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PALAEOZOIC

Contents

Cambrian

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Introduction

The Cambrian period, the oldest division of the Phanerozoic time-scale, encompasses several important global-scale environmental and evolutionary transitions. Recent advances in the understanding of Cambrian environments, faunas, and chronostratigraphy have all provided an enriched view of this critical interval in the history of the Earth – the time during which life's direct impact upon the rock record first became explicit. The term 'Cambrian' was first applied by Sedgwick (*see* **Famous Geologists: Sedgwick**) in 1835 to a series of sedimentary rocks well exposed in north Wales. The Cambrian system, as defined today, equates to only a portion of what Sedgwick originally considered to be 'Lower Cambrian'. Cambrian deposits are distributed widely, and a basic stratigraphical and palaeogeographical framework has been established for almost all regions. Nevertheless, a great deal of additional research will be necessary to secure our understanding of the geological framework in which the events of the Cambrian were structured. This article presents an overview of the defining temporal, geographical, and environmental attributes of the Cambrian, and then considers these in relation to the most striking aspect of the Cambrian system – the diversification of abundant metazoan life.

Chronostratigraphical Framework

The ratification of formal boundaries for the Cambrian system and improvements in the precision of isotope geochronology have recently resulted in substantial adjustments to views concerning the absolute age and duration of the Cambrian period. These results have fundamentally changed perspectives on the historical events encompassed within the Cambrian.

The Bounds of the Cambrian System

Formal definitions for both the base and the top of the Cambrian system have been ratified within Global Standard Stratotype Sections and Points (GSSPs) in recent years, both with type sections in Newfoundland, Canada. The base of the Cambrian system is currently placed at the occurrence of the trace fossil, *Treptichnus pedum*, 2.4 m above the base of Member 2 of the Chapel Island Formation at Fortune Head, Newfoundland. The base of the subsequent geological system, the Ordovician system, is placed at the first occurrence of the conodont, *Iapetognathus fluctivagus*, at a level of 101.8 m, within Bed 23, in the measured section of the Lower Broom Point Member, Green Point Formation at Green Point, western Newfoundland.

Stratotype points are located at the occurrence of diagnostic markers within particular stratotype sections, and both the top and the base of the Cambrian system rely on the occurrence of fossils. Such boundaries commonly relate to the stratigraphically lowest occurrence of the diagnostic marker fossil in the stratotype section. In the case of the base of the Cambrian, this is not so, because unequivocal specimens of *Treptichnus pedum* have recently been described some 4 m below the GSSP at the stratotype section. The occurrence of other *Treptichnus* specimens still lower in this faulted section could compromise the utility of this section as a stratotype. Nevertheless, the diversification of trace fossils during the Precambrian–Cambrian boundary interval was a significant evolutionary event, and offers the possibility of global correlations based on the impressions of homologous morphological characteristics.

The absolute ages of both the base and the top of the Cambrian system rely on recent U–Pb zircon dating of volcanic deposits intercalated within sedimentary successions. Suitable volcanic deposits are not known from the critical intervals of either of stratotype sections. Hence, all absolute age estimates of the boundaries of the Cambrian rely on radioisotopic dates obtained from other sections that have been correlated with the stratotypes using alternative criteria, such as fossils or geochemical signatures. The base of the Cambrian system is commonly considered to be at about 542 Ma. This view is based on a minimum date for the first appearance of *Treptichnus pedum* of 539.4 ± 1.0 Ma in the Swartkloofberg section of Namibia, and a maximum age of 543.3 ± 1.0 Ma based on the occurrence of an assemblage of Ediacaran fossils in the same section. An age of 542 Ma also corresponds with a sharp negative excursion in carbon isotope ratios found in several parts of the world. Nevertheless, Ediacaran fossils have recently been recovered from rocks bearing *Treptichnus pedum* in South Australia, and the exact correlation of the Namibia section with the Newfoundland stratotype awaits resolution. The maximum age of the Cambrian–Ordovician boundary has recently been estimated from latest Cambrian volcaniclastic sandstone beds in north Wales to be 489 ± 0.6 Ma. The minimum age is 483 ± 1.0 Ma based on a Tremadocian ash from Nova Scotia.

Stratigraphical Subdivision of the Cambrian System

Formal stratigraphical stages have been established for Cambrian sequences around much of the globe. These sequences are correlated using cosmopolitan fossils, isotopic signatures, and correlative stratigraphical surfaces. Certain key horizons, characterized by distinctive and widespread markers, can be correlated with some accuracy around the globe. Other portions of the Cambrian are less securely correlated due to such factors as faunal endemism (partly real, partly the result of provincial biases in taxonomic descriptions) or questionable alignments of isotopic profiles. All global correlation schemes for Cambrian stratigraphical sequences (e.g., **Figures 1** and **2**) should be viewed as provisional.

The Cambrian period is commonly divided into three portions (**Figure 3**), although the global utility and bounds of these divisions have yet to be formalized. The perception of the nature of the Cambrian period has changed dramatically recently. The decision to place the base of the system near the first occurrence of *Treptichnus pedum* has meant that the first appearance of trilobites (and some other skeletonized macrofossils) occurs after about one-third of Cambrian time had passed. Furthermore, the discovery that the oldest trilobites date from around 520 Ma has dramatically reduced the apparent duration of the trilobite-bearing Cambrian to an interval of approximately 35 million years in duration. This suggests that the biostratigraphical zones of trilobite-bearing portions of the Cambrian are of a time resolution comparable to those of Mesozoic ammonites, on average as short as 1 million years.

