appendages – a feature typifying the insects and an unrelated group, the Myriapoda – as early as the mid-

Cambrian. *Waptia* may suggest such a reduction. Further, the sensory structures on its carapace, abdomen and telson suggest that its sensory systems were as elaborate as those of certain extant malacostracans, particularly basal groups like the phyllocarids. The degree to which central ganglia might have been elaborated, even in the case of trilobites and other arthropods that have gone extinct can, to some degree, be inferred from sensory and central innervation patterns of extant species.

PRIAPULID ORIGIN OF TREPTICHNIDS: EVIDENCE FROM EXPERIMENTAL ICHNOLOGY

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The major evolutionary events that characterize the Precambrian-Cambrian transition are accompanied by profound ecological changes in the composition of benthic communities, the nature of the substrate, and the occupation of marine ecospace. The increased animal activity on and within the substrate is attested by numerous trace fossils, such as the cosmopolitan *Treptichnus pedum*, whose first appearance is used as the GSSP to mark the base of the Cambrian. In spite of its stratigraphical importance, the trace makers of *Treptichnus*, and more generally the treptichnids, have long remained an enigma. Our experimental ichnology with Recent worms solves this puzzle. Well-preserved treptichnids from the Cambrian of Poland, Sweden, Greenland, China and other regions closely resemble horizontal traces produced by Recent priapulid worms in laboratory conditions. This suggests that priapulids created treptichnids, and allows the construction process of the trace to be reconstructed in three dimensions.

Treptichnids are sub-horizontal burrow systems, produced in the sub-surface and generally preserved as positive hyporeliefs. They typically consist of a series of subcylindrical segments that join each other at angles varying between 20° and 90°. Our data clearly show the segmented pattern of treptichnids to arise from the successive retraction and reorientation of the worm's proboscis. They also indicate that the striae present along the segments of treptichnids were probably imprinted in sediment by the external ornament of the worm (e.g. scald rows on proboscis), used as anchoring features. The size range and overall morphology of treptichnids are consistent with those of priapulid worm body-fossils in Cambrian lagerstätten (e.g. Maotianshan Shale, China). The segments of numerous treptichnids are directed upwards, and are interpreted as the probing branches of the burrow system towards the water-sediment interface. Although the exact function of these probings is unclear, they may have been part of the worms' feeding strategy, and would suggest random predation upon small epibenthic invertebrates. The gut contents of Cambrian priapulid worms, which sometimes contain diverse epibenthic organisms such as hyoliths and tiny arthropods, strongly support this interpretation. The antiquity of treptichnids, with possible occurrences below the Precambrian-Cambrian boundary, would designate priapulids as one of the oldest infaunal inhabitants of the substrate.

FROM LIMBS TO JAWS — THE NATURE OF THE MOUTHPARTS OF ANOMALOCARIDIDS

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Anomalocaridids, known from North America, South China, Australia and Europe, have long been regarded as giant Cambrian predators. The discovery of *Schinderhannes bartelsi* (showing an unusual combination of anomalocaridid and euarthropod characters) from the Devonian Hunsrück Slate greatly extends the stratigraphic range of this group of animals. Characteristic features of the anomalocaridids include a pair of frontal (preoral) great appendages and a circular mouthpart. Recently, intensive excavation in localities of the Chengjiang biota and the Burgess Shale led to the growing number of new specimens, which elucidate many aspects of anomalocaridid morphology, diversity, ecology and affinity. Phylogenetic analyses popularly place anomalocaridids in the stem group of euarthropods. However, the nature of the anomalocaridid mouthparts remains obscure.

Among several genera of anomalocaridids, the mouthparts of *Hurdia* are most commonly preserved, which consist of a circlet of 32 plates, the inner margin of each plate armed with small projections (teeth), with four larger plates arranged perpendicularly and separated by seven smaller plates. Examination of anomalocaridid specimens from the Chengjiang biota, the Kaili biota and the Burgess Shale suggest that the mouthparts have a limb nature. Evidence includes the presence of articular membranes between adjacent plates, and successive overlap from the larger plates to smaller plates. These are typical characters of segmented arthropod appendages, each plate representing a skeletal ring of podomere and two adjacent podomeres articulated by articular membranes. Additionally, the smaller teeth fringing the inner margin of plates are probably homologous with endites of arthropod limbs and ventral spines in the frontal appendages of anomalocaridids. The mouthparts of anomalocaridids are here interpreted as four pairs of fused, modified head appendages succeeding the frontal appendages. Each of the four perpendicularly arranged larger plates forms by fusion of two limb bases: the anterior and posterior larger plates represent a fused structure between two bases of the second and fifth pair of head appendages, respectively; the right- and left-side larger plates are fusions of two bases of adjacent limbs (the third and fourth pairs of head appendages) in the right and the left, respectively. In *Hurdia*, also possibly in *Parapeytoia*, many rows of teeth are present within the central opening of the mouthparts. These extra rows of teeth are interpreted as sclerotized structures lining the wall of the buccal cavity and the foregut, which are functioned as gastric mills for further processing the food. The new interpretation of anomalocaridids bearing five pairs of head appendages further supports their relationships with arthropods.

EPISODIC BIO-RADIATIONS AND EXTINCTIONS DURING THE PRECAMBRIAN-CAMBRIAN TRANSITION: INSIGHT FROM SOUTH CHINA

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Earth experienced major biological and environmental revolutions during the Precambrian-Cambrian transition. Most notable was the advent and radiation of animals following the termination of the extreme glaciations around 635 Ma. The sedimentary successions of South China preserve a wide range of facies and exquisitely preserved fossil biotas (e.g. the Weng'an and Chengjiang biotas). These well-exposed sequences offer an unsurpassed opportunity to study these major bio- and geo-events, and their interactions and causal relationships. Accumulating data from many disciplines has demonstrated four bio-radiations and four mass extinctions across the Precambrian-Cambrian transitional interval in South China, which may be applicable on a global scale. The first bio-radiation is evidenced by the rapid appearance of the large acanthomorph acritarchs shortly after the extensive glaciations of the Cryogenian period. These organic microfossils are unique to the early Ediacaran period; they probably represent diapause egg cysts of the earliest metazoans. They became extinct before the advent of an extensive negative carbon isotope excursion (the DOUNCE, Shuram or Wonoka event), with a nadir of -12% . The second bio-radiation produced the megascopic Ediacara-type biotas widely distributed later in the Ediacaran period. These became extinct near the Precambrian-Cambrian boundary (542 Ma), coinciding with the base of a major negative carbon isotope excursion (the BACE event). It may have taken 20–40 million years for life to recover from the end-Ediacaran mass extinction. The abrupt appearance and diversification of the small shelly fossils (SSF) represents the first episode of the Cambrian explosion. However, the SSF experienced a mass extinction before the first appearance of trilobites, and the onset of the second episode of the Cambrian explosion – which is amplified by the global abundance of fossil lagerstätten between 521–515 Ma. A major mass extinction of the Cambrian fauna, notably the archaeocyathid and Redlichiid-Olenellid trilobites, took place around 515–510 Ma.

During the Precambrian-Cambrian transition, positive carbon isotope excursions tend to coincide with times of bio-radiations, while negative excursions seem to correspond to the major mass extinctions.

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THE TAPHONOMY OF THE TRILOBITE ELRATHINA CORDILLERAE FROM THE GREATER PHYLLOPOD BED, BURGESS SHALE

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To deduce how closely fossil assemblages represent original faunal composition, one must quantify the amount of alteration caused by transport and decay. Trilobites, with their multiple parts, provide a sensitive index of post-mortem disturbances in fossil lagerstätten, and are thought to be excellent biostratigraphic indicators. Here we examine the taphonomy of the most common polymerid trilobite from the Burgess Shale biota, *Elrathina cordillerae*. In particular, we consider what constraints its taphonomy provides on the transportation of a vagrant benthic element of the Burgess Shale fauna. Our studies focus on specimens collected by the Royal Ontario Museum on oriented slabs within homogeneous mudstone layers, those at about 245 cm (–245), and 420 cm (–420) below the base of the Phyllopod Bed respectively. These two fossil assemblages were selected for their abundant specimens, making it possible to examine patterns of clustering as well as patterns of disarticulation.

The –420 layer contains a spatially variable, but relatively low density, concentration of *E. cordillerae*. Six slabs, yielding 124 specimens, were examined. 90% of specimens were articulated dorsal exoskeletons, commonly associated with dark staining thought to represent decay fluids. Notable dorsal flexure occurred in more than half of these specimens. Some rare specimens are preserved with limbs. Other material includes an articulated axial shield, conjoined thoracic segments, and isolated cranidia. The articulated dorsal exoskeletons show a wide array of postures, and are almost evenly split between specimens inverted or inclined toward bedding (52%) and those preserved dorsal side up (48%). These exoskeletons do not show a preferred orientation in azimuth. Their size distribution is approximately normal, with a mean glabellar length of 5.45 mm. Preservation of soft tissues or decay fluids (limbs and dark stain) suggests the rapid burial of live animals. The patchy distribution, lack of preferred orientation and clear size sorting, favors preservation *in situ* after swamping and failed extraction.

Specimens from the –245 layer occur at a higher density than in –420, and appear to be distributed in a patchier pattern, with some particularly dense concentrations. Of the 116 total trilobite specimens found on three slabs from this layer, only 18% are articulated dorsal exoskeletons, with a mean glabellar length of 3.96 mm. The postures of these specimens are varied, and include both enrolled and folded specimens. The remaining specimens from –245 show varying degrees of disarticulation, ranging from axial shields with associated but detached free cheeks that are plausibly molt configurations, to isolated, conjoined thoracic segments. The presence of abundant “ptychopariid” protaspids associated with much larger skeletal debris suggests little or no size sorting. The –245 level apparently represents a longer period of accumulation than –420, but evidence of transportation is lacking. Despite the range of preservational styles – suggesting different degrees of time averaging between the beds studied – neither indicates any significant transportation of *E. cordillerae*.

THE EVOLUTION OF SHELL COMPOSITION IN BRACHIOPODS

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The ability to secrete mineralized hard parts is crucial to many animal phyla, as it enables the formation of structural components that commonly define the overall shape of the organism. Because of this fundamental role, biomineralizing systems evolve relatively conservatively, and only rarely show a drastic change in composition. Brachiopods are an example where this has happened: while the subphylum Linguliformea exclusively uses apatite as its mineral component, the other two subphyla Rhynchonelliformea and Craniiformea secrete calcite shells. As the oldest known brachiopod faunas from the Tommotian already contain both phosphatic and calcitic taxa, the split between these two fundamental biomineral systems must have occurred at the very base of the phylum.

Recent work has shown that the shell structures and compositions of early Cambrian brachiopods are more diverse than generally assumed. They transcend the traditional pigeonholes of phosphatic and calcitic shells, and include shells which may have been entirely organic, and shells that are microstructurally and compositionally intermediate between the typical organophosphatic and calcitic types. In order to reconstruct the sequence of shell mineral acquisition, we need an unambiguous stem group that allows us to polarize shell composition.

Currently, the most compelling scenario roots brachiopods within tommotiids. This is supported by the shared shell-penetrating setal tubes of tannuolinids and various problematic brachiopods, and by the recent discoveries of articulated scleritomes of the apparently sessile tommotiids *Eccentrotheca* and *Paterimitra* which suggest that the bivalved brachiopod body plan evolved through the successive shortening and simplifying of a multi-element tube. New microstructural data now provide additional independent evidence suggesting that organophosphatic skeletal secretion in tommotiids is homologous with paterinids, the oldest known organophosphatic brachiopods. Most studied tommotiid taxa and several paterinid taxa exhibit prominent polygonal structures that permeate the entire sclerite.

The transition from tommotiids to paterinids included a gradual shift from a comparably dense lamination with micron-sized laminae to increasingly larger laminae with a decreasing phosphate/organic ratio. The observed microstructural changes probably reflect an adaptation to a more fluctuating phosphorous availability resulting from the switch of the presumed vagrant life style of basal tommotiids to the sessile life style of more derived tommotiids. The origin of calcitic shells from such organophosphatic ancestors was probably also driven by the need to permanently maintain sufficient phosphorous levels for general metabolism. The amounts of phosphorous needed for shell secretion would have made it particularly difficult to thrive in nutrient poor regions such as many tropical reef environments, in which calcitic brachiopods prospered.

EXCEPTIONAL PRESERVATION OF EARLY TERRESTRIAL COMMUNITIES IN LACUSTRINE PHOSPHATE ONE BILLION YEARS AGO

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Good terrestrial fossil assemblages are rarely seen before the Devonian (*c.* 350 Ma). Evidence for freshwater and terrestrial life in the Precambrian has therefore been circumstantial, and none has yet come from freshwater phosphate. We here demonstrate that phosphate from the *c.* 1200–1000 Ma Mesoproterozoic lake sediments of the Torridon Group (NW Scotland) preserve a remarkable picture of freshwater and terrestrial phototrophic ecosystems. Ephemeral lakes and streams, which developed in intermontane basins within the interior of the supercontinent of Rodinia, periodically experienced prolonged desiccation and phosphate precipitation. Microbial remains comparable with modern eukaryote (chlorophyte) algae and cyanobacteria reveal delicate cellular and sub-cellular structures, including desiccation-resistant cysts and aplanospores. These data suggest that Earth's terrestrial biota and its associated phosphorus cycle were well established on land by *c.* 1000 Ma.

EXCEPTIONAL PRESERVATION OF MICROBES IN THE LATE EDIACARAN LONGMYNDIAN SUPERGROUP, UK

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The study of historical and new collections from the Longmyndian Supergroup sheds new light on Ediacaran microbial communities and taphonomy. First reported by Salter in 1856, and noted by Darwin in the *Origin of Species* in 1859, a range of macroscopic bedding plane markings are already well known from the Longmyndian supergroup. Here we report filamentous and sphaeromorph microfossils, variously preserved as carbonaceous films, by aluminosilicate permineralization and as bedding plane impressions. This supports a long-suspected link between wrinkle markings and microbes, and draws further attention to our hypothesis for a taphonomic bias towards high-quality soft tissue preservation in the Ediacaran Period.

ONTOGENY, VISION AND LIFE HABITS OF SPHAEROPHTHALMUS ALATUS (BOECK) FROM THE FURONGIAN OF BORNHOLM

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Abundant specimens of *Sphaerophthalmus alatus*, which occurs together with *Mesoctenopyge tumida*, are present in the Furongian of Bornholm. All the specimens are incomplete and disarticulated. The described ontogeny is based upon detached cranidia, librigenae (though commonly incomplete), and pygidia, together with some protaspides. Early meraspid cranidia are remarkably similar in shape to those of full grown adults, being narrow and highly convex. Each librigena has a well preserved ovoid – subspherical eye. The smallest eyes are *c.* 250 µm in length, and about 200 µm in height, with about 70 lenses of less than 30 µm in diameter; the largest are 550 µm long, and 500 µm in height, with about 150 lenses. The largest lenses are up to 34 µm in diameter; these occur towards the top of the eye, where the hexagonal close packing is fairly regular. Packing is less well constrained in the centre of the eye, and more regular where the lenses become smaller towards the base of the eye. The visual field is virtually panoramic, from 0 to 180 degrees in a horizontal plane, and below the equator to 90 degrees above, but the fields of the two eyes do not overlap. The eye-parameter (main visual field) lies at about 5.4 µm rad, which corresponds to recent compound eyes adapted to dim light conditions. The sensitivity of the eye is comparable to the living *Nautilus* pinhole eye. The greatest depth at which the eye could function would be no more than 150 m in clear waters.

Two forms of juvenile pygidia are found in our material; one belonging to *S. alatus*, the other to *M. tumida*. The pygidia of the adult *M. tumida* are unknown, and we have had problems in relating these juvenile forms to the correct adult species. The form with an initially serrated margin is considered to belong to *S. alatus*; that with a stout central spine to *M. tumida*. The body of *Sphaerophthalmus* is poorly known, but probably resembles that of *Ctenopyge* (= *Eoctenopyge*) *angusta*, which is in many ways intermediate between *Ctenopyge* and *Sphaerophthalmus*, and which could have been placed in either genus.

From the studies of the optical systems (eye parameter and visual field), *S. alatus* appears to be adapted to a benthic life. This is consistent with previous reconstructions, which show the genal spines arranged horizontally but splayed out laterally. A more extreme adaptation for a benthic life is that of *C. angusta*, in which the long genal spines would have acted as sled runners on the mud. *S. alatus*, however was probably capable of swimming; the related *S. humilis* has genal spines which in life pointed downwards so it could not have lived on the sea floor. The contemporaneous *M. tumida* likewise has well preserved eyes which are distinctly kidney shaped, and the two forms are not easily confused. The ontogeny and optics of this species are still being investigated.

PROVIDING A PALAEOECOLOGICAL AND GEOCHEMICAL CONTEXT FOR CLOUDINA IN WESTERN NORTH AMERICA

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Biom mineralized skeletons of benthic organisms are first recorded in the latest Neoproterozoic with the appearance of *Cloudina*, a small (length up to 1 cm; 2–4 mm diameter) tube-dwelling organism. *Cloudina* were examined from the Precambrian Reed Formation, and the overlying lower member of the Deep Spring Formation, at several localities in eastern California and western Nevada. These western North America *Cloudina* localities contrast with other *Cloudina* localities in that the assemblages occur in level-bottom sedimentary settings, unlike the biohermal settings found elsewhere. *Cloudina* preservation varies significantly at the study sites, from relatively complete tests to fractured debris, occurring primarily in shell beds. Microstratigraphic and diagenetic analyses in thin section give further evidence for transportation before final deposition.

In addition to paleoecological analyses, this study also provides concentration and isotopic analyses of carbonate-associated sulfate, which gives insight to the redox conditions of the oceans during this critical interval in Earth history. Samples collected at high stratigraphic resolution from the *Cloudina* localities in the Reed and Deep Spring Formations provide a record of latest Neoproterozoic $\delta^{34}\text{S}$. Using sulfate as a proxy for changing oceanic conditions, we gain insight into how oxygenation of the oceans may have played a role in the evolution of *Cloudina* and the subsequent Cambrian radiation.

A broader context of these cloudinids is necessary for establishing a baseline towards understanding how early biomineralizers evolved in response to the ongoing “agronomic revolution” of increasing bioturbation that was occurring during the Neoproterozoic-Cambrian transition. Our ability to provide this broad context is enhanced by the physical and microbial structures within the interbedded siliciclastic strata in this region. The *Cloudina* in western North America occur before the Precambrian-Cambrian boundary, and hence before the appearance of significant vertical bioturbation. The thick Lower Cambrian sections in the study area provide numerous carbonate intervals from which to assess the context of succeeding early biomineralizers. This stratigraphic interval in eastern California and western Nevada thus provides a basis on which to determine how the first biomineralizing organisms evolved as part of the “Cambrian substrate revolution”.

PALAEOECOLOGICAL ASPECTS OF CAMBRIAN BIVALVES: CONCLUSIONS FROM PERIGONDWANAN OCCURRENCES

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The palaeoecology and palaeobiology of Cambrian bivalves (=pelecypoda) is controversial due to limitations in critical taxonomic characters and poor preservation. Here we report Perigondwanan specimens from Germany, Turkey, and Morocco. Of the several hundred fossils, most are represented by steinkerns of articulated *Pojetaia* and *Fordilla* preserved in late-Early Cambrian to early-Middle Cambrian limestones. They occur in two different facies realms.

The bivalve-bearing sediments of Germany (Charlottenhof Fm.) and Turkey (Çal Tepe Fm.) are bioclastic wackestones and floatstones of a shallow subtidal, open-marine environment within a transgressive system. The fauna is autochthonous to par-autochthonous and mainly represented by echinoderms and cancelloriids, but trilobites, hyoliths, other molluscs, poriferans, and “small shelly fossils” (hyolithelminths, cambroclaves, *Rhombocorniculum*, *Halkieria*, etc.) also occur. In both regions, the bivalve level is immediately below nodular limestones which are interpreted as the initial drowning of the ramp or platform. For the relatively small palaeoecological window of the bivalves, a quiet and muddy, shallow carbonate environment of rather low latitude palaeogeographic regions with somewhat reduced carbonate precipitation rate is envisaged. In contrast, no bivalves occur in typical oligotrophic environments which are characterized by calcimicrobial carpets and archaeocyathan reef mounds.

Moroccan bivalves come from allochthonous limestone hash layers (Jbel Wawrmast Fm.) of a storm-influenced, high-energy intertidal to very shallow subtidal environment (nearshore to shoreface) of a transgressive regime. Along with these bivalves, reworked remains of trilobites, brachiopods, echinoderms, and various “small shelly fossils” occur. We reinterpret the habitat of the redeposited fauna as more distal (shallow, low energy platform, occasionally agitated by storms) than the definite depositional area. This palaeoecological window corresponds to that of the bivalve-specimens from Germany and Turkey, and supports the hypothesis that Perigondwanan bivalves are very sensitive to palaeoecological changes during early stages of transgression.

Several arguments point to an infaunal mode of life of *Pojetaia* and *Fordilla*: (1) laterally compressed shape, (2) general articulated preservation, (3) shell symmetry (very well-developed anterior end), and (4) lack of microbial overgrowth. The feeding strategy of the early bivalves is hard to estimate. There is no indication of a pallial sinus or a siphon as in modern species, leading to the assumption that *Pojetaia* and *Fordilla* were deposit feeders using their ciliated body and mantle surface to collect food particles. We assume that their early ontogenetic stage was lecitotrophic, with a relatively short planktonic larval phase. We take this to imply that the Cambrian palaeocontinents were more closely connected than commonly assumed. Along with poor preservation, and the absence of critical characters typical of phylogenetically younger bivalves, this makes it generally difficult to distinguish between species and variants in Cambrian taxa.

Because of their paleoecological sensitivity and the persistent taxonomic uncertainties, Cambrian bivalves should be used only carefully as biostratigraphic and paleogeographic tools.

FEEDING IN SITU: DIRECT PROOF FOR CAMBRIAN HERBIVORY AND CARNIVORY IN THE BARRANDIAN AREA (CZECH REPUBLIC)

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Several examples of *in situ* ecological interactions are presented from the Middle Cambrian Jince lagerstätte (Barrandia, Czech Republic). Primary consumption is observed in microbial mats with carbonaceous filaments, retrieved from stratigraphically higher levels of the Jince Formation, which were supposedly deposited in shallow water. Several of these surfaces contain articulated exoskeletons of the opportunistic polymerid trilobite *Ellipsocephalus hoffi*, and complete specimens of the tiny hyolithids *Jincelites vogeli* embedded inside organically preserved microbial mats. Both the trilobites and hyoliths represent an *in situ* assemblage of benthic primary consumers.

Hiding or scavenging behaviour is evidenced by several examples of the agnostid *Peronopsis integra* inside other invertebrates. Two articulated exoskeletons of *P. integra* are entombed between the hypostome and the dorsal exoskeleton of the cephalic shield of a complete specimen of *Paradoxides (Hydrocephalus) minor*; another intact exoskeleton of *P. integra* is preserved under thorax of a carcass of *P. minor*. A holaspid specimen of *P. integra*, with hypostome *in situ*, occurs inside of the hyolithid conch of *J. vogeli*. *Peronopsis* may have fed on deteriorating soft tissue of the containing organism, or dwelt within the host for protection from predation, bad weather or moulting.

Numerous articulated holaspids of *P. integra* associated with late meraspid to early holaspid specimens of *Paradoxides paradoxissimus gracilis* cover slabs with partially disarticulated large specimens of the edrioasteroid *Stromatocystites pentangularis* and/or the cystoids *Akadocrinus* in lower levels of the *P. paradoxissimus gracilis* Zone in the Jince Formation. This may indicate scavenging.

The large flattened thecae of the edrioasteroid *S. pentangularis* sometimes contain a number of the bradoriid *Konicekion*; eight to over sixty individuals may be present in a single edrioasteroid, some of which are in the “butterfly position”. This mass occurrence of bradoriids represents the oldest known direct evidence of carnivorous behaviour for these arthropods, reflecting either hunting or opportunistic scavenging.