Cambrian Palaeogeography

Palaeogeographical reconstructions for the Cambrian, constructed by different earth scientists, generally agree in terms of the overall distribution of the major landmasses, although doubts are commonly expressed about the quality of the palaeomagnetic database used to underpin such reconstructions. The assembly of the core Gondwana components is

generally considered to have been completed prior to the onset of the Cambrian. The positions and movements of many of the 'outboard' terranes that jostled about the margins of Gondwana, however, remain poorly constrained. This is particularly true of the equatorial sector of Gondwana, where faunal provinciality – commonly useful for regional demarcation – was low. Overall, Cambrian palaeogeography was characterized by open water in the northern polar region, and dominated by the major landmass, Gondwana, that stretched from the lowest latitudes in the south, across the equator, and well into the northern hemisphere. Other major landmasses, such as Laurentia, Siberia, and Baltica, were equatorial or lay within the southern hemisphere (**Figure 4**).

With the exception of the movements of minor terranes, global palaeogeography remained broadly consistent throughout the Cambrian period, with most of the changes apparently related to the rotation and dispersion of Laurentia, Siberia, and perhaps Baltica relative to a stable Gondwana. These movements, coupled with the patterns of sedimentation, are consistent with the breakup of a late Precambrian supercontinent that has been named Pannotia. Details of late Neoproterozoic palaeogeography remain hotly debated and these debates have important implications for interpreting secular changes during Cambrian time.

Cambrian Environments and Climates

The deposits of most major palaeocontinents record a substantial transgression during much of the Cambrian. Such a pattern is clearly displayed in Laurentia, where deposits encroached progressively further into the interior of the continent. Cambrian sedimentation patterns are consistent with relatively high rates of thermal subsidence, perhaps related to the fragmentation of Pannotia. In equatorial settings, particularly within Gondwana, latest Neoproterozoic carbonate platforms were drowned by relatively rapid flooding events that were followed by the deposition of phosphorites and black shales. The shoreward spread of oxygen-depleted and nutrient-enriched waters onto the shelf was associated with the replacement of fossils by secondary phosphates and within cherts. Substantial evaporite deposits developed within interior basins. In the absence of evidence of persistent glaciation, the Cambrian transgression is inferred to have been related to high rates of seafloor spreading.

The analysis of secular changes in the stable isotopes of strontium and carbon provides supplementary tools for correlation amongst sections, together with insights into the evolution of Cambrian environmental conditions (**Figure 5**). The striking rise in Cambrian stable isotopic ratios is thought to reflect enriched ^{87}Sr values due to the uplift and erosion of cratonic material. This rise in $^{87}Sr/^{86}Sr$ ratios is comparable with that seen in the Neogene, associated with the uplift of the Himalaya. Events associated with the latest stages of the prolonged 'Pan-African' orogeny (*see* **Africa:** Pan-African Orogeny) and the final consolidation of Gondwana may have been responsible, but the sequence and timing of these events remain incompletely resolved.

Investigations of Cambrian seawater chemistry, both directly from fluid inclusions and indirectly from inorganic and organic precipitates, suggest that Cambrian seawaters were generally characterized by relatively low Mg/Ca ratios. This is consistent with the deposition of calcitic, as opposed to aragonitic, biomineralized metazoan skeletons. The late Proterozoic to Cambrian interval witnessed the transition from an 'aragonite sea' to a 'calcite sea', corresponding to a transition from 'icehouse' to 'greenhouse' climatic conditions, and a change from $MgSO_4$ to KCl late-stage salts in evaporites. When viewed in the context of trends seen throughout the Phanerozoic, such transitions correspond with long-term changes in plate tectonic regime. The rapid seafloor spreading associated with the breakup of Pannotia probably drove changes in mid-ocean ridge brine fluxes, caused a global sea-level rise, and increased global volcanism.

Marked fluctuations in Cambrian carbon isotopic ratios over short time-scales have been noted in association with the base of the Cambrian and the Early–Middle Cambrian boundary. In these cases, the excursions were towards lighter carbon isotopes. A more prolonged, positive excursion towards the heavier isotope, ^{13}C, has been defined within the Late Cambrian Steptoean stage within Laurentia, Kazakhstan, and portions of core and outboard Gondwana. The determinants of such fluctuations are complex because carbon isotopic ratios are influenced by multiple factors. Explanations commonly invoked include alternations between periods of well-oxygenated, warmer waters on continental shelves and periods in which the shelves were flooded by cooler, oxygen-poor waters. These explanations receive additional support from marked periodic fluctuations in macrofaunal diversity that roughly parallel the excursions, at least in some cases. Cambrian oceans were similar to oceans throughout the Phanerozoic in that oxygen penetrated the sediment–water interface even within deep ocean basins. Recent models of atmospheric oxygen levels throughout the Phanerozoic suggest that O_2 constituted between 10% and 20% of the composition of the atmosphere. Although these estimates are subject to considerable uncertainty, they suggest that Cambrian