TRILOBITE TAPHONOMY OF THE LATHAM SHALE (LOWER CAMBRIAN), CALIFORNIA: A BURGESS SHALE-TYPE DEPOSIT OF WESTERN LAURENTIA

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The Early Cambrian Latham Shale (Mojave Desert, California) has yielded a diverse fauna including abundant olenelloid trilobites, and rare unmineralized taxa, such as algae and anomalocaridids. A >500-specimen sample from the formation shows that the most abundant trilobite species include *Olenellus clarki*, *Mesonacis fremonti*, and *Bristolia bristolensis*, with the abundance rank of species varying greatly between localities. *O. nevadensis*, *B. mohavensis*, *B. harringtoni*, *B. insolens*, and *B. anteros* were also present in lower quantities. The frequency distribution of the olenelloid trilobite fragments indicates the absence of size-based sorting. Of the total sample, 97.8% were isolated complete or partial cephalons. Only 1.4% were complete articulated thoraxes (with articulated cephalons in most cases). Orientation data indicate that the cephalons show no statistically significant up-down trend, and azimuth orientations of the long axis of the glabella show no obvious preferred trend. Taphonomic results suggest that the Latham Shale trilobites were deposited in a quiet-water setting in the inner detrital belt with little current activity and generally long bottom exposure times for moults and carcasses.

In the up-down orientation of the sclerites; mean, mode, and range of cephalon widths; and percentage of complete specimens, trilobites of the Latham Shale differ markedly from other abundant trilobite deposits at certain sites in the Spence Shale of Idaho and the Bright Angel Shale of Arizona. In contrast to the Latham, the trilobites in these latter deposits are more frequently articulated, and show a moderate to strong preference in up-down orientation. These taphonomic differences likely result largely from relatively faster burial in higher-energy environments. Possible differences in decomposition patterns between the Early Cambrian trilobite taxa of the Latham and those of the Middle Cambrian taxa of the Spence and Bright Angel may also have an impact.

ISOXYS AND TUZOIA WITH SOFT-PARTS FROM THE EMU BAY SHALE: COMPARISON WITH MATERIAL FROM OTHER CAMBRIAN LAGERSTÄTTEN

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Abundant material from Buck Quarry, a new outcrop of the lower Cambrian (Series 2) Emu Bay Shale lagerstätte (Kangaroo Island, South Australia), contains preserved soft-bodied features previously unknown from the original Big Gully locality. This has allowed the revision of *Isoxys communis* and *Tuzoia australis*, two bivalved arthropod taxa described in 1979 by Glaessner. The collections have also produced fossils that represent two new species, one of each of *Isoxys* and *Tuzoia*. Among the soft parts preserved in these taxa are stalked eyes, digestive structures and cephalic and trunk appendages.

Comparison with species of *Isoxys* with soft-parts from the Burgess Shale, the lower Cambrian Maotianshan Shale (China) and the Sirius Passet assemblage (Greenland) show that the genus exhibits a considerable range of morphologies of cephalic appendages, ranging from long and spiny to short and spineless. However, the nature of the postcephalic appendages seems more conservative, with a small endopod and a well developed exopod fringed with setae. Other non-mineralized structures, such as stalked eyes and digestive structures are very similar across the genus.

Tuzoia is also widespread (Canada, eastern and western USA, south China, Australia, Czech Republic), but preservation of soft parts is extremely rare: out of more than four hundred specimens studied by Vannier and colleagues, only three specimens of *T. burgessensis* and *Tuzoia* sp. from the Burgess Shale have preserved soft parts. In contrast, soft part preservation in *Tuzoia* from the Emu Bay Shale is more common, being present in 5% of specimens. Both Australian species preserve soft parts in the form of eyes, while the appendages and other anatomy of these taxa remain elusive. The Australian species fall within the lower and upper size range of the genus, with the larger species from the Emu Bay Shale only surpassed in size by *Tuzoia* sp. from Bohemia; both exceed 13 cm in maximum sagittal length.

THE ORIGIN OF THE PALAEOSCOLECIDA AND SOME OTHER CAMBRIAN WORMS

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Cambrian lagerstätten preserve an enormous variety of palaeoscolecids and other ecdysozoan worms. Palaeoscolecids were first discovered 130 years ago, and for over a century were affiliated with the annelids. However, the group possesses many characters which are absent in annelids: a terminal mouth and anus; an inverting proboscis with pointed scalds; a thick integument built of diverse plates; sensory trunk tubuli, tumuli, and flocculi; and caudal hooks. These features have been taken to indicate an affinity with the Cephalorhyncha or Cycloneuralia. These two phyla unite some “primitive” worms (priapulids, kinorhynchs, loriciferans, and nematomorphs) with a retractable proboscis (at least in their larval stages), a circumpharyngeal brain, and some other features also found in leg-bearing ecdysozoans.

The Palaeoscolecida, and many other Cambrian ecdysozoan worms (including *Ancalagon*, *Fieldia*, and *Louisella*), are commonly treated as representatives of the Priapulida, or as relatives of the Nematomorpha. However, the elaborated cuticle of these Cambrian worms is comparable with the cuticle of larval priapulids and other cephalorhynchs. In contrast, introverts of the Palaeoscolecida and most Cambrian ecdysozoan worms are much less complex than those of modern cephalorhynchs. Thus, we propose that these Cambrian worms represent a stem-group of the Cephalorhyncha.

The Palaeoscolecida share some of their morphological features with the Xenusia (leg-bearing Cambrian ecdysozoans). Xenusia commonly possess a terminal mouth; proboscis (although not retractable); midgut diverticulae; and a thick integument built of diverse three-layered plates. They also possess telescopic walking appendages (lobopods) similar to those of the Onychophora and the Tardigrada. The most primitive Cambrian ecdysozoan worms bear a non-retractable proboscis and midgut diverticulae, while both the Palaeoscolecida and the Xenusia share a complete (although highly variable) set of cuticular plates, with a common microstructure. This suggests that stem-group cephalorhynchs are decedents of xenusian-like ecdysozoans, whose body form was modified in adaption to a burrowing lifestyle. This caused the loss of walking appendages, and acquisition of a retractable proboscis and “worm-like” body during an adaptation to burrowing life-style. The loss of limbs occurs independently in many animal clades (over 100 times among the tetrapods, for example), and is often accompanied by axial elongation; however, the reaquisition of limbs is rarely observed. These changes garner more efficient locomotion, the ability to navigate crevices, and the ability to burrow. On this basis, we consider it more likely that cephalorhynchs were derived from limb-bearing xenusian-like ecdysozoans, and not vice versa. We propose *Facivermis* as a representative “intermediate form” – this semi-burrowing sedentary worm bore lobopods around a terminal mouth; an annulated, limbless, plate-bearing trunk; and a terminal anus.

MORPHOLOGY OF EXTANT PLANKTONIC CTENOPHORES AND CNIDARIANS: CONSIDERATIONS FOR INTERPRETING ANCIENT FORMS

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Among the most intriguing of fossils, because of their relative phylogenetic position to the earliest metazoans, are some soft-bodied forms attributed to gelatinous plankton such as scyphozoan jellyfish and ctenophores. Fossils thought to belong to these groups have been reported from several Burgess Shale-type deposits including the celebrated Chengjiang biota of Yunnan, China.

Because so little of the structure of these animals is preserved, and only under unique conditions, recognition of homologous structures such as tentacles and ctenophore comb rows in both fossil and extant forms is often problematic. Given the difficulty of obtaining intact specimens, contemporary representatives of these organisms are often unfamiliar even to marine biologists and invertebrate zoologists, let alone paleontologists.

Here we present unique macroscopic and microscopic view of living jellies and ctenophores, with special focus on diagnostic features that might be of value in identifying fossil counterparts from Burgess Shale-type deposits in particular.

EVIDENCE OF MOULTING IN PALAEOSCOLECID WORMS FROM CHENGJIANG

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The palaeoscolecidians are a group of fossil priapulid-like worms which bear a variety of trunk ornaments, including sclerites, plates, and platelets with several central nodes. They have a wide distribution and are known from the Early Cambrian to the Late Silurian; they were a significant component of benthic and endobenthic Cambrian communities. Morphological data supports the placement of the group as an Ecdysozoan clade, basal to the lobopods and arthropods. While there is abundant evidence of moulting in lobopods and arthropods, direct evidence of moulting in palaeoscolecidians is lacking. The fossil record of palaeoscolecidians predominantly consists of trunk fragments and discrete sclerites, which cannot preserve evidence of moulting. However, soft tissues are rather abundant in the Early Cambrian Chengjiang biota.

There are two methods used in recognizing moults. The first is to identify new sclerites located beneath the older ones, which we contend can be recognized in some well preserved *Cricocosmia* specimens, as well as in other palaeoscolecids. A similar record of moulting has been reported in the Chengjiang lobopod *Microdictyon*. The other approach considers the preservation status of worms in event beds: moults are usually strongly twisted, and lack a proboscis and guts, which clearly differentiates them from poorly-preserved body fossils. However, we have yet to observe palaeoscolecid moults preserved within their burrows. We suggest that moulting style differs in various worms, and that breakage of the cuticle, perhaps caused by the scalids, occurred between the trunk and the pharynx.

EXCEPTIONAL PHOSPHATIC PRESERVATION IN THE LOWER CAMBRIAN COMLEY LAGERSTÄTTE OF ENGLAND

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The exceptional preservation of embryos and small, non-mineralizing metazoans in early diagenetic phosphate provides a unique window onto evolution across the Proterozoic–Phanerozoic transition. However, a poor understanding of the underlying taphonomic mechanisms limits the palaeobiological inferences that can be drawn. In particular, it is not known whether the conspicuously narrow range in taxonomy and body size of the preserved organisms is governed by intrinsic biological properties, or whether it reflects conditions of preservation in a shared ecological or environmental setting. Furthermore, there is disagreement as to whether the various assemblages represent the products of a common taphonomic pathway.

We contribute new empirical data to the debate through a detailed analysis of the Lower Cambrian Comley lagerstätte of England, which has yielded exceptionally preserved soft parts of phosphatocopines and thus represents one of the earliest known occurrences of phosphatized micro-arthropods. Our re-excavation of a classic locality, combined with petrographic and energy-dispersive X-ray analysis, has allowed a new, high-resolution reconstruction of the Comley sequence, while extensive new collections of microfossils have revealed a preservational spectrum with implications for the depositional and post-burial environment. Through comparison with broadly contemporaneous assemblages, we find that the shallow depositional setting of the Comley sequence is comparable to that of the embryo-bearing facies of the Doushantuo Formation (Neoproterozoic, China), although the style of phosphatization is closer to that of the arthropod-dominated, quiet-water Orsten deposits from the middle to late Cambrian of Sweden. We question whether the apparent diversity of depositional settings is genuine or artefactual, and explore the implications for understanding the history of this phosphatization window and of the life that it reveals.

THE COLLEPLAX – A HOMOLOGOUS STRUCTURE IN THE ONTOGENY OF EARLY CAMBRIAN STEM RHYNCHONELLIFORM BRACHIOPODS

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The ontogeny of fossil and recent brachiopods has been of great importance in deciphering phylogenetic relationships of the clade. The resolution within the clade could be improved with a better understanding of the ontogeny of Early Cambrian brachiopods. One poorly-understood Early Cambrian group is the order Chileida, which has been considered to belong within the calcareous-shelled crown group Rhynchonelliformea, in the class Chileata. The chileids are amongst the earliest known brachiopods with a calcareous and strophic shell, but as they are known mostly from rather coarsely silicified shells, their early life history has been largely unknown. A unique find of well-preserved phosphatized material of a chileid from the Flinders Ranges, South Australia, shows that their early ontogeny closely parallels that of the unusual Early Cambrian paterinate-like *Salanygolina* from Mongolia. In both *Salanygolina* and the new chileid, the anterior margin of the well defined ventral larval shell is indented by an unrestricted notch that, through later ontogeny, develops into an umbonal perforation, directly anterior to the umbo. In subsequent ontogenetic development, this sub-triangular perforation is enlarged by resorption and covered posteriorly by the colleplax – a triangular plate – in the umbonal perforation. The colleplax structure was first described from the equally enigmatic Palaeozoic order Dictyonellida (Rhynchonelliformea, Chileata); the colleplax in *Salanygolina* is considered to be homologous with that of the chileates. As proposed in the original description, the foramen and colleplax clearly represent integral parts of an attachment structure that developed early in the ontogeny and was retained in the adult. This type of colleplax holdfast cannot be considered homologous with the pedicle of the Cambrian paterinids, such as *Micromitra*, which are famously found still-attached to sponges in the Burgess Shale. However, it is possible that the earliest larval attachment of the chileids and *Salanygolina* can be compared with the paterinid pedicle, emerging between the valves; we infer that the first larval pedicle was thus homologous to the adult pedicle of paterinids.

Uniquely preserved scleritomes of early Cambrian tommotiids from South Australia show that they represent sessile stem brachiopods. Study of the early ontogeny of the derived tommotiid *Paterimitra* shows that its early life history closely parallels that of the brachiopods; it has a brachiopod-like bivalved larval shell, which is also provided with a colleplax structure, here considered to be homologous with that of *Salanygolina* and the chileids. However, in *Paterimitra* the colleplax-structure does clearly not function as an adult holdfast. We propose that *Salanygolina* and the chileids, as well as the tommotiid *Paterimitra*, belong to the stem of the crown group Rhynchonelliformea.

APPENDAGES OF EARLY CAMBRIAN EOREDlichIA (TRILOBITA) FROM THE CHENGJIANG BIOTA, YUNNAN, CHINA

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The Early Cambrian Chengjiang biota in Yunnan, southern China, has yielded many articulated exoskeletons of the spiny redlichiid trilobite *Eoredlichia intermedia*, some with exceptionally preserved appendages. Each of the paired, uniramous antennae of a medium-sized holaspis consists of 46–50 short segments (articles), each of which bears a fine spine near its inner edge. Behind the antennae there are twenty one pairs of biramous limbs: three pairs are situated underneath the cephalon, one pair underneath each of the fifteen thoracic segments, and probably three pairs underneath the small pygidium. The endopod consists of a broad basis and seven podomeres, of which the last is divided into three terminal spines. The exopod is blade-like, and according to one interpretation is dorsally hinged to the basis of the endopod – an alternative suggestion being that both the endopod and exopod are split from the basis, the latter being independent and not forming part of the endopod. The exopod has a prominent anterior rim, and possesses about forty long filaments along the posterior margin, and short setae along the rounded distal lobe. The basic appendage features of the redlichiid trilobites are comparable to those of other known Cambrian polymerid trilobites, such as *Olenoides*, that belong to more distantly related clades. The gut, preserved in three specimens, has the form of a straight, tubular alimentary canal, with nine pairs of diverticulae, four belonging to the cephalon and five to the thorax. *Eoredlichia*, like many other Cambrian trilobites, is best interpreted as a scavenger/predator.

THE EARLY CAMBRIAN GUANSHAN FAUNA — A NEW BURGESS SHALE TYPE FOSSIL LAGERSTÄTTE FROM YUNNAN, SOUTHWEST CHINA

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The Guanshan fauna, a new konservat-lagerstätte from the Botomian (Early Cambrian) of eastern Yunnan, SW China, is slightly younger than the famous Chengjiang fauna. Fossils of non-mineralized taxa are found in the Wulongqing Formation (previously assigned to the Wulongqing Member of the Canglanpu Formation) from the lower *Palaeolenus* Zone to the upper *Megapalaeolenus* Zone.

The Guanshan fauna is diverse. The arthropods (including trilobites and non-trilobite arthropods, bivalved arthropods, and some new taxa) are the most abundant and dominant group, followed by the brachiopods. The brachiopod and paleoscolecid

assemblages are diverse, and soft-tissues are occasionally preserved. Vetuliciliids, hyolithids and anomalocaridids are commonly recovered. Sponges, chancelloriids and eocrinoid echinoderms are relatively rare, and lobopods rarer still. Not even putative macroalgae have been found.

The Wulongqing Formation is composed of mudstones interbedded with siltstones. The underlying Hongjinshao Formation represents deltaic and flood deposition, indicated by thick sandstone layers with large cross bedding, flute casts, and ripples. Basal conglomerates define the base of the Wulongqing Formation, probably representing a regional transgression in SW China. Non-mineralized fossiliferous layers generally show graded interbedded silt and mudstone with erosive bases, indicating rapid deposition from distal storms. Sedimentological and taphonomic analyses indicate that the unusual preservation of the unmineralized fossils results from smothering by storm-induced rapid burial, producing autochthonous or parautochthonous assemblages. Wrinkle structures and microbe-induced sedimentary structures imply the possible presence of microbial mats.

This fauna is almost contemporaneous with the Early Cambrian Chengjiang Fauna, but its composition is more reminiscent of Middle Cambrian fossil lagerstätten such as the Kaili Biota and the Burgess Shale. This provides a new window into the diversity and dynamic of Early Cambrian marine communities, with great significance for our understanding of the Cambrian Explosion and early animal evolution.

A MIDDLE CAMBRIAN BURGESS SHALE-TYPE FAUNA FROM SHANDONG PROVINCE, EASTERN CHINA

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Soft-bodied Cambrian faunas have a worldwide distribution. Within China, most occur in a wide area of the Yangtze platform, represented by the Chengjiang fauna from Yunnan Province and the Kaili fauna from Guizhou Province. The stratigraphy has been well established in the Early to Middle Cambrian Huabei platform on the basis of fragmented trilobites. Few soft-bodied animals have been so far reported from the Huabei platform.

Complete, well-preserved trilobites are abundant in the Middle Cambrian Xuzhuang Formation (Zhangxia Stage), Feixian, Shandong, eastern China, which is near the south margin of Huabei platform. This fauna is preserved in black to greenish shale, and is dominated by the trilobite *Maotunia*. The trilobites *Manchuriella*, *Changqingia*, and *Eymekops* were also present. Many trilobites were preserved as complete individuals; isolated cephalons and pygidia of *Pseudoperonopsis* occur in several beds. Other soft-bodied animals are present, including sponges, chancelloriids, arthropods (e.g. *Isoxys*), putative echinoderms, problematica (e.g. *Banffia?*), and other unidentified fossils. Brachiopods and hyoliths are also very common.

This Burgess Shale-type fauna helps to reveal the diversity, distribution and evolution of soft-bodied animals in the Cambrian.

COMPARATIVE PALAEOECOLOGY OF CHANCELLORIIDS IN THE MAOTIANSHAN SHALE AND WHEELER SHALE BIOTAS: NON-ADAPTATION TO THE CAMBRIAN SUBSTRATE REVOLUTION

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Chancelloriids were a taxonomically enigmatic group of Early and Middle Cambrian animals noted for their unusual sponge-like morphology. They lived in the midst of the Cambrian substrate revolution, when increasing bioturbation in shallow subtidal unlithified seafloors led to a transition from firm Proterozoic-style substrates to soft Phanerozoic-style substrates with a well-developed mixed layer.

We compare the ecology of two exceptionally preserved chancelloriids: *Allonnia*, from the early Cambrian Maotianshan Shale biota, southwest China; and *Chancelloria eros*, from the middle Cambrian Wheeler Shale of Utah. Both these localities exhibit an extremely low level of bioturbation, with an ichnofabric index of 1. This suggests that firm Proterozoic-style substrates still dominated both environments.

Allonnia is interpreted as a shallow sediment sticer adapted to firm substrates. Its morphology reflects this lifestyle: specimens often exhibit tapered blunt basal ends, and lack structures for attachment to hard substrates. These features are shared with *Chancelloria*, suggesting that it too was a shallow sediment sticer. It is possible that the chancelloriids were restricted to firm substrates, and that their failure to adapt to the changing substrate conditions of the Cambrian substrate revolution led to their extinction in the late Cambrian.

ELDONIA AND WIWAXIA FROM THE CAMBRIAN OF THE BARRANDIAN AREA (CZECH REPUBLIC)

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We examined Burgess Shale-type soft-bodied fossils from the Cambrian of the Barrandian area, Czech Republic. One specimen of *Eldonia* sp. was discovered in the Paseky Shale (Holsiny-Horice Formation, Pribram-Jince Basin) at Kočka Hill, Brdy mountains. It is part of a very low diversity *Kodymirus* assemblage, which is dominated by arthropods. Among them, only the stem-chelicerate *Kodymirus vagans* is very abundant (more than one thousand exoskeletal fragments were found). The larger stem-group aglaspideid *Kockurus grandis* and the tiny, crustacean-like *Vladicaris subtilis* are comparatively rare (both known from several tens of fragments). The macroscopic alga *Marpolia spisa* also occurs infrequently (several tens of fragments discovered). Ichnofossil diversity is low, suggesting that the low diversity of the body-fossil assemblage is not a taphonomic

artefact. Most traces were apparently produced by arthropods, and can be attributed to the aforementioned species.

We identified rare specimens of the pterobranch *Rhabdotubus robustus* from the “Orthisovy lumek” (Orthis Quarry) near Skryje (Tyrovce Member, Buchava Formation in the Skryje-Tyrovce Basin). We defend the interpretation of this organism as a dendroid graptoloid. Seven isolated *Wiwaxia* sclerites (six scales and one spine) are preserved on surfaces bearing *R. robustus*. Although the poor preservation quality prohibited detailed analysis of sclerite morphology, there are no obvious differences from the type species *W. corrugata*.

EARLY CAMBRIAN STEM-GROUP BRACHIOPODS FROM SOUTH CHINA

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The early Cambrian is a key period in brachiopod evolution. Members of the crown group make their first appearance, and join the company of many enigmatic stem group forms. Many stem-group brachiopods and brachiopod-like fossils have been recovered from Lower Cambrian rocks in South China, including some cap-like small shelly fossils (eg., *Tianzhushanella* and *Lathamella*), some tommotiids (eg., *Micrina* and *Tannuolina*), *Heliomedusa* and possible halkieriids. These fossils are important for studying the origin and early evolution of brachiopods.

Many cap-like SSFs (c. 18 genera) from the pre-trilobitic Cambrian were previously described as brachiopods. Though their shells may originally have been calcareous, the fossils are usually preserved by secondary phosphatisation. Only two genera (*Tianzhushanella* and *Lathamella*) may conceivably be related to brachiopods. The other genera are molluscs, junior synonyms of other genera, or enigmatic fossils with whose status as a genus is questionable. *Tianzhushanella* is often taken as a senior synonym of *Lathamella* since both genera are cap-like and bear a pair of recessed cavities in the umbonal region. Recent SEM examination of the holotype of *T. ovata* shows 7 rows of nodes on the surface of the internal mould, opposing the synonymy of the genera. Unlike the bivalved *Apistoconcha* and *Aroonia* from the lower Cambrian of South Australia, both *Tianzhushanella* and *Lathamella* from South China have been only recovered with one type of valve, without “ventral” and “dorsal” differentiation. It remains unclear whether they were univalved, or bivalved with two nearly equal valves.

Heliomedusa from the Chengjiang Biota was referred to the craniopods or discinids, but the distinctive pustulose ornamentation on the shell of *H. orientalis* may indicate affinities to the early Cambrian stem-group brachiopod *Mickwitzia*.

DEPOSITIONAL ENVIRONMENTS AND GEOCHEMISTRY OF THE SHIYANTOU SILTSTONE, YUNNAN, CHINA

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The Early Cambrian Shiyantou Siltstone of Yunnan Province immediately underlies the Yu'an-shan Shale, which contains the Chengjiang Biota. The Shiyantou occupies a critical stratigraphical interval in the history of life: Small Shelly Fossils appear in the immediately underlying Yuhucun Formation, and the first appearance of trilobites occurs immediately above the Shiyantou, in the lowermost Yu'an-shan Shale. We examined a core drilled through the Yu'an-shan and Shiyantou at Haikou, Kunming to better resolve the geochemistry and depositional setting of this sequence.