Siberian platform			Australia		China		Spain
Stages	Trilobite, Archaeocyath, and Small Shelly Fossil Zones		Archaeocyath Zones	Trilobite Zones (Stages)	Stages	Trilobite and Small Shelly Fossil Zones	Stages
Amgan	*Schistocephalus*	1		*Xystridura templetonensis/ Redlichia chinensis*	Maochuangian	*Yaojiayella*	Leonian
Toyonian	*Anabaraspis splendens*	3			Lungwangmiaoan	*Redlichia nobilis*	
				(Ordian/ Early Templetonian)		*Redlichia chinensis*	
	Lermontovia grandis/ Irinaecyathus shabanovi- Archaeocyathus okulitchi beds	2	*Archaeocyathus abacus beds*		Tsanglangpuian	*Hoffetella*	Bilbilian
	Bergeroniellus ketemensis	1		*523 Ma		*Megapalaeolenus/ Palaeolenus*	
Botomian	*Bergeroniellus ornata*	4	*Syringocnema favus beds* [EB]	*Pararaia janeae* *525 Ma		*Drepanuroides*	Marianian
	Bergeroniellus asiaticus	3		*Pararaia bunyerooensis*		*Yunnanaspis/ Yiliangella*	
	Bergeroniellus [SB] *guraril*	2	Unnamed beds				
	Bergeroniellus micmacciformis/ Erviella	1		*Pararaia tatei*	Chiungchussuan [CG]	*Malungia*	
						Eoredlichia/Wutingaspis	
Atdabanian	*Fansycyathus lermontovae*	4	*Jugalicyathus tardus*	*Abadiella huoi*		*Parabadiella/ Mianxidiscus*	Ovetian
			Spirillicyathus tenuis			*Lapworthella/ Tannuolina/Sinosachites*	
	Nochoroicyathus kokoulini	3	*Warriootacyathus wilkawillinensis*				
	Carinacyathus pinus	2					
	Tetecoscinus zegebarti	1					
Tommotian *535 Ma	*Dokidocyathus lenaicus/ Tumuliolynthus primigenius*	4			Meishucunian		Cordubian
	Dokidocyathus regularis	2/3					
	Nochoroicyathus sunnaginicus	1				*Siphogonuchites/ Paracarinachites*	
Nemakit- Daldynian *545 Ma	*Purella antiqua*	2					Alcudian
	Anabarites trisulcatus	1				*Anabarites/ Protohertzina/ Arthrochites*	

Figure 1 Correlation chart for the major regions of Lower Cambrian rocks. CG, Chengjiang fauna; EB, Emu Bay Shale; MC, Mount Cap Formation; SB, Sinsk fauna; SP, Sirius Passet fauna; RW, Ruin Wash fauna. Modified with permission from Zhuravlev AY and Riding R (2000) *The Ecology of the Cambrian Radiation*. New York: Columbia University Press. © Columbia University Press, 2000.

oxygen profiles and levels in both ocean and atmosphere were essentially modern in aspect.

As noted above, the Cambrian marked a transition interval between 'icehouse' and 'greenhouse' climatic conditions. The details of this transition are poorly resolved, however. Direct evidence of warm conditions in the later Cambrian, derived from oxygen stable isotope ratios, is questioned by some authorities. Yet, the presence of widespread evaporites suggests warm conditions, at least in the equatorial Gondwana region. Broad, but indirect, climatic indicators, such as the distributions of evaporites, ironstones, and carbonates, are consistent with climatic gradients similar to those that characterized much of the Palaeozoic. Recent suggestions of Early Cambrian glacial deposits in West Africa are yet to be accepted generally, but it is likely that the overall climatic conditions warmed through the Cambrian.

Morocco		Baltic Platform		Laurentia	Avalonia	
Stages	Trilobite Zones	Trilobite, Small Shelly Fossil & Ichnofossil Zones	Acritarch Zones	Trilobite Zones	Stages	Trilobite, Small Shelly Fossil & Ichnofossil Zones
Tissafinian	Ornamentapsis frequens	Eccaparadoxides insularis	"Kibartay"	Albertella	*511 Ma	Protolenus
				Plagiura/Poliella		
	Cephalopyge notabilis	Proampyx linnarssoni	Volkovia dentifera/ Liepaina plana	RW		
	Hupeolenus					
Banian	Sectigena	Holmia kjerulfi		Bonnia/ Olenellus	Branchian	
	Antatlasia guttapluviae					
	Antatlasia hollardi		Heliosphaeridium dissimilare/ Skiagia ciliosa	MC		Callavia broeggeri
Issendalenian	Daguinaspis			"Nevadella"		
	Choubertella					Camenella baltica
	Fallotaspis tazemmourtensis	Holmia inusitata		SP		
	Eofallotaspis	Schmidtiellus milkwitzi	Skiagia ornata/ Fimbriaglomerella membranacea	"Fallotaspis"	Placentian	
		Rusophycus parallelum				Sunnaginia imbricata
						No fauna known
		Platysolenites antiquissimus	Asteridium tornatum/ Comasphaeridium velvetum			Watsonella crosbyi
						"Ladatheca" cylindrica
						No fauna known
						"Phycodes" pedum
		Sabellidites	"Rovno"			Harlaniella podolica

Figure 1 Continued

Information on Cambrian terrestrial conditions is sparse, and the transition between marine and terrestrial sedimentary rocks is difficult to determine in many Cambrian sequences, partly because fine-grained sedimentary particles were easily winnowed in the absence of binding by macroflora. Definitive non-marine sedimentary structures are relatively rare within Cambrian sandstones. Nevertheless, the common tacit assumption of an abiotic terrestrial realm during the Cambrian is probably unrealistic. A diverse microbiota may have existed in some settings. Furthermore, there is abundant trace fossil and sparse body fossil evidence of both diploblastic and triploblastic metazoans active in marginal marine environments, together with spores that are apparently non-marine in origin.

Due to the decreasing rotation speed of the Earth, the Cambrian year would have contained more days