Surface exposures of Shiyantou are highly weathered and friable, and appear featureless in outcrop. Analysis of core material reveals that the Shiyantou is comprised of amalgamated, 0.4–3.0 cm thick, event beds, which are characterized by alternating quartz silt–black shale laminae, typically several millimetres thick, with significant basal scour between events. Rarely, ripple cross laminations are present. Abundant pyrite occurs throughout the Shiyantou, and is typically restricted to thin black shale laminae, whereas authigenic calcite preferentially occurs as a pore-filling phase in thin silt laminae. Both of these authigenic phases are completely lost from surface exposures due to intensive weathering in the shallow subsurface. Moderate bioturbation (ichnofabric index 3) of 2–3 cm depth is prevalent throughout the Shiyantou, indicating that oxic bottom waters prevailed at least periodically during the accumulation of the unit. Pyrite occurs throughout the section as dispersed grains and as larger aggregate clusters. Petrographic and $\delta^{34}\text{S}$ analyses of individual grains isolated from whole rock by HF extraction and $\delta^{34}\text{S}$ transects across individual large grains and aggregates provide constraints on the chemical conditions that prevailed in the waters overlying the Shiyantou and during sulfate reduction in the organic rich sediments.

THE EARLY CAMBRIAN ARTHROPOD GUANGWEICARIS: ITS SOFT TISSUES AND EVOLUTIONARY SIGNIFICANCE

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Based on newly discovered fossil material with excellently preserved soft tissues, we have investigated the morphological details of the appendages of the Early Cambrian Fuxianhuia-like arthropod *Guangweicaris*. We discuss its phylogenetic relationships, and its bearing on the evolution of early arthropods. Although its body segmentation is

typical of *Fuxianhuia*-like protoarthropods, advanced characteristics of euarthropods are clearly displayed in the appendages and antennae, suggesting a key position of *Guangweicaris* in the transition from protoarthropods to euarthropods. *Guangweicaris* is a non-trilobite arthropod documented only from the Early Cambrian Guanshan fauna of Yunnan, China. This animal consists of 18 body tergites. The head is composed of two tergite-bearing segments: the eye-bearing segment, and the antennal segment. A shield-like structure is present as a widely expanded tergite, just like in other *Fuxianhuia*-like arthropods. These features are considered typical characteristics of protoarthropods. The trunk (body tergites from 3-17) is divided into two parts: the thorax, with 8 tergites; and the abdomen, comprising 7 tergites. Three thoracic tergites are covered by the shield-like structure, the so-called “second head tergite”. Posteriorly, there is a triangular tail spine and a pair of lateral flaps (the last body tergite).

The eyes of *Guangweicaris* are similar to other *Fuxianhuia*-like arthropods (including *Shankouia*, *Fuxianhuia* and *Chengjiangocaris* from the Lower Cambrian Chengjiang Biota), which are thought to be borne on short, tubular stalks. The antennae of *Guangweicaris* are unusual, as they are flagelliform in shape and composed of at least 23 short annuli. This morphology is regarded as a derived euarthropod character. Other euarthropod characters are also present in the limbs. The limbs of *Guangweicaris* are neither tubular with a multi-annulated main rod, nor – as described for *Fuxianhuia* – like a sclerotised lobopod. Rather, the multi-jointed limbs comprise an 8-10 podomere endopod, a flap-shaped exopod, and a possible rigid basipod.

We consider *Guangweicaris* as a “derived *Fuxianhuia*-like protoarthropod”. This research may help reshape current hypotheses of early arthropod evolution.

GOGIID EOCRINOIDS (ECHINODERMATA) FROM THE LOWER AND BASAL MIDDLE CAMBRIAN, YANGTZE PLATFORM, GUIZHOU PROVINCE, CHINA

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Thousands of new specimens of *Sinoeocrinus* and *Globoeocrinus* (basal Middle Cambrian: Kaili Formation) and *Guizhoueocrinus* (Lower Cambrian: Balang Formation), from the eastern margin of the outer shelf/upper slope of the Yangtze Platform (Guizhou Province, China) have greatly enhanced our knowledge of ontogenetic development, heterochrony and functional morphology in these groups. Guizhou gogiids are similar to, but are more primitive than, those of western Laurentia and southern Gondwana. Thecal height is used as a proxy for development. Ontogeny and emplacement of brachioles is similar in all three genera.

Guizhoueocrinus is the most primitive genus known. In both the theca and the stalk, its plates are poorly organized, and independent of the ambulacra. The number of thecal and stalk plates in *Sinoeocrinus* and *Globoeocrinus* is reduced by pedomorphosis. Nearly half the stalk plates in *Sinoeocrinus*, and all those in *Globoeocrinus*, are juvenile in character.

Sutural pores are restricted to thecal plates, and are emplaced in three series: (1) just below the ambulacra; (2) just above the stalk/theal juncture; and (3) over the rest of the theca. Pores change from round to oval as the organisms mature; this transition is observed in juvenile *Globoeocrinus*, early mature *Sinoeocrinus*, and in the second row of plates in juvenile-to-mature specimens of *Guizhoueocrinus*. The pores peramorphically become triangular in mature *Sinoeocrinus*, and in late-juvenile to mature *Globoeocrinus*.

Apparent soft-part preservation associated with *Guizhoueocrinus* suggests that respiratory tissue resembled papillae, which bowed inwards like a pocket. In *Globoeocrinus* and *Sinoeocrinus*, the (probable) respiratory surface area falls off relative to thecal volume. Respiratory efficiency was maintained by pressurizing the theca, by covering both the mouth and anus, then circulating coelomic fluid by peristaltic gut pumping, to propel the fluids past the inwardly directed respiratory tissue. The attachment disks of gogiids were 'glued' to the substrate, probably with collagen.

THE EARLY CAMBRIAN BALANG FAUNA, EASTERN GUIZHOU, CHINA

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The Early Cambrian Balang Formation (eastern Guizhou, China) is composed of gray to gray-greenish silty shale or muscovite-rich shale and mudrock. It was deposited in a slope facies belt juxtaposed between the Yangtze platform to the west and the Jiangnan basin to the east. Trilobite biostratigraphy places the fauna in Cambrian Series 2 (Dunyunian Stage, equivalent to the late Chanlangpuian and Botomian), between the Early Cambrian Chengjiang Biota and the Middle Cambrian Kaili Biota. The age-equivalent Guanshan Biota was preserved in shallow water settings, whereas the Balang Biota was preserved in deeper water, in shelf margin to slope facies.

The upper part of the formation yields an important Burgess Shale-type biota, including a diverse skeletal fauna, non-mineralized invertebrates, algae, and a rich ichnofauna. The eocrinoid *Guizhoueocrinus* and the trilobite *Redlichia* (*Pteroredlichia*) are the most common and characteristic taxa of the fauna. The fauna also contains trilobites, trilobitomorpha, bradoriids, large bivalved arthropods, coelenterates, brachiopods, priapulid worms, molluscs, stalked eocrinoid echinoderms, hyoliths, cancelloriids, brachiopods, phyllocarids, bradoriids, and palaeoscoleids.

The preservation of an unusually large quantity of high quality articulated eocrinoid specimens, including those preserved attached to skeletal fragments of hyolithids, trilobites and bradoriids, indicates that the fauna was smothered and rapidly buried by obrution events. Only one species of eocrinoid is present; it exhibits a complex ontogeny involving changes in ambulacral symmetry, position and number of thecal plates and sutural pores, and number and disposition of brachioles.

THE NEOPROTEROZOIC DZABKHAN BIOTA: ALGAE, MICROFOSSILS, TRACE FOSSILS AND PROBLEMATIC REMAINS FROM WESTERN MONGOLIA

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The Ediacaran-Cambrian boundary marks one of the most important events in geological history. However, in spite of the tremendous progress in Ediacaran-Cambrian stratigraphy and palaeontology, the location of this boundary – and indeed the most appropriate way to subdivide Cambrian and Ediacaran stratigraphy – is still a hot topic.

We examined Ediacaran-Cambrian siliciclastic-carbonate sections in southwest Mongolia, which contain both ichnofossils and small shelly fossils. These fossils allow the age of the strata to be determined. *Treptichnus pedum* proved to be an inadequate marker for the Ediacaran-Cambrian boundary in the Dzabkhan Zone. The association of ichnofossils present alongside the first appearance of *T. pedum* is typical of younger ichnozones, correlating to the Upper Tommotian–Lower Atdabanian ichnozone III, and the *Rusophycus avalonensis* ichnozone from Newfoundland.

The Eastern European platform contains Ediacaran sediments which are associated with glacial deposits at their base, and yield an Ediacara-type fauna. Microfossils have been derived from silicified, carbonate and phosphate layers of the upper part of the Tsaganolom Formation, which lies above the glacial Maikhanuul diamictites. The Dzabkhan microfauna contains algae, large acanthomorphic acritarchs, multicellular thalli, sponge spicules and problematic remains. This complex is comparable to Ediacaran assemblages such as Doushantuo of South China, Pertataka of Central Australia and the Ediacaran of the East European Platform. The Ediacaran-Cambrian transitional layers contain problematic Ediacara-type fossils. Problematic cyclic organisms from the Tsaganolom Formation are morphologically similar to the common Ediacaran genera *Beltanelloides*, *Beltanelliformis* or *Nemiana*, but poor preservation prohibits a rigorous identification.

The Ediacaran-Cambrian boundary can be established more precisely at the base of the Tommotian Stage by the presence of the SSF associations, trace fossils, microfossils and bioherm-forming algae.

A CRITICAL REVIEW OF THE OCTOCORALIAN FOSSIL RECORD (CNIDARIA: ANTHOZOA)

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Octocorals have a rather disjunct representation throughout the geological record. The earliest possibly date back to Ediacaran faunas and today they are as diverse and widely represented as soft and horny corals (Alcyonacea and Gorgonacea), sea pens (Pennatulacea), as well as blue corals and stoloniferans (Helioporacea and Stolonifera) and some other small groups. They are generally characterized by a lightly chitinized exoskeleton (e.g. Gorgonacea) or endoskeletons with microscopic calcareous sclerites or axial rods (e.g. Alcyonacea, Pennatulacea). All have poor preservation potential, which is clearly the principal reason for their rarity and occasional absence in the fossil record.

Despite this, over the decades a number of Palaeozoic octocorallian fossils have been described. In many of these, understanding higher-level taxa has not been possible, largely as a result of poor preservation of the microstructure. After detection of skeletal carbonate hydroxylapatite in recent gorgonaceous octocorals, previously unknown in modern coelenterates, several Early Cambrian phosphatic 'problematica' have occurred regarding relationships to octocorals appear now in another light. Similarly, fossils of the Ediacaran leaf-like presumed pennatulids have been described from Cambrian rocks – the earliest of these is *Priscopennamarina* from the Early Cambrian of eastern Yunnan, China. The Middle Cambrian Burgess Shale taxon *Thaumaptilon* is also presumed to be a pennatulid, while another Burgess Shale fossil – *Echmatocrinus* – originally described as a crinoid, was later interpreted as a probable octocoral. Some Neoproterozoic phosphatized embryos have been attributed to cnidarians, but interpretations of the Ediacaran and Cambrian pennatulid-like fossils and probable octocorals are not always accepted with regard to the further Phanerozoic fossil record.

The early fossil record, evolution and phylogeny of Octocorallia and Anthozoa, including recent molecular analyses, is still in a state of confusion, and more work is needed before either hypothesis can be accepted or rejected.

EDIACARAN SEEPAGE-RELATED CLOUDINA-MICROBIALITES FROM SOUTHERN NAMIBIA

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Little is known about the lifestyle of the calcified tube organisms of the *Cloudina* group. This late Proterozoic group, whose overall morphology slightly resembles modern calcified worm tubes, were the first animals with calcified skeletons. The modern seep-related vestimentiferan worm tubes of *Escarpia* are composed of chitin; in few cases we note the beginning of CaCO₃ (aragonite) mineralisation on the chitin surfaces. The calcified skeleton of *C. hartmannae* exhibits a more complicated microstructure. The

calcareous skeleton, which was probably originally aragonitic, appears to be produced by an enzymatically controlled biomineralisation.