Kazakhstan & Siberia			Australia			China
Ungurian	*Dilelokephalina*	1	Warendian	*Cordylodus lindstromi*		Xingchangian
Batyrbayan	*Euloma limitaris/ Batyraspis*		Datsonian	*Cordylodus prolindstromi*		Xingchangian
				Hirsutodontus simplex		
		1		*Cordylodus proavus*		
	Lotagnostus hedini		Payntonian	*Mictosaukia perplexa*		Fengshanian
	Harpidoides/Troedsonia					
	Lophosaukia			*Neoagnostus quasibilobus/ Shergoldia nomas*		
	Trisclcagnostus trisulcus	3		*Sinosaukia impages*		
Aksayan	*Eolotagnostus scrobicularis*	2	Iverian	*Lophosukia*		Changshanian
				Rhaptagnostus clarki prolatus/ Cazbnaia sectarix		
	Neoagnostus quadratiformis			*Rhaptagnostus clarki patulus/ Caznaia squamosa/ Hapsidocare lilyensis*		
	Oncagnostus ovaliformis			*Peichiashania tertia/ Peichiashania quarta*		
	Oncagnostus kazachstanicus			*Peichiashania secunda/ Peichiashania glabella*		
	Pseudagnostus pseudangustilobus	1		*Wentsua iota/ Rhaptagnostus apsis*		
Sakian	*Ivshinagnostus ivshini*	3		*Irvingella tropica*		
	Pseudagnostus "curtare"	2	Idamean	*Stigmatoa diloma*		
	Oncagnostus longifrons			*Erixanium sentum*		
				Proceratopyge cryptica		
	Glyptagnostus reticulatus	1		*Glyptagnostus reticulatus*		
Aysokkanian	*Glyptagnostus stolidotus*	6	Mindyallan	*Glyptagnostus stolidotus*		Kushanian
	Agnostus pisiformis	5		*Acmarhachis quasivespa*		
Mayan	*Leiopyge laevigata/ Aldanaspis truncata*		Boomerangian *495 Ma	*Erediaspis eretis*		Changhian
		4		*Damesella torosa/ Ascionepea jantrix*		
	Anomocarioides limbataeformis			*Holteria arepo*		
				Proampyx agra		
		3		*Ptychagnostus cassis*		
	Anopolenus henrici/ Corynexochus perforatus		Undillan	*Goniagnostus nathorsti*		
				Doryagnostus notalibrae		
				Ptychagnostus punctuosus		
		2		*Euagnostus opimus*		
Amgan	*Pseudanomocarina*		Late Templetonian/ Floran	*Acidusus atavus*		Hsuchuangian
		3		*Triplagnostus gibbus*		
	Kounamkites	2		*Xystridura templetonensis/ Redlichia chinensis*		Maochuangian
	Schistocephalus	1				KF

Figure 2 Correlation chart for the major regions of Middle and Upper Cambrian rocks. Global correlations for the top of the Cambrian System are not finalized, but the top of the Sunwaptan Stage of North America approximates the top of the Cambrian in these figures. Rocks above this belong to the Lower Ordovician. BS, Burgess Shale; KF, Kali fauna; MF, Marjum Formation; OR, *orsten*; WF, Wheeler Formation. Modified with permission from Zhuravlev AY and Riding R (2000) *The Ecology of the Cambrian Radiation*. New York: Columbia University Press. © Columbia University Press, 2000.

| China (cont.)	Scandinavia		North America (Laurentia)	
Yosimuraspis	Rhabdinopora	Rhabdinopora flabelliforme	Symphysurina	Ibexian
Richardsonella/ Platypeltoides	Acerocare	Acerocare ecorne / Westergaardia / Peltura costata / Peltura traniens	Symphysurina	Ibexian
Missisquoia perpetis	Peltura	Peltura scarabaeoides	Missisquoia	Ibexian
			Eurekia apopsis	
Mictosaukia cf. M. orientalis	Peltura	Peltura scarabaeoides	Saukiella serotina	Sunwaptan
Tsinania/Ptychaspis			Saukiella junia	
Kaolishania pustulosa		Peltura minor / Protopeltura praecursor [OR] *492 Ma	Saukiella serotina/ Rasettia magna	
	Leptoplastus	Leptoplastus stenotus / Leptoplastus angustatus / Leptoplastus ovatus / Leptoplastus crassicorne	Ellipsocephaloides	
		Leptoplastus raphidophorus / Leptoplastus paucisegmentatus	Idahoia	
	Parabolina	Parabolina spinulosa		
Maladioidella		Parabolina brevispina	Taenicephalus	
Changshania conica	Olenus	Olenus scanicus / Olenus dentatus	Elvinia	Steptoan
		Olenus attenuatus	Dundenbergia	
Chuangia batia	Olenus [OR]	Olenus wahlenbergi / Olenus truncatus / Olenus gibbosus	Aphelaspis	
Drepanura	Agnostus pisiformis [OR]	Agnostus pisiformis	Crepicephalus	
Blackwelderia				
Damesella/Yabeia			Cedaria	Marjuman
Leiopeishania	Paradoxides forchhammeri	Lejopyge laevigata	Bolaspidella	
Taitzuia/Poshania		Jinsella brachymetopa		
Amphoton		Goniagnostus nathorsti		
Crepicephalina	Paradoxides paradoxissimus	Ptychagnostus punctuosus		
		Hypagnostus parvifrons		
Bailiella/Lioparia		Tomagnostus fissus/ Acidiscus atavus		[MF] [WF]
Poriagraulos/ Hsuchuangia/Ruichengella		Triplagnostus gibbus	Ehmaniella	
Shantungaspis	Eccaparadoxides oelandicus	Eccaparadoxides pinus	Glossopleura	
Yaojiayella			Albertella	[BS]

Figure 2 Continued
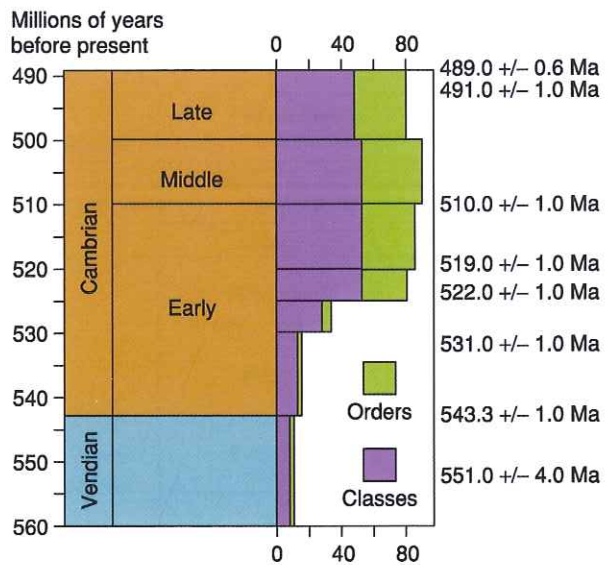
Figure 3 A broad chronology of the Cambrian, and part of the underlying Precambrian Vendian period, showing the major stratigraphical divisions of the system that are commonly used, an approximation of the diversity of metazoan order and classes, and some radiometric dates. Modified with permission from Bowring SA and Erwin DH (1998) A new look at evolutionary rates in deep time: uniting paleontology and high-precision geochronology. *GSA Today* 8: 1–7.