Adolf Seilacher reconstructed the *Cloudina* group as typical soft bottom dwellers. Some millimetre-sized *C. riemkeae* specimens are indeed common in soft micritic, lagoonal carbonates. However, we have observed large *C. hartmannae* tubes inside very large (10–12 meters high, 30–50 cm in diameter) pillar-like microbialites (“organ-pipes”) from the Zaris Mountains/ Zebra Rivier (Omkyk Member, Kuibis Subgroup, Nama Group). These microbialites have a complex structure. The inner portions of these microbialites are formed by large, cm-sized recrystallized aragonitic spherulites covered by calcified microbial matter exhibiting a typical thrombolitic structure. The outer portions of the microbialites exhibit a typical stromatolitic structure. These “organ-pipe” microbialites strongly resemble the modern ones known from Lake Van and Mono Lake. In both modern cases the microbialites grow in extremely alkaline water located at sites where Ca²⁺-rich ground water seeps. Geochemical data, from the still Sr-rich neomorphic aragonitic spherulites and all other noted carbonate phases, suggest that the microbialites from the Zaris Mountains in Namibia formed under comparable conditions.

Cloudina is very common within the thrombolitic portion of the microbialites and the occurrence is definitely autochthonous; *Cloudina* has probably filtered the seep fluids. A chemosynthetic life style cannot be excluded and will be the subject of further investigations. The occurrence of the heavy calcified metazoan skeletons in potentially Ca²⁺-rich seep fluid environments support the idea that Ca²⁺-detoxification was a driving force of the beginning of an enzymatically controlled biomineralisation.

THE EYES OF LEANCHOILIA, AND WHAT THEY MAY TELL US

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Leanchoilia represents one of the most common non-trilobite arthropods known in the Lower and Middle Cambrian, characterized by great first appendages which are supported by three anterior filaments. A vigorous discussion about the systematic position of this genus followed Walcott’s 1912 description of the genus. Although substantial material had been used in all previous investigations, the presence or absence of eyes remains one of the most controversial characters of its morphology. Walcott himself described *L. superlata* to have pedunculate eyes, as had been proposed for *L. illecebrosa*. On the other hand, there is a long history of observations describing two pairs of pits on the head, interpreted as eyes attached near the front of the ventral underside of the headshield. The reconstructions made between 1935 and 1983 did not show any eyes, and the genus was considered to be blind.

In this study, we investigated roughly fifty specimens of *L. illecebrosa* from the Chengjiang and Haikou areas (Yu’anshan Member, Heilingpu; former Qiongzhusi Formation). Just four of these specimens possessed ventrally stalked eyes. These stalks differ from the pendulum-like eyes of *Alalcomenaeus*. They are very narrow, and at the distal end they

are structured rather like a bunch of grapes, with about 100 separate spherical units on the visual surface. Their shape is comparable to the stalks of some crustaceans, or other Chengjiang arthropods. These lenses have a diameter of *c.* 60 μm and indicate (by calculation) a lifestyle under dim light, probably at the sea-floor at a water depth of under 200 m. The delicacy and low preservation potential of their stalks explains their rarity. Likewise, the fine structures of the visual surface have only a limited chance of preservation, and can usually only be observed in Chengjiang fossils using light microscopy with the most tangential light. If *Leanchoilia* was a free-swimming animal, the low resolution of its eye would not allow the formation of an image sufficient for hunting or the detection of predators. If, on the other hand, it lived on the sea floor, its eyes may have enabled it to detect priapulid worms by observing their movements in the ground when disturbed by the digging actions of *Leanchoilia's* great appendages. We interpret the pitlike eyes described by previous authors as ocellar eyes, in agreement with previous work which showed that no facets are recognisable. We interpret these four dorsal ocelli as homologous to typical dorsal median eyes of arthropods, which are, in general, a euarthropodean autapomorphy.

It may therefore be concluded that, like many modern arthropods, *L. illecebrosa* has two kinds of eyes – two stalked ventral eyes, and four dorsal (ocellar) median eyes. Its stalked eyes indicate that *Leanchoilia* was a bottom dweller, able to detect worms as prey in the sediment of the sea-floor.

DORYPYGE PERCONVEXALIS (TRILOBITA, MIDDLE CAMBRIAN) FROM ZANSKAR REGION OF NORTHWEST HIMALAYA: SIGNIFICANCE IN GLOBAL CORRELATION

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Dorypyge perconvexalis occurs very sparsely in the late-Middle Cambrian *Lejopyge laevigata* Zone, and the lower part of the *Proagnostus bulbosus* Zone, in Himalayan India. Six pygidia and two cranidia have been collected from alternating shale-lime grainstone beds of the Teta Member (Karsha Formation) exposed along the Tangze-Yogma-Kuru section of the Kurgiakh valley in southeastern Zanskar (Zanskar-Spiti Basin). This is the first report of the genus *Dorypyge* from the region.

The Indian Himalayan species is assigned to *Dorypyge perconvexalis* based on characters of the pygidium, including deep and clearly defined pleural and interpleural furrows; one pair of long and stout posterolateral spines; dense, medium granular ornamentation; and the absence of a lateral border and border furrows. The Indian species can be differentiated from the type species of *Dorypyge*, *D. richthofeni*, by its wide and relatively short axis; incised pleural and interpleural furrows; five pairs of marginal spines, with the last pair longer and stouter; and lack of a lateral border. It differs from a third species, *D. Bisulcata*, in possessing only a single pair of long, stout posterior spines.

New findings indicate the occurrence of this species in the Wangcun and Paibi sections, northwestern Hunan, China, where it occurs in the *Wanshania wanshanensis* Zone to *Listracina bella* Zone. However, in the Zanskar region of Zanskar-Spiti Basin, this species is found at a stratigraphically lower level, in association with trilobites of the *Lejopyge laeivigata* Zone to *Proagnostus bulbosus* Zone (equivalent to the *Pianaspis sinensis* Zone to *Wanshania wanshanensis* Zone of Hunan).

Dorypyge is globally widespread in rocks of middle Middle Cambrian age; species occur in late Middle Cambrian successions in Australia and China, and elsewhere in Laurentia and Gondwana.

MICRORNAS AND METAZOAN PHYLOGENETICS: BIG TREES FROM LITTLE GENES

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Knowledge of the phylogenetic relationships between modern organisms allows the reconstruction of morphological characters shared by the last common ancestor of the crown group. With this knowledge, fossils can be correctly placed along the stem-lineage, thereby giving insight into the order of character acquisition during the evolution of that clade. Sequence-based molecular phylogenetics has provided robust answers to many phylogenetic questions, but many areas of the metazoan tree have remained recalcitrant, yielding either poorly resolved or conflicting trees. This is particularly true for fast, deep radiations such as the Cambrian "explosion" of animal life. New approaches may be needed to resolve these problems. MicroRNAs possess three properties that give them tremendous potential as phylogenetic markers: (1) new microRNA families are continually being incorporated into metazoan genomes through time; (2) they show only rare instances of secondary loss, and only rare instances of substitutions occurring in the mature gene sequence; and (3) they are almost impossible to evolve convergently. Because of these three properties, we propose microRNAs as a novel type of data that can be applied to virtually any area of the metazoan tree, to test among competing phylogenetic hypotheses or to forge new ones.

We have coded a presence/absence matrix for all known and newly-discovered conserved microRNA families from 36 metazoan taxa that span the range of metazoan evolution. This matrix includes nine taxa whose microRNA complement was determined during the course of this study by applying 454 pyrosequencing technology to small RNA libraries. Parsimony analysis of the matrix demonstrates that microRNA datasets are capable of robustly resolving almost all nodes in the metazoan tree, including the placement of acoel flatworms, the monophyly of Eumetazoa, and the relationships among annelids that are recalcitrant in many molecular analyses. When homoplasy indices for this matrix are compared to matrices using the same taxa but assembled using data from morphological characters, 18S rDNA, PCR-amplified nuclear housekeeping genes, ESTs or complete mitochondrial genomes, microRNAs have the least homoplasy of any dataset used in

metazoan phylogenetics. This suggests not only that microRNAs hold high promise for resolving difficult phylogenetic problems, particularly the phylum- and class-level divergences during the Ediacaran and early Paleozoic, but highlights the extreme conservation of microRNAs and the intense selection pressures operating on these genes over evolutionary timescales.

ECHMATOCRINUS FROM THE BURGESS SHALE: A CRINOID OR AN OCTOCORAL?

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Echmatocrinus brachiatus from the Middle Cambrian Burgess Shale was originally described as the earliest known crinoid-like fossil, and was generally accepted as an echinoderm and crinoid precursor or sister group. An alternative interpretation, as an early skeletized octocoral (Cnidaria), has also been proposed.

Morphologic features of *Echmatocrinus* indicating likely echinoderm affinities include: (1) the plated stalk, conical cup, and erect, uniserial, articulated “arms” that resemble those in other early crinoids, (2) the apparent sutured, polygonal plates covering all parts of the body, (3) the reticulate ornament that resembles other known Burgess Shale echinoderms, (4) the resemblance of this ornament to stereom, although with a larger pore size, (5) the presence of aligned crystals in the thin pyrite film, possibly indicating single-crystal original plating, (6) the soft appendages (tube feet?) branching alternately off the arms in the holotype, (7) the curled tips of the arms like those seen in some living crinoids, (8) the apparent internal ligaments holding the arm segments together, (9) tiny plates lying alongside many arms that appear to be open cover plates, and (10) a disklike attachment structure at the distal tip of the stalk, similar to early crinoid holdfasts.

Problems in assigning *Echmatocrinus* to the echinoderms include: (1) lack of convincing pentameral symmetry (5 or 10 arms), (2) lack of convincing stereom in the body plates, (3) lack of pentameres or organized columnals in the stalk, (4) lack of large, organized, plate circlets in the cup, especially radials beneath the arms, (5) the large, alternating, tube feet instead of smaller tube-foot triads, and (6) no moldic specimens that preserve convincing polygonal plating or sutures.

Morphologic features of *Echmatocrinus* indicating likely octocoral affinities include: (1) overall similarity of *Echmatocrinus* cup and arms to the large, soft-bodied, living octocoral *Alcyonium*, (2) thin imbricate scales covering many deep-sea octocorals, and (3) average number of tentacles is about 8 in known *Echmatocrinus* specimens. Problems in assigning *Echmatocrinus* to the octocorals include: (1) the fact that *Alcyonium* is colonial, with many individuals attached to a common base, (2) solitary octocorals are rare today and have not been described as fossils, (3) heavily plated octocorals have large fanlike colonies with hundreds of tiny polyps, unlike *Echmatocrinus* that is not fan-shaped and 25-30 times larger, (4) all living octocorals have eight tentacles, with almost no variation, vs. 6-9 arms in different specimens of *Echmatocrinus*, (5) no octocoral has ligaments in the tentacles, (6) no octocoral has tiny cover plates on the tentacles, and (7) *Echmatocrinus*

doesn't resemble sea pens, the only octocorals that are reputed to occur in the Late Proterozoic and Cambrian. Although not conclusive, more features favor an echinoderm and basal crinoid assignment for *Echmatocrinus* than an unspecified octocoral assignment.

SMALL SHELLY FOSSILS FROM THE MIDDLE CAMBRIAN STEPHEN FORMATION, BRITISH COLUMBIA, CANADA

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In the Stanley Glacier area, Kootenay National Park (British Columbia, Canada), only the upper member (Waputik Member) of the Stephen Formation (*Ehmaniella* zone, Middle Cambrian) is present. The member consists of six shale-dominated parasequences which grade upwards into pack- or grainstones. It is underlain by cryptalgal laminites of the upper Cathedral Formation, and overlain by nodular carbonates of the Eldon Formation. Fourteen carbonate horizons have been sampled for acetic acid preparation, ranging from the uppermost Cathedral Formation to the lowermost Eldon Formation. Acid residues include common trilobites (e.g., *Elrathina*, *Pagetia*), inarticulate brachiopods (obolids, acrotretids, acrothelids, and paterinids), various morphologies of enigmatic sclerites (probably re-crystallized echinoderm ossicles), and internal molds of hyolith cones. Helcionellids, sponge spicules, chancellorids, and bradoriids are present but rare. The fauna and faunal associations vary with respect to stratigraphic position, and paleoenvironments inferred from sedimentological data. Furthermore, the various inarticulate brachiopods, some of which were previously only known from shale preservation, display new details on shell structure and shell morphology.