than at present, and each day would have been shorter than 24 h. The Cambrian year was likely to have been about 420 days long. If the shorter distance between the Earth and its moon resulted in a stronger tidal action during the Cambrian, as might also be expected, Cambrian epeiric seas may have been dominated by tides. However, there is no observational support for increased tidal dominance in the Cambrian relative to comparable recent settings. Overall, Cambrian environmental conditions were apparently primarily controlled by the global tectonic setting. The dispersion of the continents, rates of thermal subsidence, and sea-floor spreading strongly influenced both the accumulation of sedimentary rocks and their preservation potential. Cambrian environmental conditions were similar to those seen at other parts of the Phanerozoic and essentially modern in aspect. In marked contrast, several aspects of ocean chemistry and stratification during the Neoproterozoic apparently differed significantly from the Phanerozoic conditions. Hence, the Neoproterozoic–Cambrian interval remains a fascinating and important time of environmental transition, in addition to encompassing critical biotic transitions.
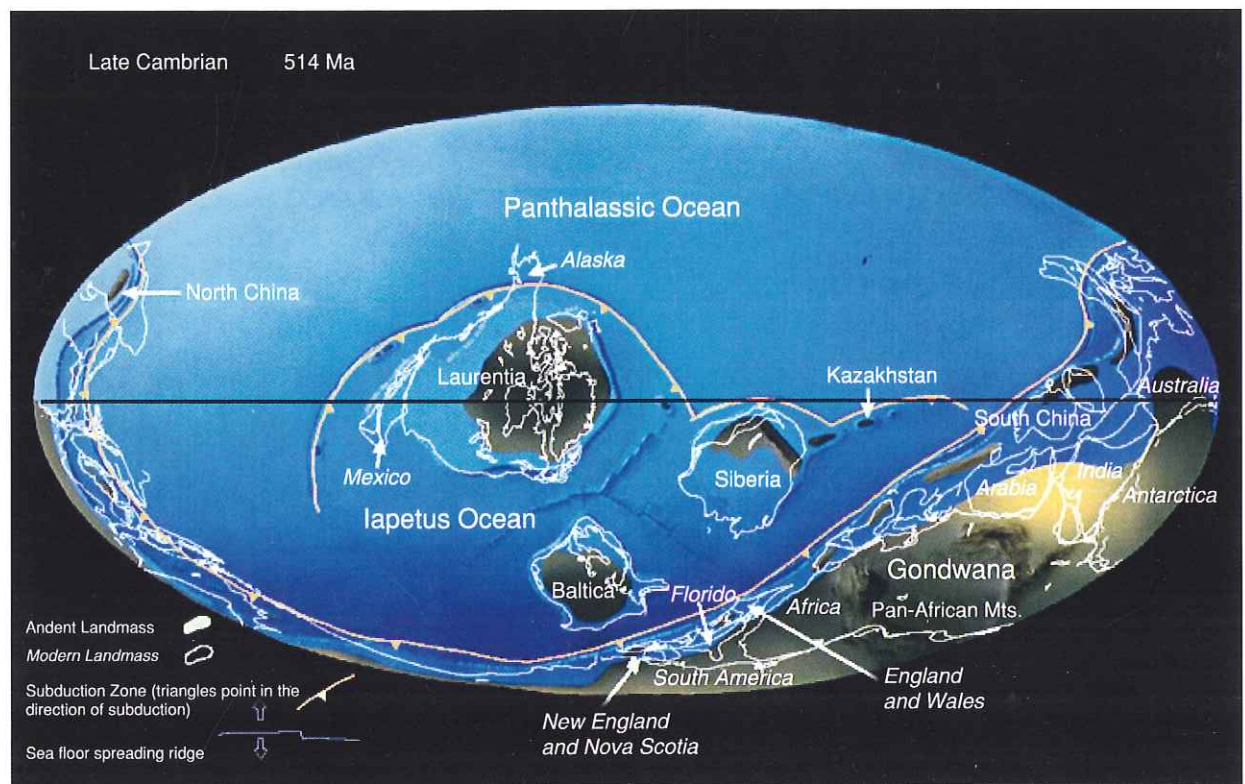

Figure 4 A reconstruction of Cambrian palaeogeography at approximately 514 Ma. Reproduced with permission from Chris Scotese and the Paleomap project.
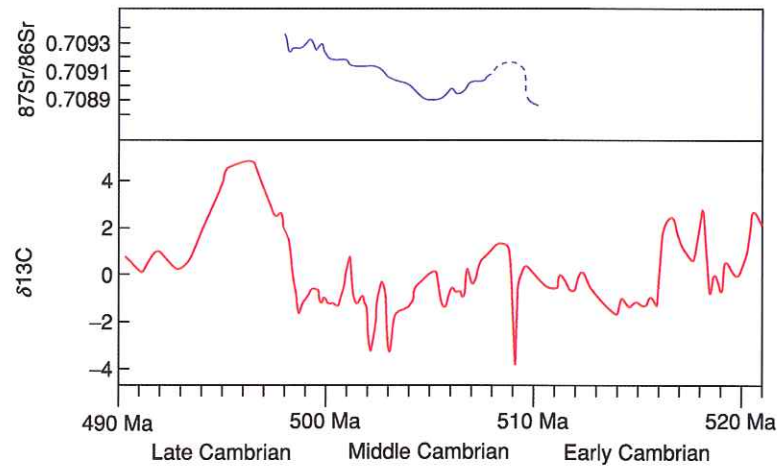
Figure 5   Secular changes in carbon and strontium isotope values during the Cambrian. Modified with permission from Montañez IP, Oselger DA, Banner JL, Mack LE, and Musgrove ML (2000) Evolution of the Sr and C isotope composition of Cambrian oceans. *GSA Today* 10: 1–7.