PLACEMENT OF THE STAGE 5, SERIES 3 GSSP (APPROXIMATELY THE "LOWER-MIDDLE" CAMBRIAN BOUNDARY): AN UPDATE

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Placement of the "Lower-Middle" Cambrian boundary has been, and still is, controversial. It is difficult to correlate the boundary, as presently recognized, in different regions of the world. The "Lower-Middle" Cambrian working group of the Cambrian Sub-commission of the ICS is presently tackling the problem. At present the traditional boundaries, recognized by the last appearance of *Olenellus* (olenellids) in Laurentia; first occurrence of *Paradoxides* (paradoxids) in Baltica and the Mediterranean; and the last occurrence of *Redlichia* in China, are not suitable.

After vigorous discussion about the attributes of the different potential biohorizons, each member of the Working Group was asked to vote for two likely FAD horizons. Working

Group members include representatives from Australia, Canada, China, England, Germany, Korea, Russia, Spain, Sweden, and the United States. Twenty-three out of 25 members voted, their first choice was given a full point and their second choice a half point. The members suggested that two biohorizons are the most likely candidates for the definition of Stage 5/Series 3 lower boundary, which is roughly equal to the “Lower-Middle” Cambrian boundary. The favoured horizon is the FAD of *Oryctocephalus indicus*, both in total points (12.5) and first place votes (11). The second favoured horizon is the FAD of *Oryctocara granulata* in total points (9.5) and in second place votes (11).

The location of the potential GSSP is still being considered. There are two possible GSSP locations using the FAD of *O. indicus*. The most likely location is in the Kaili Formation at the Wuliu Section near Balang, Guizhou, China where it occurs just above the LAD of *Redlichia*, matching the traditional boundary in eastern Gondwana. The second location is in the Emigrant Formation at the Split Mountain, Nevada, USA, where the boundary is located 15 m above the last occurrence of olenellid trilobites. However, the Split Mountain section is condensed; correlation to other locations in Nevada indicates a stratigraphic thickness of 30–50 m between the FAD of *O. indicus* and the LAD of olenellids. At present, the Kuonamka Formation at the Molodo River section, Siberian Platform, Yakutia, Russia is the only likely location for a GSSP using the FAD of *Oryctocara granulata*. This section is very well exposed, but is condensed and remote; the climate restricts access to two months per year.

There are many problems that hinder the progress in establishing a GSSP. First and foremost is the correlation between palaeogeographical regions. To perform this correlation, some other problems need to be addressed, and more data collected. Problems include: (1) the taxonomic identification (and agreement) and ranges of *O. indicus* and *O. granulata*; (2) the paucity of data on carbon and sulfur isotopes, REE, magnetostratigraphy, and sequence stratigraphy; and (3) the taxonomic evaluation (and data collection) of brachiopods, hyolithids, acritarchs, molluscs, and small shelly fossils.

THE OLDEST BIVALVED ARTHROPOD ASSEMBLAGE FROM THE EARLY CAMBRIAN OF SOUTH AUSTRALIA

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Bradoriids and phosphatocopids are small bivalved arthropods that were an important component of Cambrian faunal assemblages before disappearing in the middle Ordovician. Historically considered to be ancestral ostracods, appendage morphology of exceptionally preserved specimens from China and Sweden suggests that both groups are only distantly related to extant and fossil Ostracoda. Bradoriids are currently thought to be a potential sister group to the Crustacea and phosphatocopids a sister group to the crown group Eucrustacea. Bradoriids and phosphatocopids had a worldwide distribution during the Cambrian and have been recorded from all the major Cambrian lagerstätten.

They have been sporadically documented from Cambrian successions in central and northern Australia equivalent to Cambrian Series 2 (Stage 4) and Series 3 (Stage 5 to Guzhangian). The diverse faunas from older parts of the traditional lower Cambrian in South Australia (Series 2, Stage 3) remain to be fully described.

Bradoriids occur coevally with the first trilobites on several continents, but appear slightly earlier than the first recorded trilobite (*Abadiella*) in southern China. The oldest bradoriids previously documented from South Australia were svealutids from the Lower Cambrian (*Abadiella huoi* Zone, Atdabanian equivalent). These occur in association with species belonging to the Hipponicharionidae and Monsateriidae. The oldest phosphatocopid in Australia (*Indianidae* gen. et sp. indet.) has also been documented from this trilobite zone in South Australia.

Recent systematic investigations by the authors have revealed well preserved, diverse (total of 8 taxa) and prolific bradoriid and phosphatocopid assemblages (including new taxa) in acid resistant residues from the lower Cambrian Ajax Limestone in the northern Flinders Ranges. In the Ajax Limestone, the first bradoriids occur some 20 m below the FAD of the zonal trilobite *A. huoi*. This pre-trilobitic occurrence suggests an early Series 2, Stage 3 age for the assemblage and represents the oldest bivalved arthropod assemblage hitherto known from the lower Cambrian succession of South Australia. The recognition of distinct bradoriid assemblages associated with the *A. huoi* (Atdabanian), *Pararaia tatei*, *P. bunyerooensis* and *P. janeae* (all Botomian) trilobite biozones in South Australia indicates great potential for future regional, and possibly intercontinental, biostratigraphic correlation.

PRECAMBRIAN–CAMBRIAN FOSSIL RECORD OF POLYPOID SCYPHOZOANS

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Recent molecular studies indicate that the phylum Cnidaria originated during the Proterozoic Eon. However, the fossil record of Precambrian cnidarians is problematical. Various Ediacaran fossils that were originally interpreted as cnidarian medusae or polyps have been removed from this group, and the cnidarian affinity of various polyp-like fossils from the lower–middle Cambrian has also been called into question.

The scyphozoan cnidarians are characterized today by a prominent medusoid stage and a relatively inconspicuous polyp. Ediacaran and Cambrian scyphozoan have large polyps, which in some cases are encased in a phosphatic periderm. The Ediacaran *Vendoconularia triradiata*, known from a single Ediacaran specimen, is most similar to conulariid scyphozoans (Late Cambrian to Late Triassic) – although unlike these fossils it may have lacked a mineralized periderm. Certain more-or-less tubular genera from the Lower to Middle Cambrian have also been interpreted as scyphopolyps. *Hyolithellus* and *Byronia* are most similar to the peridermal tubule of extant coronates, and were probably coronate polyps themselves. *Cambrorhytium* and *Cambrovitus* were probably polypoid

scyphozoans or hydrozoans. *Sphenothallus*, whose range continued to the Permian, was either a scyphozoan or hydrozoan polyp. It occurs both in shallow shelf carbonates and in dark shales deposited in deep slope settings. The Lower Cambrian small shelly fossils (SSFs) *Arthochites*, *Carinachites*, *Emeiconularia*, and *Hexaconularia* have been interpreted as conulariid scyphozoans. Together these four genera exhibit certain gross morphological characteristics that appear to be shared only with Late Cambrian and younger conulariids. However, the laminar microstructure and internal skeletal structures (septae, carinae, and transverse walls) of these SSFs is not conulariid-like. Further, *Hexaconularia* exhibits a distinct apical region, probably an embryonic shell, which is absent in conulariids. The apparent absence of conulariids or conulariid-like fossils in middle Cambrian strata presents another problem for the hypothesis of a conulariid/scyphozoan affinity for conulariid-like SSFs.

Like modern scyphozoan polyps, *Byronia*, *Cambrorhytium*, *Cambrovitus*, and *Sphenothallus* were sessile organisms that were attached by an apical holdfast to biological substrates such as brachiopod shells or other tubular fossils. With the possible exception of *Sphenothallus*, all of these taxa appear to have been solitary. None of the conulariid-like SSFs exhibit a basal holdfast or other intrinsic evidence (e.g. close association with possible substrates) of a sessile mode of life.

ARTHROPOD VISUAL PREDATORS IN THE EARLY PELAGIC ECOSYSTEM EXEMPLIFIED BY ISOXYS

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Fossil specimens with exceptionally preserved soft parts from the Maotianshan Shale (c. 520 Ma) and Burgess Shale (505 Ma) biotas indicate that the globally distributed bivalved arthropod *Isoxys* was probably a non-benthic visual predator. We obtained new evidence from the functional morphology of its powerful prehensile frontal appendages which, in conjunction with large spherical eyes, are thought to have played a key-role in the recognition and capture of swimming or epibenthic prey. *Isoxys* swam and steered using its flap-like telson while beating its multiple setose exopods. The appendage morphology of *Isoxys* suggests a close relationship with the megacheirans, a widespread group of (probably) predatory arthropods characterized by a pre-oral 'great appendage'. Functional morphology and taphonomy both suggest that *Isoxys* was able to migrate through the water column, possibly exploiting hyperbenthic niches for food. The palaeoecology of *Isoxys* supports the notion that off-bottom animal interactions, associated with complex feeding strategies and behaviours (e.g. vertical migration, hunting), were established by the Early Cambrian. It also suggests that a prototype of pelagic food chain was already present, at least in the lower levels of the water column.

THE GUT CONTENTS OF OTTOIA (PRIAPULIDA) FROM THE BURGESS SHALE: IMPLICATIONS FOR THE RECONSTRUCTION OF CAMBRIAN FOOD CHAINS

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Ottoia prolifica (Walcott, 1911) is one of the most abundant priapulid worms of the Middle Cambrian Burgess Shale fauna, and often occurs in large numbers on the surface of bedding planes – suggesting gregarious habits. Its “banana-shaped” body is divided into an anterior introvert (proboscis) armed with longitudinal rows of hook-like scalds and spines, and a posterior annulated trunk bearing terminal hooks. Some specimens are preserved with the introvert invaginated into the anterior part of the trunk. Those showing a fully everted introvert display a long, cylindrical pharynx lined with small pharyngeal teeth. The detailed morphology of the pharyngeal region suggests that *Ottoia* was a predator that probably used a feeding mechanism comparable with that of large Recent priapulids (e.g. *Priapulidus*) – i.e. seizing prey with the everted pharynx, and drawing it into the gut by inverting the pharynx and retracting the introvert.

O. prolifica was infaunal, as indicated by individuals preserved within their burrows. The scald rows and the trunk hooks are likely to have anchored the body in the surrounding sediment at some points in the burrowing process.

Preliminary study of abundant material from the Walcott Quarry Shale (Burgess Shale Formation) reveals gut contents in numerous specimens of *O. prolifica*. Hyolith exoskeletal fragments, such as cones, opercula, and the helens of *Halophrentis carinatus*, are the most common food remnants preserved in the *O. prolifica* gut. Brachiopods (e.g. *Micromitra burgessensis*), bradoriids (e.g. *Liangshanella burgessensis*), and small trilobites (agnostid and non-agnostid larval stages) are present at a smaller frequency. These gut contents bring direct evidence that *Ottoia* fed on a variety of small, epibenthic, mostly slow-moving prey. Clusters of unrecognizable microscopic elements, typically concentrated within the posterior part of the gut, suggest that other types of prey were consumed by *Ottoia*. Appropriate methods (scanning electron microscopy, CT-scan) are expected to reveal their composition. Elongated masses of very fine black material are also frequent in the posterior gut and may represent digested residues. These also require detailed morphological and chemical analysis. Although there is no doubt that *O. prolifica* was an infaunal worm that lived in burrows and fed at the water-sediment interface, its feeding behaviour – that is, whether or not it was a selective feeder – requires clarification.

TRILOBITE TRANSPORT, TAPHONOMY AND TURBIDITES: THE CAMBRIAN CONASAUGA SHALE LAGERSTÄTTE REVISITED

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In 1916, Charles Walcott suggested that the Conasauga Shale (Coosa River, northwestern Georgia, USA) was Middle to Upper Cambrian in age. His initial assessment has not been refuted. The Conasauga Shale is composed of inner shelf (Middle Cambrian) and mid-shelf (Upper Cambrian) strata, composed of abundantly mineralized trilobites along with other Burgess Shale-like organisms of Walcott renown. Exceptional trilobite preservation in the Conasauga lagerstätte is thought to occur in relatively oxic, shallow-water facies – in direct contrast to the anoxic shelf-to-slope facies represented by the Wheeler and Burgess Shale lagerstätten. We hypothesise that the Conasauga Shale also may contain outer shelf-to-slope deposits similar to the Wheeler Shale.