The Neoproterozoic–Cambrian Evolutionary Radiation

Cambrian Life

The morphological and taxic diversity of trace fossils expanded markedly in association with the basal Cambrian boundary. Surficial trails of simple morphology present in Late Neoproterozoic Ediacaran assemblages were joined by varied morphologies, suggesting motile, triploblastic organisms that mined the sediment infaunally and possessed complex anterior–posterior body patterning. The first traces that can be attributed to the scleritized appendages of arthropods also occurred at about 530 Ma, significantly before the appearance of arthropod body fossils, but after the base of the Cambrian system.

Biomineralized skeletons were present in the latest Neoproterozoic, but were uncommon there relative to their abundance in the Early Cambrian. The pre-trilobitic Cambrian contains a myriad of relatively small biomineralized fossils, collectively known as 'small shelly fossils'. These were commonly composed of calcium carbonate or calcium phosphate and displayed shapes that ranged from simple conical tubes to highly sculptured plates. The diversity of these forms increased through the lowermost Cambrian. Although the phylogenetic relationships of many small shelly fossils remain obscure, in some instances considerable progress has been made in assessing their affinities. Whilst some small shelly fossils represented protective skeletons surrounding the bodies of a variety of diploblastic organisms, others are known to be components of a sclerite meshwork containing hundreds or thousands of separate units that covered portions of the external surface of triploblastic organisms (**Figure 6**). The synchronous biomineralization of numerous separate metazoan and protist lineages, together with the appearance of Foraminifera that agglutinated inorganic minerals to their external surfaces, suggests that the possession of a reinforced external surface conferred a selective advantage in the Early Cambrian. This pattern, together with evidence from body fossil size and mouthpart anatomy of some Early Cambrian arthropods, suggests that Cambrian marine ecologies were structured with significant feedback between higher and lower food chain levels.

The appearance of trilobites marked the start of the traditional Cambrian fauna, as it has come to be known following Jack Sepkoski's static modelling of Phanerozoic marine diversity. This assemblage of fossils, based on the record of biomineralized fauna, was dominated by certain basal trilobite, linguliform brachiopod, echinoderm, and poriferan clades, and persisted into the lower Ordovician. Although the designations 'Cambrian fauna' and 'Palaeozoic fauna' aptly describe the marked contrast in the composition of biomineralized faunas, dynamic modelling of diversity does not suggest that these two faunas behaved as distinct ecological entities. Moreover, it is clear that basal representatives of many of the clades that rose to dominance in the Ordovician were also present in the Cambrian.

Cambrian benthic macrofossils were also characterized by a periodic series of major evolutionary radiations and extinctions. Several of these extinctions (e.g., those associated with the Early to Middle Cambrian transition) had a cosmopolitan effect,

Figure 6 The Early Cambrian triploblastic metazoan *Halkieria evangelista*. Note the external surface consisting of multiple skeletal elements. Each element individually constitutes a 'small shelly fossil', many of which were combined on a single individual. Photograph: John S. Peel.

during which important groups, such as the archaeocyathid sponges and olenelloid trilobites, were exterminated. Marked episodes of diversity expansion were typically followed by stratigraphically sharp extinctions. These striking cycles of diversity fluctuation occurred repeatedly during the Cambrian, and have been documented most clearly in the Late Cambrian 'biomeres' of Laurentia. Although the mechanisms responsible for the biomere pattern are still debated, it appears that large-scale eustatic changes of sea-level, probably coupled with fluctuations in seawater temperature and oxygen levels, were driving factors.

Cambrian Faunal Provinces

The distributions of Cambrian taxa can be used as tools for both biostratigraphical correlation and palaeogeographical reconstruction. Geologically short-lived, abundant, and cosmopolitan species (e.g., agnostoid trilobites) have great utility for global correlations.

Other forms had more restricted distributions, with their geographical ranges limited by barriers (e.g., temperature tolerances, the inability to cross deep ocean basins; **Figure 7**). Distributions of fossils can be used as independent criteria to constrain palaeogeographical reconstructions based on other data. Laurentian shelf faunas were apparently the most distinctive, which is consistent with the notion that Laurentia was geographically isolated during Cambrian times. A wide-ranging shelf fauna also occurred about the peri-Gondwanan margin, although restriction of some elements to specific regions suggests some palaeolatitudinal limits on faunal distribution. In general, species adapted to cooler waters had more widespread occurrences than those restricted to equatorial shelf environments. Additionally, the occurrence of Cambrian faunas diagnostic of one province surrounded by rocks of another province has proved key to the recognition of Cambrian microcontinents.

The Neoproterozoic–Cambrian Biotic Transition

The traditional criterion for recognizing the base of the Cambrian is the first appearance of macrofossils in the stratigraphical record – the change from 'hidden' to 'obvious' life. Although it is certain that Cambrian global tectonics favoured the accumulation and preservation of fossils, and may even have fuelled evolutionary radiation, the extent to which Cambrian tectonic settings triggered the metazoan radiation is less clear. Clarification of this depends on a knowledge of the nature of biotic diversity and structure prior to the base of the Cambrian. If the clades that first appeared in the Cambrian had phylogenetic origins significantly prior to the base of the Cambrian and had also assumed their 'modern' ecological roles within Neoproterozoic ecosystems, the appearance of abundant fossils in the Cambrian may be related to conditions that favoured both biomineralization and the preservation of shelfal sediments. Alternatively, the Cambrian might chronicle the fundamental steps in metazoan phylogenetic and ecological diversification, in which case clues for the trigger might be sought within Cambrian deposits.