Here, we interpret these deep-water deposits as turbiditic facies composed of thinly laminated siliciclastic shales interbedded with siltstones. In these putative turbiditic beds, impressions of trilobite elements (e.g., free cheeks, genal spines and thoracic segments) are common, and complete trilobites are rare. Molted elements are usually size-sorted and occur as mono-element assemblages, suggestive of current sorting in turbiditic flows. When complete specimens occur, the dominant trilobite is *Elrathia antiquata*, a species that may live in exaerobic conditions like its southwestern relative, *E. kingii*. In thin sections, iron-oxide pseudomorphs after pyrite are present, an indication of rapid trilobite burial in relatively anoxic conditions. Thus, the Conasauga lagerstätte may also contain trilobite hardparts that were entombed via deep-water turbidites, not unlike other Cambrian lagerstätten.

EVOLUTIONARY REDUCTION OF THE FIRST THORACIC LIMB IN BUTTERFLIES

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One of the factors contributing to the evolutionary success of the arthropods is their segmented body plan. Most segments bear a pair of appendages, with anterioposterior differentiation of appendage identity (tagmosis) as a feature of their evolution. The diversity of appendage morphology in Cambrian arthropods is significant in a number of hypotheses about their phylogenetic relationships. The developmental processes governing the specification of appendage identity are therefore an important field of study in arthropod evolution. Studies of crustaceans have demonstrated the ability of the Hox genes *Ubx* and *Scr* to effect evolutionary transformations of one limb type into another by their presence or absence in a body segment. As the evolution and

differentiation of arthropod limb types in the Cambrian radiation is one of the essential questions in the diversification of the phylum, the investigation of development is crucial to resolving the processes by which this occurred.

Limb development has received some attention in crustaceans, but the genetic controls leading to differentiated appendage types are not known in insects. The first thoracic (T1) limb of butterflies in the family Nymphalidae is reduced so much that it cannot be used for walking; it gives the family the common name “brush-footed butterflies”. The function or development of this limb has never been investigated (it is potentially significant in courtship and feeding). SEM of the T1 leg in the nymphalid butterfly *Bicyclus anynana* shows the absence of all five tarsal limb segments and the absence of two claws at the distal terminus. Proportionally, there is a significant reduction in the length of the distal segments of T1 compared with T2 and T3. In contrast, in the pierid butterfly *Pieris rapae* (an outgroup of Nymphalidae) all tarsal segments are present. Transformation of the regular thoracic walking leg into the brush-foot may be initiated by homologues of the crustacean Hox genes, or changes in expression downstream in the limb developmental network. One candidate gene is *Dll*, which is involved in the outgrowth of distal limb structures. *Dll* is not expressed in insect mandibles, which have the least distal outgrowth of all appendages. Thus, the nymphalid brush-foot could lack *Dll* expression, leading to the fusion or loss of distal limb outgrowths (especially tarsal segments). Therefore, developing *B. anynana* limbs were stained with antibodies against *Dll* to reveal its expression pattern. Future work will include applying similar methodologies to other extant arthropod taxa, particularly those with anterior specialization of limbs (e.g. crustacean maxillipeds, branchiopod first antennae). Sampling of phylogenetically diverse arthropods provides a basis for inferring ancestral character states. Knowledge of character states is crucial for determining polarity of limb character evolution, and therefore homology of limb types. Fossil arthropods with preserved limbs from Palaeozoic lagerstätten must be included in the phylogenetic dataset, as they provide crucial records of stem-group morphology, filling in some of the gaps created by subsequent extinction. With this joint approach of developmental gene expression and fossil morphology, the developmental mechanisms underlying the origin of arthropod limb types, such as the Cambrian great appendages or phyllopodous limbs, may be elucidated.

THE OLDEST KNOWN EXAMPLE OF TRILOBITE ECDYSIS (CHENGJIANG BIOTA, EARLY CAMBRIAN)

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Moulting is a requisite process in arthropod growth, but direct evidence of active ecdysis is rare in the fossil record. Here we describe the trilobite *Eoredlichia intermedia*, from the Early Cambrian Chengjiang Biota of south China, in the act of moulting. The more-or-less undisturbed ecdysial specimen is approximately 40 mm in length and shows the freshly moulted animal emerging at an angle from the old exoskeleton. The shed librigenae are rotated counterclockwise through 180°. Five thoracic rings are visible on the new exoskeleton and eleven on the exuvium; adults of this species possess 15 thoracic

segments. The hypostome of the emergent animal is preserved in place, attached to the rostral plate. The exoskeleton of the moulted trilobite is markedly different in colour from the exuvium, partly reflecting the lack of pervasive calcification. The new specimen provides the first unequivocal evidence of moulting activity in trilobites during the Early Cambrian.

THE EARLY RADIATION OF CAMBRIAN SPONGES FROM GUIZHOU, SOUTH CHINA

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Since sponges are the most primitive group of multicellular animals, it is logical that they should have a long fossil record. Well-preserved sponge fossils are common in early Cambrian black shales throughout China, and elucidate the detailed mechanics of the “Cambrian Explosion” and the early radiation of sponges.

We examined sponges from the Lower Cambrian Niutitang Biota and the Middle Cambrian Kaili Biota, Guizhou. 40 distinct genera are known from the Niutitang Biota. In addition to cnidaria, arthropods, algae, and molluscs, sponges are the dominant group, comprising 55% of the genera-level diversity. The Leptomitidae (Demospongea) are the dominant sponges. The abundance of well preserved sponges in this Early Cambrian Formation suggests that the sponges had already undergone an explosive radiation by the end of the Qiongzhusian stage; sponges must have relatively abundant shortly after the Precambrian-Cambrian boundary.

The Kaili Biota is of earliest Middle Cambrian age. It preserves seven sponge genera, which comprise a mere six percent of the biota. As in the Niutitang, Demospongea dominate sponge diversity in the Kaili: six genera belonging to the Demospongea, with the only other genus representing Hexactinellida. The Kaili sponges increase our knowledge of early sponge diversity, and provide an important record of sponges from the Middle Cambrian of China.

NEW DATA ON THE ENIGMATIC EARLY CAMBRIAN BRACHIOPOD HELIOMEDUSA ORIENTA FROM SOUTH CHINA

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The organization of the lophophore is a key diagnostic character for the definition of higher brachiopod taxa, and has a pivotal role in phylogenetic analysis of this group. In all

extant Lingulata, there is a double row of lophophore filaments at the (early) trocholophe stage, whereas in extant calcareous-shelled brachiopods (Craniiformea and Rhynchonelliformea), the trocholophe stage has only a single row of filaments. However, the lophophore is very rarely fossilized, so organizational evolution can often only be inferred.

Heliomedusa orientata, one of the numerous puzzling brachiopods from the Lower Cambrian Chengjiang lagerstätten of Yunnan, southwestern China, has a well-preserved lophophore set in a striking disposition. Based on a comparative study of lophophore disposition in *H. orientata* and the extant discinid *Pelagodiscus atlanticus*, the in- and excurrent pattern and shell orientation of *H. orientata* are described and discussed. Reconstructions of lophophore shape and function are based on numerous specimens and comparison with *P. atlanticus*. The lophophore is composed of a pair of lophophoral arms that freely arch posteriorly, rather than coiling anteriorly as commonly seen in fossil and Recent lingulids. Attached to the dorsal lobe of the mantle, it has neither calcareous nor chitinous supporting structures, and is disposed symmetrically on either side of the valve midline. The mouth can be inferred to be located at the base of the two brachial tubes, slightly posterior to the anterodorsal projection of the body wall. The lophophoral arms bear laterofrontal tentacles with a double row of cilia along their lateral edge, as in extant linguiliform brachiopods. In addition to tentacles, the main brachial axes are ciliated, which presumably facilitated transport of mucous-bound nutrient particles to the mouth. In terms of overall shell shape, setal arrangement and external micro-ornament, *H. orientata* exhibits links to the purported stem-group brachiopod *Mickwitzia*, which challenges recent interpretations of an affinity to discinids. The combination of morpho-anatomical characters, such as lophophore palisades, dorsal and ventral visceral regions and muscular markings, suggests that *Heliomedusa*, probably together with the cosmopolitan small shelly fossil *Mickwitzia*, represents a stem group brachiopod closely associated with lingulates.

SPATIAL VARIATION IN THE DIVERSITY AND COMPOSITION OF THE EARLY CAMBRIAN MAOTIANSHAN SHALE BIOTA: TAPHONOMIC VERSUS ECOLOGICAL CONTROLS

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Early Cambrian konservat-lagerstätten with Burgess Shale-type preservation are thought to preserve relatively unbiased records of metazoan ecosystems in the immediate aftermath of the Cambrian radiation. The degree to which species diversity and composition vary between these different ecosystems, and the factors controlling these variations, are poorly known; they have not been quantitatively explored at the level of entire fossil assemblages. The Maotianshan Shale Biota in Yunnan, China may potentially

represent a good model for addressing these questions, since abundant fossils of this biota are known from many localities. In this study, we quantitatively analyzed spatial variation in species diversity and biota composition based on published diversity data for 10 localities and 19,688 specimens; and from new systematic field collections in 3 localities with comparable sedimentary features spanning 150 km. All localities are regarded as sub-contemporaneous based on the presence of the subzonal trilobite *Eoredlichia-Wutingaspis*.

Our study demonstrates that the diversity of the Maotianshan Shale Biota shows strong spatial variation. High diversity (210 species) characterizes the Chengjiang-Haikou-Anning areas, where the fossil-yielding strata consist of stacked couplets of thin, mm-scale single-event and background mudstone layers. Moderate diversity (55 species) characterizes the Malong-Qujing areas, where the fossil-yielding strata are composed of indistinctly bedded shale showing remnant lamination. Low diversity (26 species) characterizes the Wuding area, where the fossil-yielding strata have been intensely bioturbated. Species composition also shows spatial variation. The proportion of arthropod species varies from 33.9% to 69.9%, while priapulids range from 3.8% to 17.6%, poriferans from 0 to 18.8%, brachiopods from 0 to 9.1%, lobopods from 0 to 7.1% and hyoliths from 0 to 7.7%.

Our analyses indicate that spatial variation in the diversity and species composition of the Maotianshan Shale Biota was primarily controlled by the local geological setting, which influenced both ecological and taphonomic factors.

ECHINODERMS IN THE KAILI BIOTA

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The Kaili Biota, which is earliest Cambrian Series 3 in age, is one of the most important Burgess Shale-type biotas. It is preserved in grey-green shale in the middle-upper part of the Kaili Formation (Cambrian series 2 to 3) at Balang Village, Guizhou Province, southwestern China. It contains biomineralized and non-mineralized fossils representative of 10 higher taxa and trace fossils. The most noteworthy fossils in Kaili Biota are echinoderms, soft bodied fossils and non-trilobite arthropods. The biota includes over 130 genera of animals, placing the Kaili Biota among the three most diverse Burgess Shale-type lagerstätten. The Kaili Biota is evolutionarily intermediate between the older Chengjiang biota and the younger Burgess Shale biota. The Kaili biota has 30 genera in common with the nearby (but earlier) Chengjiang biota, and 38 genera in common with the distant but more contemporary Burgess Shale, showing that the Cambrian soft-bodied fauna had a relatively cosmopolitan distribution in space, but changed significantly over time. The Kaili Biota is the only Cambrian fauna with well preserved, well represented echinoderm fossils. Echinoderms are represented by 8 genera in the Eocrinozoa (Blastozoa), Edrioasteroidea (Echionzoa), Homoiostenea

(Homalozoa), and one novel family. Gogiid eocrinoids are most common, with over 10 000 specimens collected; they include *Sinoeocrinus*, *Globueocrinus*, *Balangicystis*, *Lyracystis*, *Curtoeorinus* and the stalkless "*Kailieocrinus*". "*Kailidicus*" is the first Edrioasteroid discovered in the Cambrian of China.

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