It is now apparent that the base of the Cambrian did not coincide with the phylogenetic appearance of most of the clades, both metazoan and protist, that became common in Cambrian rocks. Although metazoan divergence patterns and times based on molecular data are fuzzy, they are consistent in several major aspects, placing the origins of diploblastic organisms before the triploblasts at least tens of millions of years before the base of the Cambrian. Furthermore,
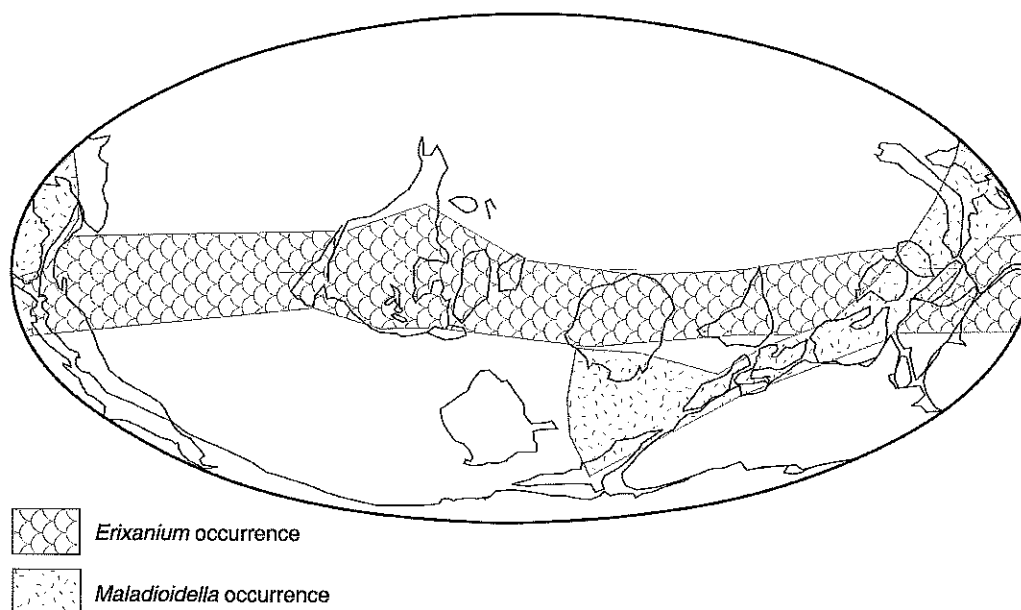
XXX *Erixanium* occurrence

.·.· *Maladioidella* occurrence

Figure 7   Contrasting biogeographical distributions of two widespread Late Cambrian trilobite genera. The *Erixanium* distribution was apparently constrained by factors related to latitude. In contrast, the *Maladioidella* distribution was apparently limited by open ocean basins. Modified with permission from Zhuravlev AY and Riding R (2000) *The Ecology of the Cambrian Radiation*. New York: Columbia University Press. © Columbia University Press, 2000.

direct fossil evidence of Neoproterozoic metazoans is provided by phosphatized embryos aged about 575 Ma from southern China, in addition to other various late Neoproterozoic fossils such as definitive sponges and possible cnidarians. Evidence for Neo-proterozoic triploblasts is still being debated. The phylogenetic affinities of the famous Ediacaran fossil assemblages (*see* **Precambrian: Vendian and Ediacaran**), consisting of large bodies commonly constructed metamerically, also remain hotly contested. Even for some of the best known forms, such as *Dickinsonia*, recent interpretations range from it being a member of an extinct kingdom, a multi-cellular prokaryote, a lichen, a cnidarian, and a basal triploblastic metazoan capable of movement. Unequivocal Precambrian triploblasts pursuing ecologies closely comparable to their roles in the Phanerozoic have yet to be described, although the Ediacaran *Kimberella* – which may be a mollusc with an associated grazing trail – provides the most plausible candidate.

The presence of likely Late Precambrian metazoans that differed in gross morphology and ecology from their Cambrian counterparts suggests that the transition into 'obvious life' was not merely an artefact related to the advent of biomineralized skeletons with high preservation potential (although biomineralization clearly did appear synchronously and independently during Early Cambrian time in various

metazoan and protist clades). Such a suspicion is confirmed by two other data sets that are arguably free of strong preservational biases across the Neoproterozoic–Cambrian boundary. The first of these is the record of trace fossils. Ediacaran fossils are commonly found preserved in sandstones with evidence of mat-like bedding surfaces bound by algae. Finer grained substrates, such as mudstones, were apparently quite firm throughout the Neopro-terozoic to Cambrian transition interval. Such sub-strates would have provided a suitable medium for the preservation of surficial movement traces and shallow, infaunal burrowing. Examination of the trace fossil record shows that the diversity, complex-ity, depth, and extent of bioturbation increased progressively across the Neoproterozoic–Cambrian boundary, with trends begun in the Neoproterozoic continued into the Early Cambrian. These observa-tions suggest that this interval witnessed important evolutionary innovations in metazoan size, morph-ology, and behaviour coincident with the establish-ment of benthic ecologies of essentially modern aspect. The second critical data set is the burst in morphological diversity of pelagic microflora at the onset of the Cambrian following marked conserva-tism during the late Neoproterozoic. New morpholo-gies found in the Cambrian are consistent with the presence of active pelagic herbivores (mesozooplank-ton) of which there is direct evidence from Lower

Cambrian rocks. If mesozooplankton were essential to the establishment and maintenance of the Cambrian benthic communities, as they are in modern marine communities, it could be that innovations in the zooplankton drove diversification of the Cambrian macrobenthos.

It seems that the phylogenetic origins of the clades that first appeared in the Cambrian probably pre-dated the base of the Cambrian by at least 50 Ma (and possibly far longer), as did most of the genetic regulatory architecture required to organize large, complex, body plans. This is indicated by the remarkable extent to which body patterning mechanisms are shared amongst disparate metazoan groups. For this reason, it seems unlikely that the Cambrian radiation was directly coupled to basic biological innovations that made metazoan diversity mechanistically possible. Nonetheless, the Cambrian radiation was more than a simple expansion of biotic diversity and ecological structure present in the terminal Neoproterozoic triggered by favourable tectonics. Cambrian ecologies, both pelagic and benthic, were different from those of the Neoproterozoic in ways that suggest enhanced trophic interactions and ecospace utilization. Biotic innovations coincident with the Neoproterozoic–Cambrian transition, both morphological and ecological, appear to have been critical to the adaptive radiation that clearly took place during Cambrian time.

Although there were marked differences between late Neoproterozoic and Cambrian biotas, this does not imply that the transition between the two was sharp, even on a geological time-scale. Both the sequence and apparent spacing of events are consistent with evolutionary processes and mechanisms operative today, although the rates of anatomical and behavioural innovations may have been elevated in some lineages relative to later times. This pattern, and the persistent compatibility of new data with the expectations of the evolutionary model, belies any basis for the idea that the Cambrian radiation requires alternative, non-evolutionary explanations. Furthermore, it can be argued that the types of evolutionary transformation that took place during the Precambrian–Cambrian boundary interval persisted into the Cambrian.

Many Early Cambrian body fossils arguably belong to stem group lineages of clades whose derived crown group representatives only appeared later in the Cambrian or thereafter. According to this view, many varieties of early arthropods present in Cambrian Lagerstätten (see Lagerstätten) (e.g., Chengjiang in Yunnan, China; the Burgess Shale in British
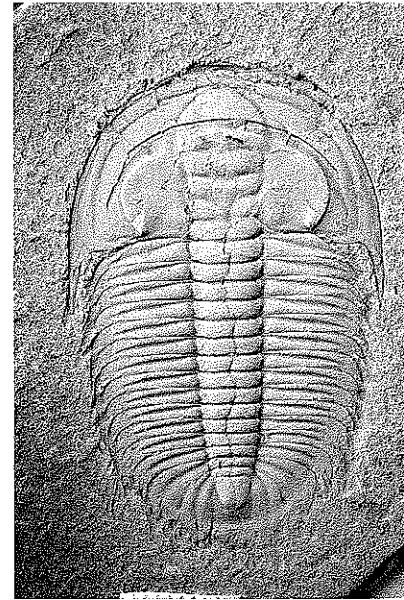

Figure 8 The Middle Cambrian trilobite, *Xystridura templetonensis*, from Australia, a typical representative of the 'Cambrian fauna'. Photograph: Nigel C. Hughes.

Columbia, Canada) represent steps *en route* to derived euarthropods, and scenarios for the evolution of basic features of arthropod morphology, such as rigid, metameric sclerites, can be postulated on the basis of character state transformations seen amongst Cambrian fossils. Although the specifics of such scenarios are subject to debate, the fact that they can be reasonably postulated affirms that major aspects of arthropod evolution were probably accomplished subsequent to the appearance of the earliest arthropod body fossils. Furthermore, the opportunity to explore the connection between the ontogenetic and phylogenetic development of body patterning in early Palaeozoic arthropods (e.g., **Figure 8**) suggests that aspects of the basic control of body plan (e.g., the numbers and varieties of segments) evolved during the Early Palaeozoic. Although such opportunities may offer a fascinating glimpse of the evolution of developmental processes, they apparently concern relatively minor adjustment of developmental systems established prior to the base of the Cambrian.

See Also

Africa: Pan-African Orogeny. **Analytical Methods:** Geochronological Techniques. **Evolution. Famous Geologists:** Sedgwick. **Fossil Invertebrates:** Trilobites. **Lagerstätten. Palaeozoic:** Ordovician. **Precambrian:** Vendian and Ediacaran. **Trace Fossils.**

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Ordovician

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Introduction

The Ordovician System, which is radioisotopically dated to have lasted from 495 Ma to 443 Ma, follows the Cambrian in the geological time-scale and is overlain by the Silurian. The Ordovician comprises the middle part of the Lower Palaeozoic, and has been traditionally divided into six series, of which two (Llanvirn and Llandeilo) have been combined to give a five-fold subdivision. These series are currently in the process of revision, largely to bring them into line with the threefold division (Lower, Middle, and Upper) used in other geological systems. It is still, however, convenient to describe Ordovician rocks in terms of five classical subdivisions, which are in ascending order: Tremadocian (489–483 Ma), Arenigian (483–463 Ma), Llanvirnian (463–*ca.* 455 Ma), Caradocian (*ca.* 455–*ca.* 448 Ma), and Ashgillian (*ca.* 448–443 Ma). Of these, the Tremadocian was previously included in the topmost part of the Cambrian by some authorities, but has now been assigned to the Ordovician by international agreement. The top of the Ordovician is marked by a major ice age and an important mass extinction of marine organisms, which forms a natural boundary with the base of the Silurian. Ordovician rocks are found on every continent except the Indian Peninsula. During the Ordovician the continental masses were widely dispersed, other than the Gondwana supercontinent. Ordovician geology, therefore, varies richly from one area to another. The Ordovician saw the inception of several marine ecosystems that are still with us today.